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Fire regimes for pine–grassland communities in the southeastern United States

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ABSTRACT

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Four combinations of season and frequency of burning were applied in Coastal Plain loblolly pine stands over a 43-year period. Overstory species composition and growth were unaffected by treatment. Above-ground portions of small hardwoods (less than 12.5 cm d.b.h.) were killed and replaced by numerous sprouts under periodic summer, periodic winter, and annual winter burning regimes. With annual summer burning, small hardwoods and shrubs were killed and replaced by vegetation typical of grassland communities. Grasses and forbs also dominated the understory of annual winter burns but numerous hardwood sprouts survived. Study results emphasize that frequent burning over a long period is needed to create and maintain the pine–grassland community observed by the first European settlers of the southeast.

INTRODUCTION

Fire has been a major ecological force in the evolution and distribution of forest types in the Southeastern United States. Ecological and meteorological evidence suggests that man- and lightning-caused fires helped shape the pine–grassland communities which were once common in the region. Komarek (1974) described these communities as having herbaceous and grass cover under open canopies of longleaf (*Pinus palustris* Mill.), loblolly (*P. taeda* L.), and shortleaf *P. echinata* Mill.) pines. Herbs and grasses once flourished in these stands because open canopies filtered sunshine rather than shading the ground. Komarek (1965) argues that the natural accumulation of fuels in grasslands, without heavy grazing, would allow summer fires caused by lightning to burn with sufficient intensity to maintain pine–grassland communities against encroaching hardwoods. Winter fires, which burn with low

intensity, would not prevent the invasion of hardwoods into grasslands (Komarek, 1965).

The evolution of southeastern plant communities was greatly influenced by the latest glacial retreat and the advent of aboriginal man, which occurred at approximately the same time. Northern migrations of plant species occurred rapidly as ice masses retreated, leaving distributions of woody plants similar to contemporary forests by the beginning of the Holocene epoch — some 10,000 years ago (Delcourt and Delcourt, 1987). Archeological evidence has established the presence of Paleo-Indians in the region as early as 12,000 years ago (Chapman, 1985). These early inhabitants possibly contended with a periglacial climate or localized permafrost (Keel, 1976). As Indian populations grew and tribes migrated, their use of fire affected a large portion of the landscape. Indians remained hunters and gatherers until approximately 800 to 1000 A.D., when corn and beans were first cultivated in the region (Hudson, 1982). Recent research indicates that Southeastern Indian populations were much larger than previously estimated, suggesting widespread use of fire for land clearing (DeVivo, 1991). The movement of Indian tribes for game and cropland created variable patterns of fire frequency across the landscape, producing a mosaic of vegetation types and stand ages (Buckner, 1989).

Early explorers of the Atlantic coast, including Giovanni Verrazano (1520s), Jacques Cartier (1530s), and Samuel de Champlain (early 1600s), described the forests as open pine and hardwood stands with grasses underneath (DeVivo, 1991). Others have suggested these open forests owed their existence to frequent burning (Bartram, 1791; Harper, 1962; Van Lear and Waldrop, 1989). Woods burning in the region remained common and unregulated until the early 1900s, when government agencies began efforts to ban fire use for forest protection and to allow pine regeneration. This ban was only partially successful and remained controversial through the 1940s and 1950s when prescribed burning for fuel reduction gained general acceptance after a series of wildfires (Pyne, 1982). Even with the extensive use of controlled burning in the Southeast today, pine–grassland communities are less common and contemporary forests often have dense understories and more hardwoods.

lower case ?

It can be difficult to appreciate the important role of fire in shaping the species composition and structure of forests. Plant community changes brought about by fire can be slow and depend on the season and frequency of burning as well as the number of successive fires used. Opportunities to observe changes in community characteristics in the presence of fire over long periods are limited. The results of a long-term study by the Southeastern Forest Experiment Station, however, may give an indication of the ecological role fire once played in the southeastern United States. The experiment, known as the Santee Fire Plot Study, was established in 1946. Various combinations of season and frequency of burning were maintained for over 40 years. This paper discusses the changes to plant communities these different

burning regimes caused over time, and identifies which regimes may have been needed to create and maintain presettlement pine–grassland communities.

METHODS

Study plots were established in 1946 on the Santee Experimental Forest in Berkeley County, South Carolina, and on the Westvaco Woodlands in neighboring Georgetown County (Lotti et al., 1960). Plots on the Westvaco site were harvested in 1984, so this paper is restricted to the Santee plots. The study area is on a Pleistocene terrace of the lower Coastal Plain at 7.5 to 9.0 m above sea level. Soils are poorly drained Ultisols of medium to heavy texture (McKee, 1982). They are considered productive for loblolly pine with a site index of 27 to 30 m for loblolly pine at age 50. More detailed site descriptions were given by Lotti et al. (1960) and Waldrop et al. (1987). In 1946, the overstory was an unmanaged, 42-year-old stand of loblolly pine pole timber that resulted from natural regeneration after logging. Study areas showed no evidence of previous burning, supporting a well-developed hardwood midstory. Common midstory species were dogwood (*Cornus florida* L.), hickory (*Carya* spp.), southern red oak (*Quercus falcata* Michx.), post oak (*Q. stellata* Wangenh.), water oak (*Q. nigra* L.), and willow oak (*Q. phellos* L.).

Five treatment plots, 0.1 ha in size, were established in each of three replications. Treatments included: (1) periodic winter burning, (2) periodic summer burning, (3) annual winter burning, (4) annual summer burning, and (5) an unburned control. All winter burning was done on December 1 or as soon afterward as weather permitted. Summer burning was done on or soon after June 1. Periodic burns were conducted when 25% of the understory hardwood stems reached 2.5 cm in diameter at breast height (d.b.h.). This prescription resulted in variable burning intervals ranging from 3 to 7 years. Annual burning was not interrupted from 1946 through 1989.

Burning techniques were selected to ensure complete coverage of the plot by fires of the lowest practical intensity. Selection was made at the time of burning based on prevalent fuel and weather conditions. In general, backing fires were used on periodically burned plots having thick underbrush or when hot and dry weather increased the risk of high-intensity fires. Headfires or strip headfires were used on annually burned plots with little underbrush and when fuels were too moist to support a backing fire.

Data to describe various characteristics of overstory and midstory trees were collected periodically throughout the study. Diameter at breast height of overstory pines was measured in 1957, 1967, 1977, 1979, and 1984. Midstory hardwoods were measured at study establishment (1946), at year 20 (1966), at year 30 (1976), and at year 38 (1984). Detailed descriptions of sampling methods were given by Klawitter (1966), Lewis and Harshbarger (1976),

Langdon (1981), and Waldrop et al. (1987).

Understory vegetation was measured again in July 1989, after 43 years of burning. A 25 x 25 m sample plot was established within each treatment plot. Two 25 m line transects were randomly located in each sample plot to determine percent crown cover for grasses, legumes, other herbs, woody vines, shrubs, and trees less than 1.5 m tall. Cover was determined by measuring the portion of a crown intersected by a 25 m transect. Where two or more crowns overlapped, the overlapping sections of the lower crown(s) were not included. The portion of each transect where understory vegetation (less than 1.5 m tall) received direct sunlight was measured at midday (between 11:00 am and 1:00 pm).

Two 0.5 x 2 m subplots were randomly located along each 25 m transect (four subplots per plot) to measure stem density or abundance. The species and genus of each plant was identified, and the number of plants per species or genus was recorded. Species not encountered in the four subplots were counted in two 1 x 25 m subplots, each of which was located adjacent to a 25 m transect. The larger subplots (1 x 25 m) were used primarily to sample relatively uncommon species. Species not encountered in subplots of either size but occurring in a 25 x 25 m sample plot were listed as present but not counted. Mean plant abundances by treatment were compared and separated by analysis of variance and linear contrast at the 0.05 level.

lower case

Detrended Correspondence Analysis (Gauch, 1982; Hill and Gauch, 1980) was used to interpret the variation in vegetation composition among treatments. The technique groups plots or communities based on similarity of species composition and relative abundance. The degree of difference between plots is indicated by standard deviation units. A separation of communities by four standard deviations generally indicates that the two communities have no species in common, while one standard deviation indicates that the communities have approximately 50 percent of their species in common (Hill and Gauch, 1980).

The study was terminated in 1989 because of severe damage to the overstory and midstory caused by Hurricane Hugo in September 1989.

RESULTS AND DISCUSSION

Overstory and midstory vegetation

Loblolly pine remained the dominant species in all treatment plots, but a few hardwoods grew into the upper canopy. At the time of the first measurement of overstory pines (1957), all plots were well stocked with an average basal area of 22.7 m^2 and 231 trees ha^{-1}. By 1984, basal area had increased to 25.3 m^2 ha^{-1} but only 149 trees ha^{-1} survived. Waldrop et al. (1987) found a lack of treatment effect on diameter or height growth, which they attributed

to the maturity of the trees when the study was installed (42 years old in 1946). Mortality over the study period was due to natural causes including ice damage and aging. The low number of overstory trees provided an open canopy. In 1989, direct sunlight reached the understory in approximately 35% of each burned plot. The midstory of unburned controls was somewhat more dense, allowing direct sunlight on only 20% of the treatment plot.

Species composition of midstory vegetation changed little during the study. Dogwood, hickory, and oaks were common on all treatment plots. However, the structure of the midstory was changed by the various burning regimes. Diameter distribution of midstory hardwoods by treatment is given in Fig. 1 using 5 cm d.b.h. classes plus classes for trees less than 2.5 cm d.b.h and greater than 17.5 cm d.b.h. At the beginning of the study, all unburned control plots appeared to be undisturbed by fire or forest management operations. Every size class of hardwoods from less than 2.5 cm to over 17.5 cm d.b.h. was present on control plots (Fig. 1a). Diameter distribution followed a reverse-J pattern with numerous stems in small size classes and only a few stems in larger classes. The number of stems in each size class varied somewhat over time as individual trees grew into larger classes. However, the reverse-J pattern remained.

Hardwood diameter distributions were altered over time by periodic winter burns and periodic summer burns. In both treatments, the number of stems in the smallest size class (0–2.5 cm) increased while those in the next two classes (2.6–7.5 cm and 7.6–12.5 cm) decreased (Figs. 1b and 1c). With periodic summer burning, numbers in the smallest size class increased from approximately 11,000 to over 19,000 stems ha^{-1} by year 30. The 2.6 to 7.5 cm size class was most affected; numbers decreased from over 1,100 to approximately 100 stems ha^{-1} in both periodic treatments. Most changes occurred during the first 20 years, but continued at a reduced rate through year 30. Hardwoods greater than 12.5 cm d.b.h. were generally unaffected by periodic winter and summer burning. These trees were old enough to be protected by thick bark and tall enough so that their buds were above the heat of the fires. Most stems less than 12.5 cm d.b.h. were too small to survive burning. However, root systems of these smaller trees survived and produced multiple sprouts. The increase in stem numbers in the smallest size class is the result of multiple sprouting. Fires were frequent enough to prevent the growth of sprouts into a larger size class. Fewer than 10% of the trees in the 2.6 to 7.5 cm d.b.h. class survived until year 30. Trees of this intermediate size class are susceptible to top-kill from occasional flare ups or hot spots. Since hot spots occur more often during the summer, fewer trees of this size class survived periodic summer burns than periodic winter burns.

Annual winter burning caused changes in the hardwood d.b.h. distribution similar to periodic winter and summer burning. Most stems in the 2.6 to 7.5 cm d.b.h. class were top-killed or girdled during the first few years. Stem

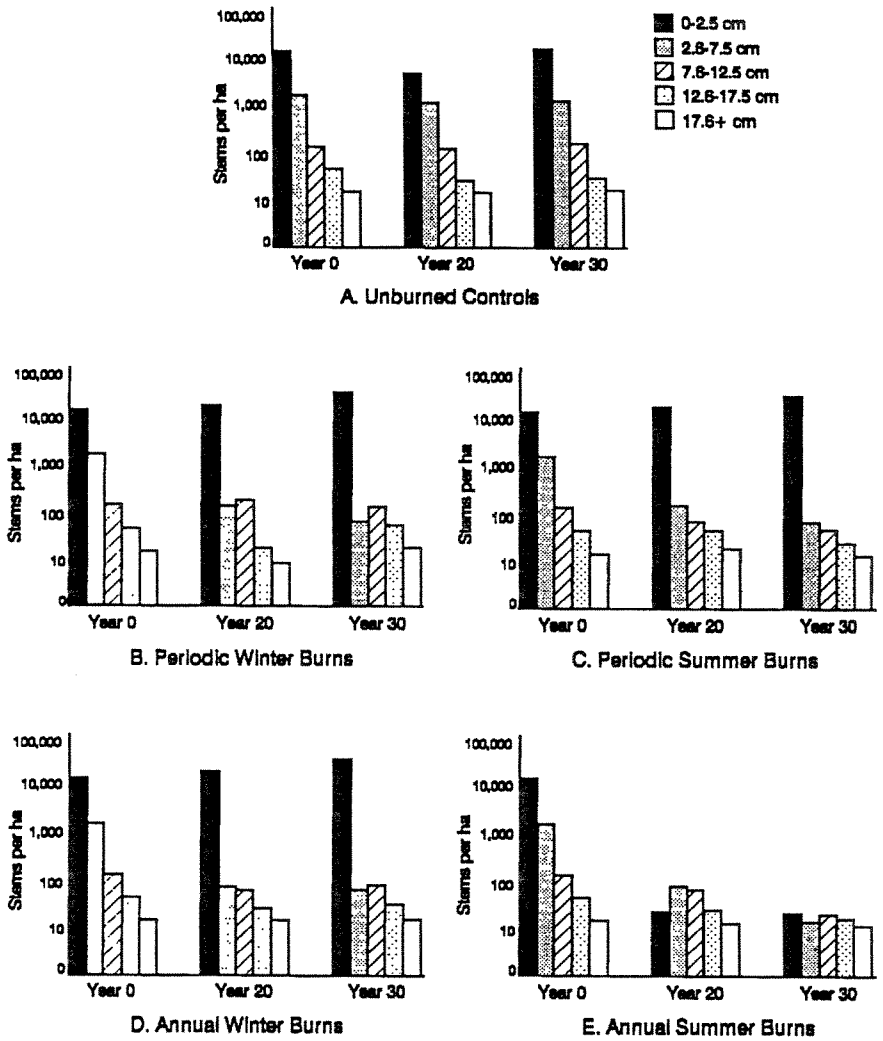

Fig. 1. Diameter distribution of all hardwoods at selected years for (A) unburned control plots, (B) periodic winter burn plots, (C) periodic summer burn plots, (D) annual winter burn plots, and (E) annual summer burn plots.

numbers in this size class were reduced from approximately 1,200 ha^{-1} to less than 100 by year 20; no additional reduction occurred through year 30 (Fig. 1d). The number of stems ha^{-1} in the smallest d.b.h. class (0–2.5 cm) increased dramatically over the 30-year period. By year 20, this size class increased from 16,000 to 21,000 stems ha^{-1}. Between years 20 and 30, that number increased to over 47,000 ha^{-1}. Most of these stems were sprouts less than 1 m tall. Since annual winter burns allowed sprouts a full growing season to recover from fire,

many root systems survived and produced larger numbers of sprouts after each fire.

Annual summer burning nearly eliminated woody vegetation in the 0–2.5 cm d.b.h. class (Fig. 1e). Root systems were weakened by burning during the growing season when carbohydrate reserves were low. Burning was frequent enough to kill root systems of all hardwood species but oaks and blackgum (*Nyssa sylvatica* Marsh.) were particularly resistant; some survived 18 to 20 annual summer burns (Langdon, 1981). A few hardwood seedlings germinated each spring but did not survive the next fire. As with other treatments, the number of stems between 2.6 and 12.5 cm d.b.h. was reduced by annual summer burning and the majority of the change occurred during the first 20 years. Numbers of hardwood stems over 12.5 cm d.b.h. were unaffected by annual summer burning.

Understory vegetation

Species composition

Species composition of understory woody plants was affected by treatment (Fig. 2a). After 43 years (1989), abundance of trees and shrubs less than 1.5 m tall on plots burned periodically in winter or summer and on plots burned annually in winter was greater than on unburned control plots. These increases were due to sprouting after top-kill of small- and intermediate-sized trees and shrubs. The large increase in numbers of shrubs was due to of the presence of huckleberry (*Gaylusaccia* spp.) and blueberry (*Vaccinium* spp.), which sprouted prolifically after fire. Annual winter burning favored sweetgum (*Liquidambar styraciflua* L.) which produced numerous sprouts after each fire. Annual summer burning eliminated understory woody vegetation with the exception of a few seedlings that were killed by the next fire. Vines were stimulated somewhat by periodic winter and summer burning but nearly eliminated by annual winter and summer burning. The abundance of woody plants in periodic winter burn plots was because these plots had been burned the winter prior to measurement.

Abundance of herbaceous plants, particularly grasses and forbs, increased with increasing fire frequency (Fig. 2b). Periodically burned areas had somewhat greater grass abundance than controls (Fig. 2b), but their understories were still dominated by trees and shrubs (Fig. 2a). The understories of annual winter and annual summer burned areas were dominated by grasses and forbs and, therefore, resembled the grassland communities described by Komarek (1974). Plots burned annually in summer had significantly higher grass abundance than periodically burned and unburned control plots. Annual winter burns created a diverse understory with numbers of grasses, legumes, and other forbs that were significantly higher than all other treatments (Fig. 2b). Also, sprouts of trees and shrubs that were missing from areas that had been

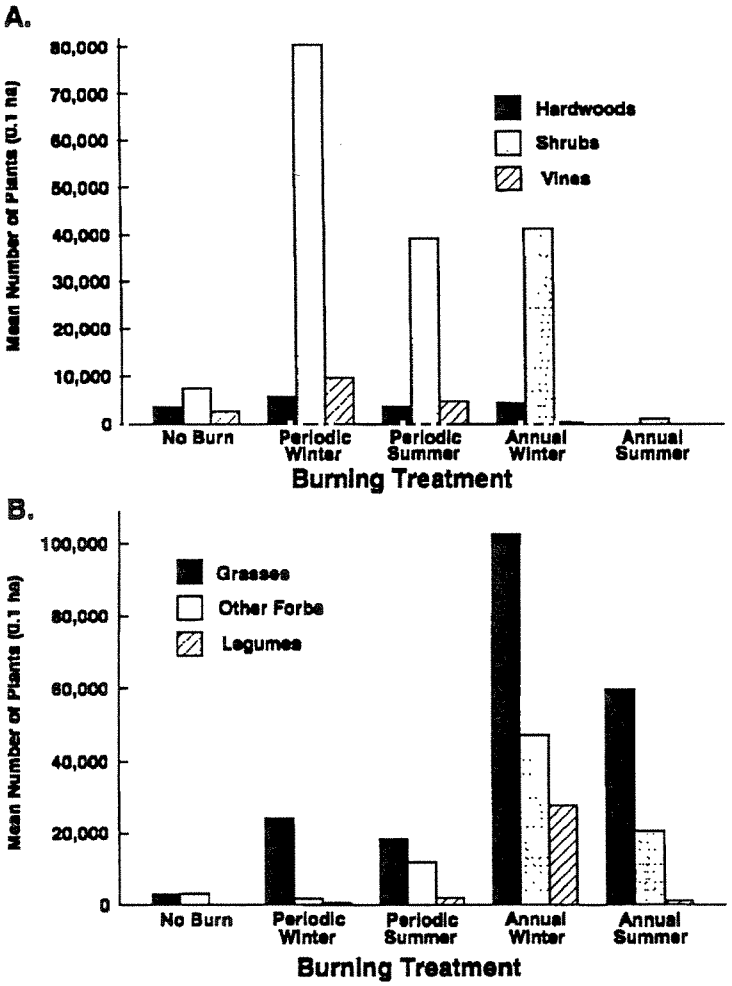

Fig. 2. Mean number of stems less than 1.5 m tall 0.1 ha^{-1} for (A) understory woody plants, and (B) understory herbaceous plants across all treatments.

burned annually in the summer were abundant in areas burned annually in winter (Fig. 2b). Legume abundance on plots burned annually in winter was higher than values reported from studies in the South that were conducted with single or periodic burns (Buckner and Landers, 1979; Cushwa et al., 1970; Speake et al., 1975).

The only detailed survey of understory vegetation on these plots, prior to the 1989 measurements, was conducted in 1967 (year 20) by Lewis and Harshbarger (1976). The period between burning and sampling differed between the two surveys for some treatments. Therefore, changes can only be presented for the unburned control, for periodic summer burning, and for annual winter burning.

Several changes to the understory occurred over the 23 years between surveys. In unburned controls (Fig. 3a), cover of understory trees and shrubs declined between 1966 and 1989, perhaps as a result of natural succession. Some trees and shrubs formerly in the understory grew into the midstory. Also, midstory hardwoods that were present in 1967 continued to grow, further reducing the amount of light reaching the forest floor.

In plots burned periodically in summer (Fig. 3b), there were few changes between years 20 and 43. At both times, the understory was dominated by shrubs and trees. A slight increase in total cover (all species) may have been caused by increased sprouting of trees and shrubs.

Greater changes were observed after annual winter burning (Fig. 3c). From year 20 to year 43, tree and shrub cover declined and grass cover increased. Although tree cover declined, the number of hardwood stems (44,700 stems ha^{-1}) was similar to the number reported by Langdon (1981) at year 30 (47,000 stems ha^{-1}). This pattern suggests that hardwood sprouts are smaller than

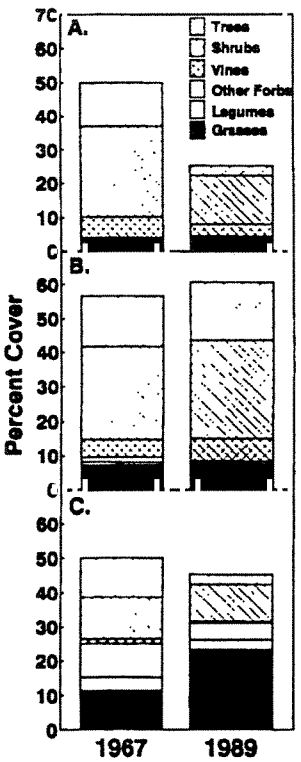

Fig. 3. Understory cover by treatment, 1967 and 1989. Treatments: (A) no-burn control, (B) periodic summer burn, (C) annual winter burn. Data for 1967 were reported by Lewis and Harshbarger (1976).

before and that sprout vigor may be declining over time. The increased importance of grasses indicates that the frequent but relatively mild disturbance associated with annual winter burning may eventually create a grass and forb community, but only after an extended number of years. Even though grasses and forbs dominate the understory, hardwood sprouts would soon regain dominance of the understory and replace the grassland community if burning were delayed a few years.

Community analysis

Detrended correspondence analysis identified four distinct plant communities associated with the following fire regimes: annual summer burns, annual winter burns, periodic burns, and unburned controls (Fig. 4). Differences between periodically burned plots and unburned control plots were not distinct; woody vegetation dominated in both situations. Annual winter and annual summer burns produced distinct understory communities, but both resembled the grasslands described by Komarek (1974). The distribution of plots along Axis 1 was interpreted as a fire disturbance gradient. The relatively large magnitude of difference across treatments (3.5 standard deviations) indicates that diversity over the landscape can be affected by season and frequency of burning. This finding supports the conclusion of Buckner (1989) that variable fire regimes created a mosaic of community types that were present in the southeast prior to European settlement. Separations along Axis 2 were less easily understood, but were interpreted as a natural variability gradient since variation of species composition decreased as frequency of

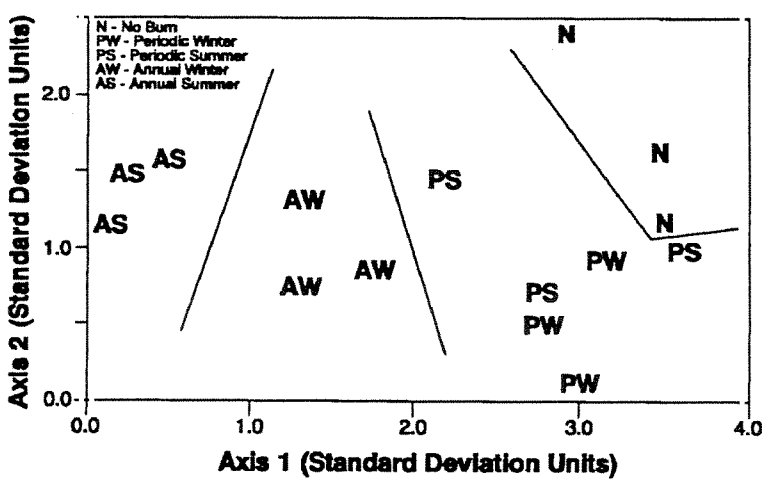

Fig. 4. Results of detrended correspondence analysis showing individual treatment plots: AS = annual summer burn, AW = annual winter burn, PS = periodic summer burn, PW = periodic winter burn, N = unburned control. Lines indicate separation between dissimilar groups of plots.

TABLE 1

Relative abundance[a] of understory species[b] in three treatment plots across fire regimes

Grp.	Species[c]	Burning Treatment											
		Unburned control			Periodic summer			Annual winter			Annual summer		
		Plot number											
		1	2	3	1	2	3	1	2	3	1	2	3
1	*Paspalum* spp.										9	R	
	Polygala lutea										9	R	3
	Hypoxis micrantha									R	1	9	7
	Rhexia spp.								R	+	9	R	R
2	*Coreopsis major*							+	9	1	+		
	Cassia nictitans							5		5	9		
	Stylosanthes biflora							4	1	8	4	9	
	Galactia macreei							9		1			
	Desmodium spp.						2	+		9	+	R	
	Tephrosia hispidula				R		R		R	9	1		
	Centrosema virginianum				R		R	9		9			
	Lespedeza spp.					+	+	+	+	9			
3	*Lobelia nuttallii*				+				9	R	+	6	4
	Aster spp.				1			1	9	2	1	+	+
	Solidago spp.				+		R	9	+	4	2	1	
	Eupatorium spp.				+	+	R	8	9	7	2	3	+
	Elaphantopus spp.				+		+	9	+		1	1	+
	Panicum spp.				3	+	1	6	9	3	6	2	3
	Andropogon virginicus				+		+		6	9	5	9	3
	Hypericum spp.				+		8		8		+	2	1
	Rubus spp.			1	4	5	5	+	1	5	+	R	
	Rhus coppalina		+		+		R	2	R	1	1	R	R
4	*Pinus taeda*		+	1	8	+	+	R	+	+	7	9	6
	Gaylussacia spp.	+	+	+	+	3	1	+	1	4	R		+
	Vaccinium spp.		1	+	1	1	6	+	3	9	+		+
	Uniola laxa	+	+	+	3	+	+	9	3	5			+
	Myrica cerifera	1	+	+	9	2	1	1	R		+		
	Liquidambar styraciflua	+	+	+	5	1	+	4	1	9			
	Smilax spp.	9	1	1	2	+	R	1	+				
	Vitis spp.	+	1	+	1	1	+	+		+	R		
	Quercus spp.	+	+	+	6	4	3	+		9			+
	Gelsemium sempervirens	+	+	+	7	9	1				+		+

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TABLE 2 (Cont'd.)

Grp.	Species[c]	Burning Treatment											
		Unburned control			Periodic summer			Annual winter			Annual summer		
		Plot number											
		1	2	3	1	2	3	1	2	3	1	2	3
5	*Cornus florida*		3	2	7	8	9				R		
	Mitchella repens		4	+	3	9	2						
	Persea borbonia	9	+	+			R						
	Lyonia lucida		+	9									

[a]Relative abundance indicated as deciles: "+" = 1–10% of the maximum abundance value observed for a given species, "1" = 11–20%, "2" = 21–30%, etc.; "R" indicates that a species was present but rare.

[b]The species list was edited to include only those species which demonstrated clear associations for a given treatment or treatments.

[c]Nomenclature follows Radford et al. (1968).

burning increased.

The distribution of species along a fire disturbance gradient reflects the relative tolerance of these species and their competitive vigor after disturbance. Relative abundance of understory species by treatment is given by a species synthesis table (Table 1) (Mueller-Dombois and Ellenberg, 1974). Only those species that demonstrate clear associations for treatments were included. Species were placed in five groups based on their distributions across treatments. Periodic winter burns were not included since sampling was during the growing season immediately following burning. Periodic summer burn plots had not been burned for 5 years.

With few exceptions, groups 1, 2, and 3 (Table 1) are herbaceous plants that have been described as "fire followers" (Lemon, 1967). Many of these plants are also associated with early successional plant communities following other types of disturbance. Other species, such as the legumes, are known to benefit directly from the effects of fire (Martin et al., 1975). Species in group 1 are found almost entirely in annual summer burn plots. These are generally opportunistic species that lack the competitive vigor to survive in other burning regimes, where more vigorous grasses and woody plants dominate. Species in group 2 are most common in annual winter burn plots. Although some are found in other treatment plots, group 2 species are primarily legumes and are less tolerant of annual summer burning and do not compete well with the hardier woody vegetation of the periodically burned plots. Plants in group 3 were common in all burned plots but absent in the unburned controls, indicat-

ing a dependence on frequent disturbance. Most species in group 3 disperse their seed broadly and compete vigorously for resources, thus enabling them to become established quickly after fire.

Groups 4 and 5 are comprised largely of woody plants (Table 1). Most of the species in these groups reproduce by sprouting but with varying degrees of vigor. Group 4 species are relatively abundant in all but the annual summer plots, maintaining their abundance primarily through sprouting. The presence of loblolly pine in group 4 was attributed to germination of seedlings which would be consumed by the next fire. Species in group 5 were relatively intolerant of frequent burning and were most common in unburned controls. Dogwood and partridge berry (*Mitchella repens* L.) were absent from annual burn plots, while redbay (*Persea borbonia* L.) and fetterbush (*Lyonia lucida* Lam. (K. Koch.)) were absent from both periodic and annual plots.

Establishment of pine–grassland communities

All tree species in the midstory and overstory of the Santee Fire Plots were well adapted to frequent low-intensity burning. Thick bark and high crowns protected the pines from damage and no fire-related mortality was observed. Hardwoods over 12.5 cm d.b.h. were protected by thick bark and most survived. During the first 20 years of the study, most hardwoods below 12.5 cm d.b.h. were probably top killed or girdled, particularly by summer burning.

The response of overstory tree species to these long-term prescribed burning treatments was considered minimal since only one major trend was observed. In burned plots, small hardwoods were replaced by large numbers of sprouts during the early years of the study. Later, those sprouts were replaced by grasses and forbs. The gradual change from small hardwoods to grasses and forbs was completed by only annual summer burning. This treatment was required for a period of 20 years to eliminate all hardwood sprouts (Langdon, 1981). This study provides evidence that sprout vigor is decreased by long-term annual winter burning, suggesting that these sprouts may eventually be eliminated. However, a large regeneration pool of hardwoods still exists after 43 years of treatment. Periodic burns did little to reduce numbers or vigor of hardwood sprouts.

This study emphasizes that frequent fires over long periods are needed to create and maintain the open pine–grassland communities reported by early explorers. Periodic burning over 43 years did little to eliminate hardwoods and it supported a dense woody understory shrub layer. Annual winter burns maintained an open understory with vegetation dominated by grasses and forbs. However, that understory also included numerous woody sprouts, which would form a dense hardwood midstory if burning were interrupted for a few years. Of all treatments tested, only annual summer burns supported the fire-dependent grasses and forbs, without hardwood regeneration, which Ko-

field sampling and Dr. Steven R. Hill, curator of the Clemson University herbarium, for assistance with species identification.

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