

# EVALUATING PYROGENICITY AND ITS EFFECTS ON VEGETATION IN LONGLEAF PINE SAVANNAS

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## INTRODUCTION

Like many habitats containing uneven-aged stands of long-lived pines, longleaf pine (*Pinus palustris*) savannas of the southeastern coastal plain are characterized by frequent fires (see reviews of Abrahamson and Hartnett 1990, Myers 1990). Common intervals between fires cited for these habitats range from as often as every year to about every 5-10 years (Christensen 1981). Three different types of evidence independently suggest high fire frequencies in pine savannas. First, high frequency of fire is deduced from numerous observations of the rapid invasion of pine savannas by hardwoods following fire exclusion (Heyward 1939, Laessle 1942, Komarek 1974, Veno 1976, Clewell 1981, Streng and Harcombe 1982, Abrahamson 1984, Platt and Schwartz 1990). Second, high frequencies of lightning strikes (e.g., Maier et al. 1979) also indicate the potential for very frequent, even annual, fires in many pine savannas of the coastal plain (Komarek 1964). Third, high frequencies of fire have occurred over periods of time long enough for evolution of a number of herbaceous and woody species endemic to southeastern pine savannas. Almost all of these species are resprouters capable of surviving fires, which also suggests a very high fire frequency (Abrahamson 1984).

Longleaf pine savanna fires are usually of low intensity. Multiple fires per decade result in only small amounts of fuel being accumulated in the intervals between fires. Fires also do not enter the canopy on a regular basis, but tend to remain confined to the ground cover, which is a mixture of grasses, shrubs, and herbaceous species that burn at relatively cool temperatures. The tendency for frequent fires when there has been little fuel accumulation and during the growing season when vegetation is green has been attributed, in considerable part, to the flammability (*sensu* Mutch 1970) of the shed needles of longleaf pine. Shed and dried longleaf pine needles are easily ignited; in addition, Williamson and Black (1981) found that litter beneath pine trees produced higher temperatures than litter beneath scrub oaks (*Quercus*) also present in xeric pine savannas. Because shed needles are located beyond the crowns of trees, fires are likely to spread into areas around trees as well. The presence of a ground cover dominated by resprouting perennials also may facilitate fire, especially when that vegetation is dominated by flammable species (e.g., *Aristida stricta*; see Wells and Shunk 1931).

These observations and data have produced a paradigm of longleaf pine

savannas as pyrogenic habitats in which fire has played an important role throughout much of the evolutionary history of the species present (e.g., see Means and Grow 1985). Indeed, studies in a number of habitats have suggested that pyrogenicity (i.e. facilitation of fire) has evolved as an adaptation whereby plants capable of surviving fires may suppress or even eliminate less fire-intolerant competitors (Mutch 1970; Rundel 1981; Williamson and Black 1981; Buckley 1984; Platt et al. 1988b; Rebertus et al. 1989). Others disagree, suggesting that pyrogenicity might be a secondary consequence of selection for other life-history characteristics (Snyder 1984).

Regardless of the evolutionary basis, patterns to the deposition of pyrogenic needles may have important consequences for vegetation patterns and processes in southeastern pine savannas. Gradients in fire intensity potentially can influence relative survival of hardwood trees, thus favoring dominance of longleaf pine (Rebertus et al. 1989). Such fire-intensity gradients also may influence survival or reproduction of herbaceous or woody species in the ground cover, thus resulting in local gradients in species composition.

Some very basic questions need to be addressed that bear on both the evolution and ecological consequences of pyrogenic fuels in longleaf pine savannas. First, is variation in abundance of longleaf pine trees associated with temperature gradients during fires in these forests? Williamson and Black (1981) demonstrated significant differences in fire temperatures beneath longleaf pines and oaks, but this could be a result of oak litter suppressing fire in a matrix of otherwise flammable fuel rather than the pyrogenic effects of longleaf needles increasing fire temperatures (Streng and Harcombe 1982). Second, if gradients in fire temperatures are created by pines, how important are they compared to other sources of variation in fire temperatures? For example, the effects of pyrogenic fuels produced by pines are assumed to be added to background fuel loads, but it is possible that flammability of the ground cover varies more than the added effects of pine needles. Finally, if significant gradients in fire temperatures are associated with longleaf pine trees, how important are the pyrogenic effects of pines compared to other characteristics of fire regimes in determining vegetation patterns and processes?

In this paper, we examine whether variation in fire temperatures is related to pyrogenic litter of longleaf pine trees in two different north Florida savanna communities (xeric sandhills and seasonally flooded flatwoods). We then use data from an ongoing long-term experimental field study to compare the responses of vegetation to fire temperatures and season of burning, another important environmental variable that may influence responses of vegetation to fire (Platt et al. 1988a). Two specific aspects of the role of pyrogenicity of longleaf pine are addressed and compared with effects of burning season. First, are pines favored over oaks in areas with hotter fires, as is predicted by the pyrogenicity hypothesis? Second, are there differences in composition and flowering patterns in the ground-layer vegetation related to fire temperature gradients? Results of this study thus enable us to evaluate the

importance of variation in fire intensity produced by pyrogenic fuels relative to other characteristics of fire regimes in longleaf pine savannas.

## METHODS

### Design of The Long-term Study

This study was conducted within the framework of an ongoing (since 1981) study of the effects of variation in characteristics of fire regimes on vegetation in pine savannas on the St. Marks Wildlife Refuge (Wakulla County, Florida). In each of two habitats, xeric sandhills (Fig. 1) and seasonally flooded flatwoods (Fig. 2; see Platt et al. 1988a for description of the habitats), 16 areas of about 2-5 ha each were selected on the basis of similarities in the density of longleaf pine and wiregrass (*Aristida stricta*). In the sandhills, the density of scrub oaks also was used to select the areas for the study. To minimize edge effects, sampling was restricted to a 1-ha plot within each area. A pretreatment burn was applied to all plots in the winter of 1980-81 to establish similar times since the last burn for all plots.

Three treatments were included in the study: habitat (sandhills or flatwoods), frequency (annual or biennial fires), and season of burn (eight different times during the year). Frequency and season of burning were randomly assigned to plots within habitats. In each habitat, beginning in November, 1981, two plots were burned during each of the following two-week periods: late November, early January, late February, early April, late May, early July, late August, and early October. The following year (beginning in November 1982), one of each of the two plots assigned to a given season of burn was reburned (i.e., annual burns). The next year (beginning in November 1983), both plots designated for burning at a given time of the year were reburned. Thus one complete treatment cycle (the interval of time between successive burnings of both plots assigned to a given season of burn) was two years. Since the initiation of the long-term study, three treatment cycles have been completed on each plot.

Experimental burns were standardized as much as possible. Within each two-week period that a plot was designated to be burned, it was burned on the first suitable day (if possible) following rain. All plots scheduled for burning during any given season (i.e. two or four plots in each habitat) were burned on as few days as possible to minimize the cost to the St. Marks Wildlife Refuge, which provided equipment and most of the manpower for the experimental burns. Strip headfires were most often used to burn plots, with width of strips increasing with distance from the downwind side of the plot.

### Fire Temperature Measurements

Maximum temperatures at ground level were recorded using Tempil tablets placed in each of 24 plots burned in February, April, May, July, August, and



**Figure 1.** An experimental plot located in a sandhill habitat at the St. Marks Wildlife Refuge near Sopchoppy, Florida. This plot is burned annually each May.



**Figure 2.** An experimental plot located in a flatwoods habitat at the St. Marks Wildlife Refuge. This plot is also burned annually during the spring.

October, 1988 (during the fourth treatment cycle). A series of 12 tablets was used that melted at various temperatures ranging from 52° to 804° C. Tablets were wrapped in heavy duty aluminum foil and placed at 20 randomly selected points in each plot prior to burning. After fires, tablets were examined and maximum fire temperature assigned. Actual melting temperatures were determined using a 30-second heat exposure in a calibrated muffle oven following the procedures of Hobbs et al. 1984; the relationship obtained (Fig. 3) indicated that wrapping the tablets in aluminum foil raised the ambient temperature at which tablets melted.

The influence of longleaf pines on maximum fire temperatures was explored graphically and with simple correlation coefficients before analyzing the data statistically. Temperature data, first converted to standard deviation units for each plot, were graphed against the sum of pine dbhs within 5 m, a measure of longleaf pine importance near each subplot. Temperature data were converted to standard deviates to present data from plots with different means and ranges on a comparable scale.

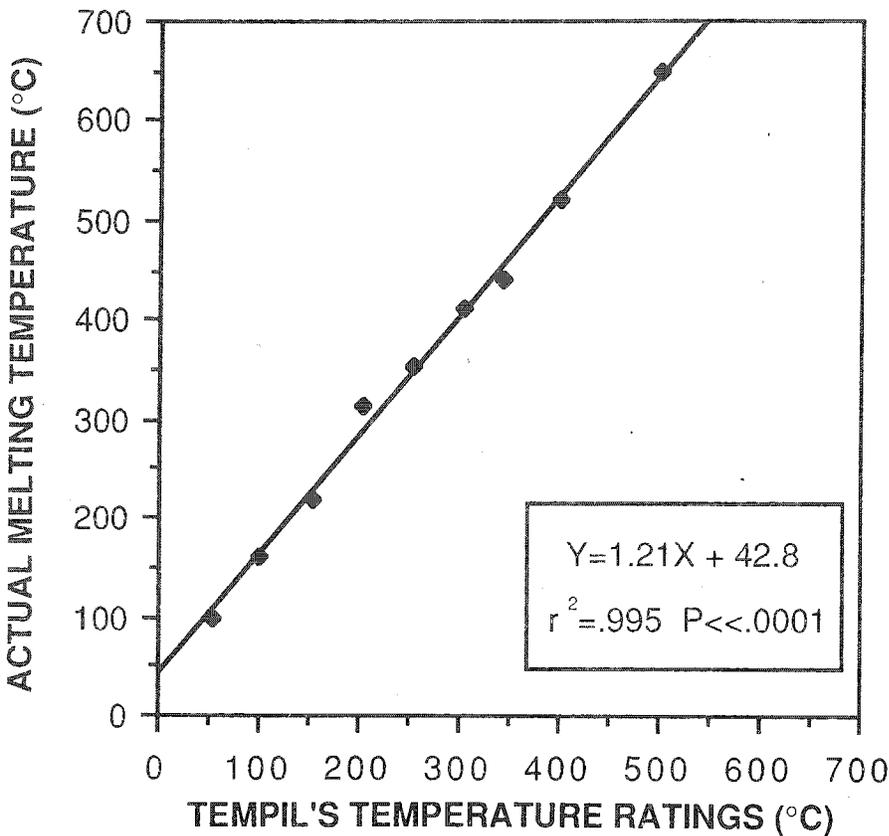


Figure 3. Relationship between Tempil ratings and melting temperatures for the heat sensitive tablets.

Because this initial phase of data analysis indicated higher maximum fire temperatures with increasing importance of longleaf pines, we used the sum of pine dbhs within 5 m as a covariate in analyses of covariance (ANCOVA). Tests were conducted for significant effects of several categorical variables, including habitat, season of burning (fall/winter, spring, summer), day of burning within season, and plot. Points occurring closer than 5 m to the border of the main plot were excluded from these analyses. Preliminary tests indicated significant differences in regression slopes between sandhills and flatwoods; as a result analyses of covariance (ANCOVAs) were run separately on each habitat. All categorical variables except plot were considered fixed variables. Day of burning was considered a fixed variable because it was stratified by month within season and because it was selected on the basis of climatic conditions by the Refuge staff rather than being allowed to vary randomly. Because factors were nested, significance testing proceeded in a hierarchical fashion, with plot effects tested against within plot variance (following removal of covariation), day effects tested against variance among plots (since plots were nested within days), and finally, season of burn effects tested against variation among days (since day was nested within season).

### **Measurements of Vegetation**

We sampled the vegetation in all plots at the end of three treatment cycles. Mortality of trees was measured. In 1980, all trees  $\geq 2$  cm dbh (diameter at breast height) in each plot were tagged with prenumbered aluminum metal tags, identified to species, and measured for dbh. Each plot was recensused in 1987-1988, prior to burns that initiated the fourth treatment cycle. Mortality was expressed as the percentage of stems in a plot that were alive in 1980, but dead (above ground) in 1987. Prior to analysis, these percentages were square-root arcsine transformed to increase normality (Sokal and Rohlf 1969). Treatment means and confidence intervals were back-transformed for presentation in this paper.

Frequency of occurrence and flowering of herbaceous species in sandhill plots also were measured in 1988. Within each plot, 100 random points were located, 20 of which were the same points used to measure temperatures at ground level during fires. All species occurring in circular plots of  $1/4$  m<sup>2</sup> around these points were recorded. Flowering also was recorded the fall after burning; these data were used to determine the frequency of flowering by fall-flowering species.

### **Temperature Effects on Vegetation**

Maximum temperatures measured during fires at the initiation of the fourth treatment cycle were assumed to be similar to maximum temperature of past fires in the same locations. We have assumed that fuel conditions at a given

location remain similar over time, producing strong temporal autocorrelation (sensu Box and Jenkins 1976) between fire temperatures in successive years at the same locations. Given this assumption, subplots were divided into cool (below the median temperature for that plot) and hot (above the median temperature for that plot) locations. To test the hypothesis that oaks are differentially eliminated in hot fires, the ratio of oak to pine mortality (for stems with dbh of 2-10 cm) was then determined for the sums of all cool and hot areas, respectively, within each plot. Evergreen oaks were excluded from these analyses because they tend to occur in dense clumps and are therefore resistant to fire regardless of proximity to pines (Rebertus 1988). Differences in relative mortality between hot and cool areas, as well as interactions with season of burning, were then tested using a split-plot analysis of variance where fire temperature was the subplot treatment and season was the main plot treatment.

Testing for temperature effects on ground cover vegetation was done using canonical correspondence analysis (Ter Braak and Prentice 1988), a form of constrained ordination where species are assumed to be distributed unimodally across environmental gradients. Constrained ordination differs from previous ordination methods in allowing direct statistical testing of the effect of an environmental variable on vegetation. The eigenvalue associated with the first axis of such an ordination is a measure of the extent of separation among species across the gradient of interest. The significance of the observed eigenvalue is evaluated using a Monte-Carlo test in which randomly generated eigenvalues are repeatedly calculated from random combinations of species and values of the environmental variable (Ter Braak 1987). A finding of insignificance is considered to have occurred when more than 5% of the randomly generated eigenvalues exceed the observed value. Such a finding suggests that species distributions along the environmental gradient do not differ more than would be expected by chance.

Vegetation data used in the ordination analysis consisted of presence/absence species data for each subplot at which fire temperatures were measured. The environmental variable of interest was temperature, expressed as standard deviates from each plot mean (again, therefore, allowing comparison between cool and hot locations in plots differing in mean temperatures). To correct for subplot differences due to background effects of main plots, a dummy variable corresponding to each main plot was used as a covariate in the analysis (thus random permutations of species and temperatures in the Monte-Carlo significance test were restricted to within main plots).

In a final analysis, we tested for effects of within-main-plot variation in temperature on flowering of the two most common fall-flowering species, *Aristida stricta* and *Pityopsis graminifolia* (nomenclature follows Clewell 1985). Flowering of these species occurs abundantly only following spring and summer fires; therefore, we classified within-plot locations as hot (temperatures during the fire greater than or equal to 520° C) or cool (temperatures less

than 520° C) only for these treatments. According to this definition, about 20% of the temperatures measured during the spring/summer fires fell into the hot category. Paired t-tests were used to test whether the percentage of flowering of *Aristida stricta* and *Pityopsis graminifolia* differed between hot and cool spots. Pairing was done within main plots in order to control for plot-to-plot variation in flowering.

## RESULTS

### Fire Temperatures

As predicted by the hypothesis of longleaf pine pyrogenicity, maximum fire temperatures within plots increased as the importance of longleaf pines increased (Fig. 4a,b). Moreover, in each habitat, maximum temperatures were consistently among the hottest temperatures at points within plots where pines were most important. Nonetheless, at points within plots where pines were absent or less important (the majority of cases) maximum temperatures were not always lower than those in areas with a greater importance of pines. Rather, a considerable range of maximum temperatures occurred in such microhabitats. Some of these measurements, especially in the flatwoods (Fig. 4b), were as hot or hotter than those observed under pines. These data strongly indicate that the effect of abundant pine litter is to impose a uniformly high temperature of burning over a variable fuel matrix that otherwise would burn with considerable local variation in intensity.

Maximum fire temperatures increased significantly with importance of pines in both habitats. The rate of increase was greater, however, in the sandhills than in the flatwoods, suggesting a lesser effect of pines on fires in the latter habitat. This difference in slopes, evident even in the standardized temperature data (Fig. 4a,b), was much more apparent in the unstandardized temperature data (Fig. 5). As a consequence of the more pronounced effect of pines, maximum fire temperatures in areas of high pine importance were much greater in the sandhills than in the flatwoods (Fig. 5).

In addition to significant effects of longleaf pines, several other factors had significant effects on temperatures measured in the fires (Table 1). Differences among plots burned on the same day were significant, suggesting unique effects of topography and fuels in the different plots. In the flatwoods, significant differences were also detected among days burned in the same season, probably reflecting climatic differences before or during fires. There was a trend towards increased temperatures in plots burned during compared to between growing seasons (Fig. 6). Nonetheless, season of burn effects on temperatures were not significant, largely as a result of the large variation among temperatures in plots burned on different days within the same season (Table 1).

Results of temperature analyses demonstrate that even though there are

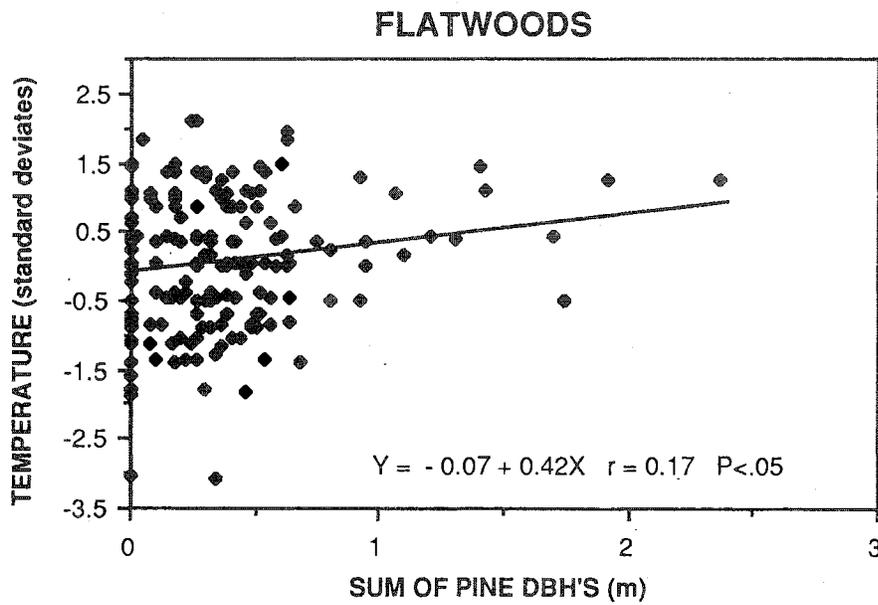
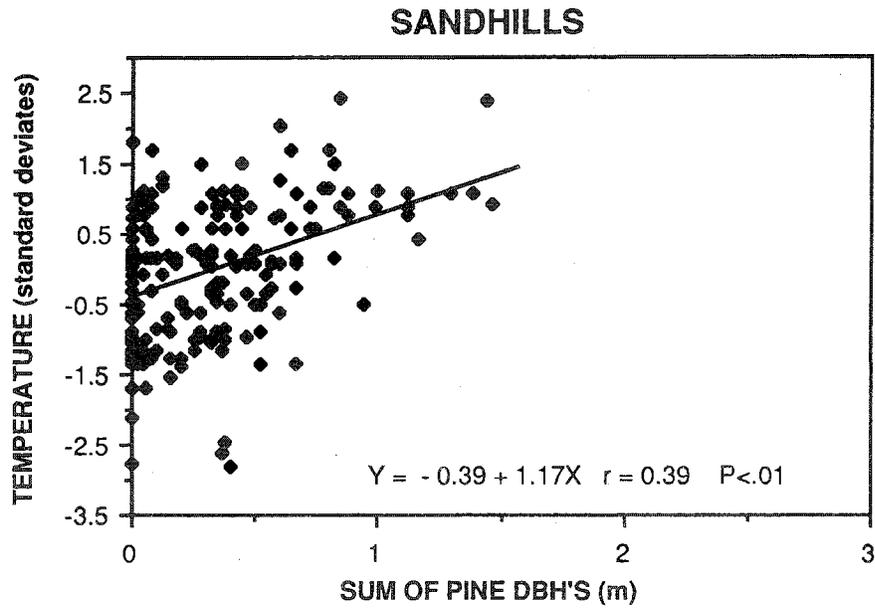


Figure 4. Scatterplots of temperature (in standard deviation units) compared to a measure of local importance of longleaf pine (sum of pine dbhs within a 5-m radius) for both habitats. Also shown are regression lines, equations, and Pearson correlation coefficients.

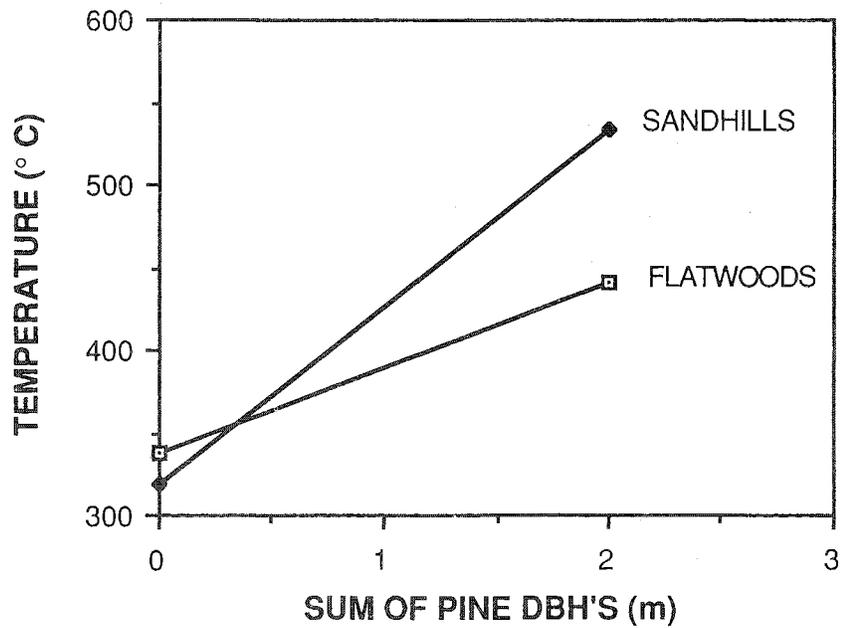


Figure 5. Regression lines of temperature on sum of pine dbhs within 5 m for unstandardized temperature data in both habitats. Regressions were adjusted for differences in sample sizes among plots.

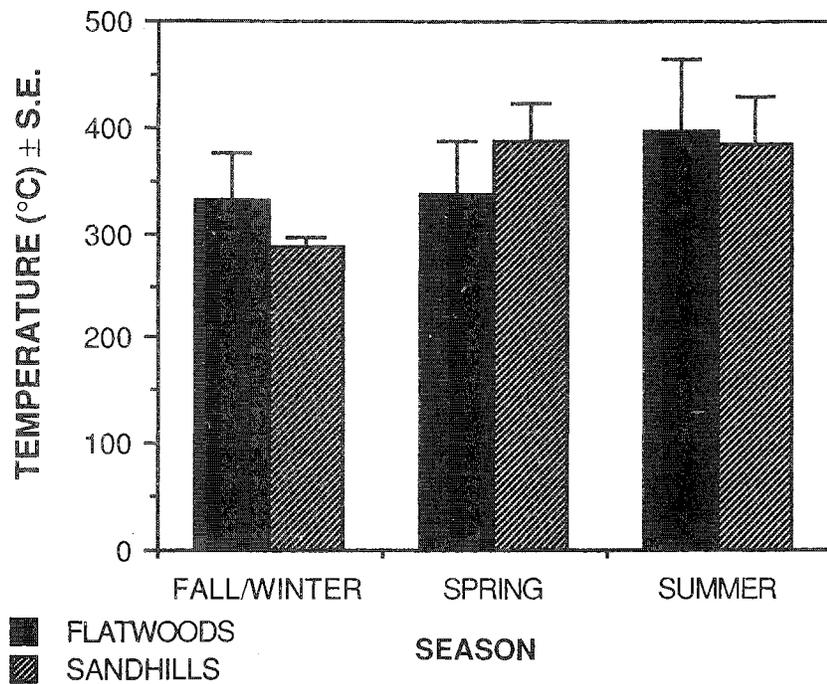


Figure 6. Seasonal trends in fire temperatures in sandhill and flatwoods habitats.

**Table 1. ANCOVA results of fire temperatures.**

<b>A. Flatwoods</b>				
Source of variation	df	MS	F	Significance
Within cells	178	6102.88	9.49	.002
Regression (within)	1	57928.15	9.49	.002
Plot within day within season (error 1)	6	16784.89	2.75	.014
Error 1	5	18431.11		
Regression (error 1)	1	32758.44	1.78	.240
Season	2	88233.85	.6	.6
Day within season	3	146940.14	7.97	.024
<b>B. Sandhills</b>				
Source of variation	df	MS	F	Significance
Within cells	179	6481.95		
Regression (within)	1	215262.47	33.21	.00001
Plot within day within season (error 1)	6	32961.73	5.09	.0001
Error 1	5	27113.29		
Regression (error 1)	1	25225.97	.93	.379
Season	2	228795.26	2.72	.27
Day within season	3	83969.41	3.10	.128

temperature gradients produced by longleaf pines in sandhill and flatwood savannas, there is considerable additional variation that is related to variation among days and local site conditions. Such variation is of a magnitude that it can potentially blur effects of temperature gradients resulting from pyrogenicity (e.g., during periods of very dry conditions, a critical threshold for mortality might occur regardless of proximity to pines).

### Vegetation Responses

Within sandhill plots, hot and cool areas (i.e., close to or away from pines) did not differ significantly in oak mortality (i.e. topkill), pine mortality, or in differences between oak and pine mortality (Fig. 7). In contrast, season of burning strongly affected oak mortality rates and, consequently, differences in mortality rates between oaks and pines. Spring burns produced about twice as much mortality of oaks as burns in other seasons, while resulting in negligible increases in the mortality of pines. These patterns were similar in areas that burned at hot and cool temperatures (Fig. 7). As a result, interactions between season of burn and hot and cool areas within plots were non-significant in all cases.

Similar results were obtained regarding the effects of spatial variability in fire temperatures on percent flowering of two of the most abundant fall-flowering sandhill species, *Aristida stricta* and *Pityopsis graminifolia*. The

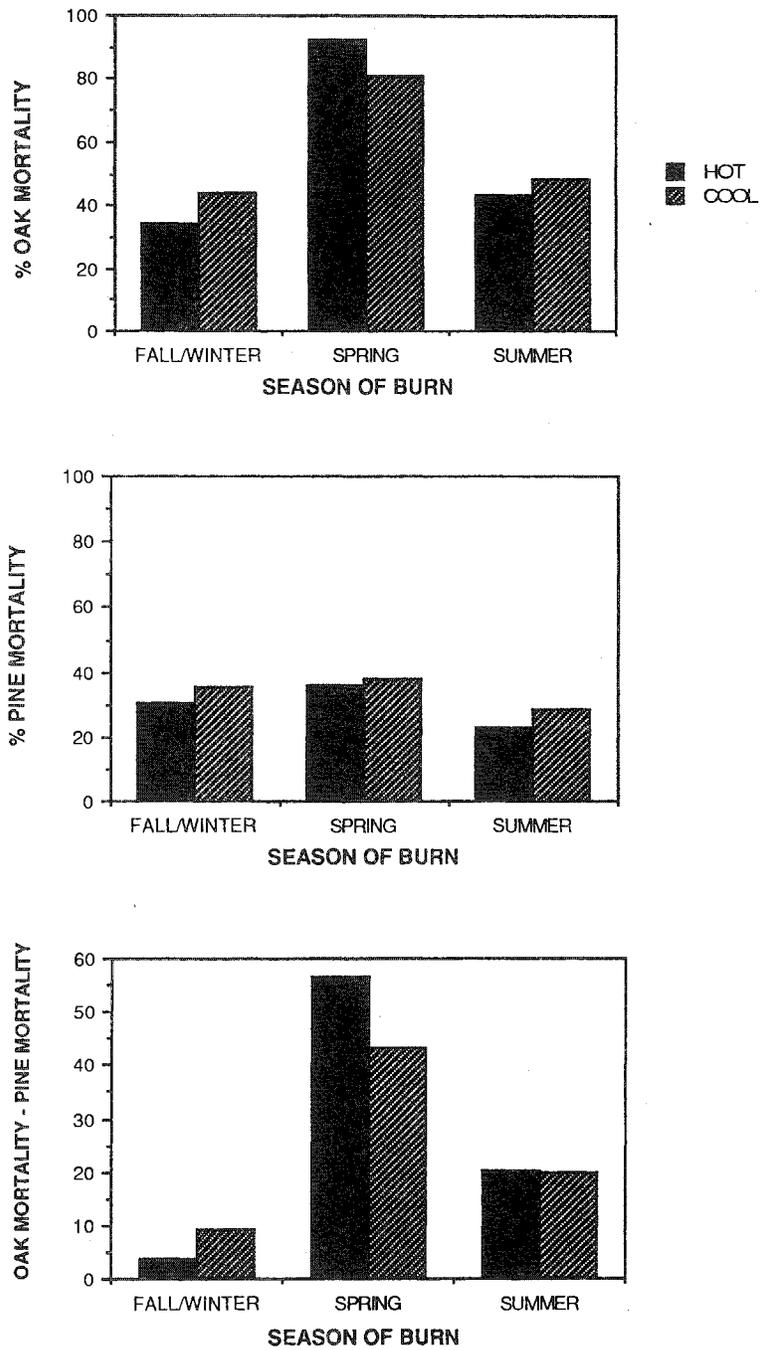


Figure 7. Relationships of oak topkill (top), pine mortality (center), and the difference between them (bottom) to season of burning and “hot” and “cool” areas within experimental plots.

spatial heterogeneity in fire temperature did not influence flowering (Table 2). Again, this was in strong contrast to results related to season of burning, for which we observed a strong positive effect of growing season burning on flowering of many species (Table 3).

Finally, we used canonical correspondence analysis (CANOCO) to test for effects of temperature variation on species composition of ground cover vegetation in the sandhills. Results again indicated negligible effects of temperature variation on vegetation. The eigenvalue for the first canonical axis was only .05, indicating very little separation among species along the presumed temperature gradient. Permutation testing performed by the CANOCO program indicated a probability of .35 that an eigenvalue of this

**Table 2. Percent flowering following spring or summer fires.**

	Hot Spots ( $\geq 520^{\circ}\text{C}$ )	Cool Spots ( $< 520^{\circ}\text{C}$ )	p#
<i>Aristida stricta</i>	79.8 (24)*	77.5 (60)	ns
<i>Pityopsis graminifolia</i>	72.1 (19)	81.6 (67)	ns

\*number of spots observed

#paired t-test with hot and cool spots paired within the experimental plot

**Table 3. Percent flowering of common fall-flowering sandhill species.**

	TIME OF BURNING				P
	Growing Season Mean (SD)		Dormant Season Mean (SD)		
GRASSES:					
<i>Andropogon</i> spp.	55.5	(13.4)	9.5	(9.9)	.0001
<i>Aristida stricta</i>	78.5	(12.7)	5.9	(7.9)	.0001
<i>Dichanthelium aciculare</i>	57.2	(13.7)	49.1	(13.9)	ns
<i>D. ovale</i>	38.1	(21.1)	51.5	(20.6)	ns
<i>Paspalum setaceum</i>	71.4	(11.7)	60.5	(24.9)	ns
<i>Schizachyrium scoparium</i>	10.2	(9.7)	0.2	(.6)	.02
SEDGES:					
<i>Scleria ciliata</i>	9.7	(11.3)	33.0	(23.7)	.03
FORBS:					
<i>Elephantopus elatus</i>	7.6	(9.0)	3.7	(4.6)	ns
<i>Lechea sessiliflora</i>	18.4	(23.7)	58.5	(5.7)	.0004
<i>Liatis</i> spp.	42.7	(19.4)	13.9	(5.0)	.002
<i>Pityopsis aspera</i>	62.6	(22.5)	10.7	(10.0)	.0001
<i>P. flexuosa</i>	43.1	(14.9)	38.1	(18.5)	ns
<i>P. graminifolia</i>	69.0	(15.0)	15.5	(12.2)	.0001
<i>Stylosanthes biflora</i>	19.2	(16.4)	1.0	(2.7)	.01

magnitude could have arisen by chance. Thus, the null hypothesis of no significant effect of fire temperature on ground cover vegetation composition could not be rejected.

## DISCUSSION

Longleaf pine produces pyrogenic fuels. The results of our study demonstrated that areas containing more and larger pines consistently had higher maximum fire temperatures. These results are consistent with those obtained by Williamson and Black (1981). We also found, however, that fire temperatures were not uniformly cooler in areas away from pines. Williamson and Black's (1981) measurements of cooler fires under oaks apparently represent only one extreme on a gradient of fire temperatures that occur independently of pines. Clearly, many other species in savanna communities produce flammable live and dead fuels, and pyrogenic effects of these species can be as important as those of longleaf pines. In frequently burned savannas, longleaf pine may be only one among many species contributing to a matrix of pyrogenic fuels which collectively serve to maintain the existence of these communities against encroachment by hardwoods. This is to be expected from an evolutionary perspective, since long-term persistence of many of these ground cover species may be at least as dependent on frequent fires as is persistence of longleaf pine.

Our results demonstrate that while fire intensity gradients are influenced by longleaf pine, they also are not as dependent on longleaf pines as previously hypothesized. This appears to be especially true in the seasonally flooded flatwoods, where increases in pine importance resulted in only minor increases in fire temperatures. Limited effects of pine trees in this habitat may be related to low production of needle litter, suggested by very low tree growth rates (Glitzenstein and Platt, unpublished data; also see Golkin and Ewel 1984). Historically, pines in the wetter flatwoods may have been present at sparse densities or even only as scattered occasional trees in open savannas. Hence, at such low densities, the pyrogenic fuels produced by longleaf pine would not likely have strongly influenced community patterns and processes. Instead, fire intensity probably was influenced primarily by herbaceous and woody ground cover vegetation, some of which is highly flammable.

Temperature gradients related in part to pyrogenic fuels of longleaf pine are present in the sandhills. Regardless, such gradients appear to be much less important than season of burning in influencing the dynamics of woody plants in this habitat. Repeated spring fires favor survival of small pines over scrub oaks while, within stands, there is no differential survival of pines relative to oaks in areas that burn at higher temperatures. Thus, our data strongly indicate that aspect dominance of sandhills by longleaf pine is a result of a higher likelihood of fire at those times of the year when scrub oaks are differentially susceptible to fire.

We found that fire intensity patterns appeared unimportant in explaining relative survivorship of oaks and pines. These results seem inconsistent with

those of Williamson and Black (1981) and Rebertus et al. (1989), who, finding lower survival of oaks beneath pine crowns than in the open, attributed these results to hotter temperatures under pines. The results of Williamson and Black (1981) and Rebertus et al. (1989) were obtained in stands that had not been burned for a number of years prior to study. We suggest that proliferation of oaks during the fire-free period suppressed the herbaceous ground cover to such an extent that fires burned with very low intensity except in the immediate vicinity of pines (see Streng and Harcombe 1982). As a result, fires intense enough to topkill scrub oaks may have been restricted to areas beneath pine crowns. In our study, in contrast, all experimental plots had a well developed ground cover resulting from repeated burning prior to the study. Under such conditions, minimum temperatures sufficient to topkill oaks may have been routinely exceeded, even in areas of limited density of pines. Moreover, we conducted multiple fires within a short period of time as part of the experimental design of our study. Repeated spring fires at close intervals may have cumulative effects on the oaks, regardless of intensity.

The above considerations suggest that the finding by Rebertus et al. (1989) of higher oak mortality in the vicinity of large longleaf pines may be more characteristic of long-unburned stands than of naturally burned longleaf pine savannas. This suggests in turn that the relative importance of longleaf pine litter in facilitating fire may be greatest in stands that have long intervals between fires (i.e., that may be on the verge of "escaping from fire" [sensu Streng and Harcombe 1982]). The longevity of longleaf pine (Platt et al. 1988b), coupled with the pyrogenic effects of accumulated pine needles, could, therefore, form a final barrier preventing conversion of savannas to other vegetation types (cf Myers 1985, 1990) and may partly explain persistence of longleaf pine islands within a landscape of less flammable vegetation (cf Kalisz and Stone 1984).

Our results also suggest that spatial differences in fire temperatures have little effect on composition and patterns of flowering of ground cover plants in frequently burned longleaf pine savannas. In contrast, season of burn strongly influenced flowering and fruiting of a number of ground cover species. Enhanced flowering responses the fall following spring burns are consistent with the suggestion that a large proportion of the herbaceous flora, including dominant warm-season savanna grasses such as *Aristida*, *Andropogon*, and *Schizachyrium*, as well as fall-flowering legumes such as *Stylosanthes* and composites such as *Pityopsis* and *Liatris*, may have evolved in association with such fires. If maintained over many years, as suggested by the seasonal patterns to lightning and flammability of vegetation, fires that occur primarily during the early part of the growing season would result in major differences in the ground cover vegetation compared to fires at other times of the year.

In conclusion, our results suggest that temperature gradients resulting from pyrogenic fuels produced by longleaf pine do indeed exist, especially in sand-hill savannas. Even in this habitat, however, pyrogenic effects of pine litter

are only one component of a highly variable matrix of fuels. Furthermore, regardless of how it may arise, spatial variation in fire temperatures appears to have much less effect on vegetation patterns and dynamics of vegetation in frequently burned savannas than does season of burn. In essence, the aspect of open pine savannas characterized by longleaf pine in the overstory and a ground cover containing abundant grasses and herbaceous forbs appears to be a result primarily of lightning-initiated fires that tend to occur repeatedly and frequently during the spring of the year.

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