Effects of Fire Regime and Habitat on Tree Dynamics in North Florida Longleaf Pine Savannas

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EFFECTS OF FIRE REGIME AND HABITAT ON TREE DYNAMICS IN NORTH FLORIDA LONGLEAF PINE SAVANNAS[1]

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Abstract. Frequent, low intensity fire was an important component of the natural disturbance regime of presettlement savannas and woodlands in the southeastern USA dominated by longleaf pine (*Pinus palustris*), and prescribed burning is now a critical part of the management of these endangered habitats. Fire season, fire frequency, and fire intensity are three potentially important, though still little understood, components of both natural and managed fire regimes. In this long-term (8-yr) study, we experimentally (through the use of prescribed burning) tested for effects of fire season (eight different times throughout the year) and fire frequency (annual vs. biennial burning), on population dynamics (recruitment, growth, mortality, change in density, and change in basal area [the total basal area of all stems in a plot]) and species composition of trees in two quite different types of longleaf-pine-dominated habitats (north Florida sandhills and flatwoods). Limited fire temperature and intensity data were also collected during one year to examine the relationship between fire behavior (temperature and intensity) and tree mortality.

Contrary to prior hypotheses, our results showed few systematic or predictable effects of season or frequency of burning on dynamics of longleaf pine. Instead, variability in the population dynamics of this species appeared to be related largely to variation in fire behavior, regardless of the season of burning.

Consistent with prior hypotheses, we found that deciduous oak species (*Quercus laevis, Q. margaretta,* and *Q. incana*) were least vulnerable to dormant-season burning and most vulnerable to burning early in the growing season. This was shown particularly by seasonal trends in the effect of burning on oak mortality (both topkill and complete kill) and, to a lesser extent, on oak recruitment. Oak densities and basal areas also declined in the spring-burned plots, resulting in a shift away from oaks and towards increased dominance by longleaf pine. Detrimental effects of spring burning on oaks were partly explained by fire behavior, but there appeared also to be an important residual effect of burning season, particularly on complete kill.

Though longleaf pine population dynamics did not differ markedly as a result of burning season and frequency, we did find important differences in pine dynamics between the two habitats (i.e., sandhills and flatwoods). In general, populations of longleaf pines in the sandhills appeared to be density regulated, while flatwoods pine populations were declining regardless of the level of intraspecific competition. This suggests that long-term persistence of longleaf pine, and perhaps other fire-adapted species in frequently burned longleaf-pine-dominated communities, may be determined by complex interactions between habitat factors and fire regimes.

Key words: burning frequency; burning season; competition; fire regimes; flatwoods; habitat; North Florida; Pinus palustris; Quercus incana; Quercus laevis; *sandhills; species change.*

INTRODUCTION

Fire is an important ecological factor in many habitats worldwide (Kozlowski and Ahlgren 1974, Wright and Bailey 1982, Crawley 1986, Trabaud 1987, Johnson 1992). In these habitats the local fire regime (sensu Fox and Fox 1987, Malanson 1987) can strongly influence vegetation composition and dynamics (e.g., Gill et al. 1981 and papers therein, Keeley 1981, Trabaud and Lepart 1981, Krueger 1984, Hobbs and Gimmingham 1987, Bowman et al. 1988, Platt et al. 1988*a*, 1991, Collins and Gibson 1990, Fensham 1990, among many others). Aspects of the burning regime that may be important include fire frequency (e.g., Trapnell 1959, Rose-Innes 1972, Noble and Slatyer 1980, Hobbs 1984, Nieuwenhuis 1987, Fensham 1990), fire intensity (Moreno and Oechel 1991*a, b*), season of burning

(Trapnell 1959, Trabaud and Lepart 1981, Le Maitre 1987, Malanson and Trabaud 1988, Platt et al. 1988a, Lonsdale and Braithwaite 1991, Swezy and Agee 1991), and regularity of burning (Keeley 1981, Malanson 1987, Rebertus et al., in press). In many areas, however, effects of different fire regimes remain poorly understood and, where important conservation or management issues are involved, controversial (e.g., Midgley 1989, Lonsdale and Braithwaite 1991, Robbins and Myers 1992, Johnson 1992).

The Coastal Plain of the southeastern United States is one area where the importance of fire as an ecological factor has long been recognized (Schwarz 1907, Harper 1911, 1962, Chapman 1932, Wells 1942, Garren 1943, Vogl 1973, Komarek 1974, Christensen 1981, Platt et al. 1988b, 1991, Platt and Schwartz 1990), but where much remains to be learned about effects of different fire regimes on vegetation (Christensen 1981, 1988). During presettlement and early settlement times, much of the landscape of this area was occupied by savannas (this term is used here to designate plant communities with an open, discontinuous tree canopy) and woodlands dominated by longleaf pine (Pinus palustris) (Bartram 1791, Baldwin 1811, Ruffin 1843, Schwarz 1907, Wahlenberg 1946, Frost et al. 1986, Silver 1990, Ware et al. 1993, Schwartz 1994, Harcombe et al., in press). Dominance of longleaf pine over other tree species is generally attributed to frequent natural burning (i.e., fire return intervals between 1 and 10 yr; see Chapman 1932, Garren 1943, Harper 1962, Komarek 1974, Christensen 1981, 1988, Frost et al. 1986, Bridges and Orzell 1989, Platt et al. 1991, Harcombe et al., in press, Rebertus et al., in press). However, except for complete fire suppression (see Heyward 1939, Streng and Harcombe 1982, Gilliam et al. 1993, Menges et al. 1993), little is known about effects of different fire return intervals on composition and dynamics of tree species in longleaf pine habitats (Rebertus et al., in press).

Another factor that may influence dynamics and composition of trees in upland habitats of the southeastern USA is season of burning. At least three reasons why this should be the case have been suggested. These are summarized below as three "hypotheses" for additional testing.

1) The "tree physiology hypothesis" postulates that seasonal variations in tree physiology and/or phenology are critically important in determining susceptibility of trees to fire (Wade and Johansen 1986a, b). This hypothesis also suggests that tree species vary in the timing of peak sensitivity to burning, so that fires at different seasons should produce different mixtures of trees. Partial support for the tree physiology hypothesis comes from several studies demonstrating that southeastern tree species do indeed differ in seasonal patterns of root carbohydrate storage and the capacity to refoliate following experimental defoliations (Hepting 1945, Woods et al. 1959, Weise et al. 1989; see

also review in Robbins and Myers 1992). One general conclusion from these studies is that deciduous hardwoods should be most vulnerable to spring fires occurring shortly after leaf expansion; in contrast, pines and other evergreens are likely to be most susceptible to fires in late summer or autumn (Wade and Johansen 1986a, b, Wiese et al. 1989, Robbins and Myers 1992).

2) The "ambient temperature hypothesis" is based largely on a series of fire-behavior equations relating height of crown scorch (i.e., needle kill or bud kill) to fireline intensity, windspeed, and ambient air temperature (cf. Van Wagner 1973, Johnson 1992). According to these equations, height of scorch increases in a curvilinear fashion with increasing air temperature, assuming constant fireline intensity and wind speed (the reason is that if plant tissue is warmer to start with, a lesser increase is required to raise the temperature to a lethal level). Since air temperatures vary seasonally (i.e., from a minimum in midwinter to a maximum during the middle of the growing season), it might be expected that crown scorch, and related aspects of tree dynamics (e.g., mortality, growth), would also vary with season of burning (Robbins and Myers 1992).

3) The "tree physiology" and "ambient temperature" hypotheses may apply to virtually any tree species. However, the third hypothetical effect of season of burning on tree dynamics is unique to longleaf pine. This hypothesis, which we will term the "brown spot control hypothesis", is derived from several studies which appear to demonstrate a positive effect (i.e., increased growth or reduced mortality) of spring burning on juvenile longleaf pines (Bruce 1951, Maple 1977, Grelen 1983). Each of these authors suggested that this effect might be due to especially effective control of brown spot fungus (Scirrhia acicola) by spring burning (this fungus is known to infest juvenile longleafs).

Despite the above hypothetical relationships and a fairly large number of empirical studies (see reviews by Garren 1943, Wade and Johansen 1986b, Robbins and Myers 1992, Streng et al., in press), the effect of season of burning on dynamics and composition of southeastern trees is not well established. In part, this is due to design and analysis problems with at least some of the empirical studies (see Robbins and Myers 1992, Streng et al., in press). Perhaps the major reason for continued uncertainty, however, is that no previous study has included a complete set of seasonal burning treatments. Thus, it has been impossible to test statistically for seasonal trends in the effects of burning.

In this paper we present results from a long term (14 yr and still continuing) experimental study of the effects of different fire regimes on trees in north Florida longleaf pine savannas. [Data on understory plants have also been collected (see Platt et al. 1988a, 1991, Brewer and Platt 1994a, b, Streng et al., in press) but these will not be discussed here.] The study was designed in part to test for effects of habitat (sandhills vs. flatwoods) and frequency of burning (i.e., annual

TABLE 1. Surface fuel loadings (in kg/m^2) in the two habitats during the study period. Data are based on eight 0.25-m^2 samples from each burn treatment plot (see Streng et al., *in press* for details on sample locations and collection dates). Data are presented separately for plots burned annually (A) and biennially (B) during 1984, due to differing times since last burn.

| | Flatwoods | | | | | Sandhills | | | | |
| | | 1984 | | | | | 1984 | | | |
	1983	A	B	1985	1988	1983	A	B	1985	1988
No. plots:	16	8	8	16	16	16	8	8	16	16
Time since fire (yr):	1	1	2	1	2	1	1	2	1	2
Fuel type										
Standing woody	.22	.16	.20	.18	.14	.04	.02	.04	.02	.04
Standing forb	.04	.03	.02	.05	.03	.03	.03	.02	.03	.03
Standing grass	.15	.13	.17	.11	.15	.19	.09	.13	.08	.12
Pine litter		.19*	.33*		.40		.44*	.76*		.62
Grass litter		...	...		.03		...	...		.04
Twigs + bark		...	...		.14		...	...		.19
Other litter		.11†	.26†		.11		.07†	.13†		.05
Grand total		.62	.98		1.00		.65	1.08		1.09

* Includes pine twigs and bark.
† Includes non-pine twigs, bark, and grass.

vs. bienniel burns), and we also collected some data on fire behavior effects (especially on tree mortality). However, the most useful feature of the experimental design was that it also included (and still does) a wide range of seasonal burning treatments. Thus, for the first time, we were able to rigorously evaluate prevailing hypotheses about effects of fire season on longleaf pine and associated tree species.

METHODS

Study area

The study was conducted in the Panacea Unit of the St. Marks National Wildlife Refuge, which is located in Wakulla County, Florida, $\approx$32 km south of Tallahassee. Established in 1931 to protect migrating waterfowl (Zontek 1966), the refuge also contains >7800 ha of upland habitats, most of it dominated by longleaf pine (Reinman 1989). The original timber was removed early in the present century, and most stands are now second growth (Reinman 1989). However, there is no history of soil disturbance, and the kinds and numbers of understory species are typical of those found in old growth longleaf pine savannas of the region (Platt et al. 1988a, 1991).

Little is known about fire history prior to establishment of the refuge, though it appears that open range burning (in late winter) was still common in the area in the late 1920s (as it is today on large tracts of private land) (Zontek 1966). After the government acquired the land, a policy of complete fire suppression was instituted, which lasted for most of the next decade (Zontek 1966). Controlled burning by refuge staff began in the early 1940s and a burning rotation of 4–6 yr was prescribed for most longleaf-pine-dominated habitats (Zontek 1966). In practice, this goal was seldom met, and actual fire return times averaged closer to 8 yr during most of the last five decades (Reinman 1989).

Sandhills.—Drier longleaf pine savannas (Subxeric Gulf Coastal Plain type of Peet and Allard, *in press*) are found in the St. Marks refuge on higher elevation sites ($\approx$12 m above mean sea level), with deep, moderately to excessively drained, acid, sandy soils (Typic Quartzipsamments in the Ortega and Lakeland series) (Allen 1991). These soils are representative of the very xeric Entisols that are common on deep sand deposits throughout western Florida (Brown et al. 1990). In the refuge, the main canopy of these sandhill sites is dominated almost exclusively by longleaf pine. However, there is often a well developed midcanopy (usually $\leq$9 m in height) consisting of several species of xerophytic oaks. Turkey oak (*Quercus laevis*) is generally the most common species, but bluejack oak (*Q. incana*) and sand post oak (*Q. margaretta*) may also be locally abundant (nomenclature follows Clewell 1985, except as otherwise noted). Three other oak species, sand live oak (*Q. geminata*), myrtle oak (*Q. myrtifolia*), and upland laurel oak (*Q. hemisphaerica*) occur occasionally in dense patches. The ground cover is dominated by wiregrass (*Aristida beyrichiana*; Peet 1993) and grass-leaved goldenaster (*Pityopsis graminifolia*), though many other herbaceous plants and some small shrubs are also common (Platt et al. 1991 includes a species list and photograph of this habitat type; see also Christensen 1988, Myers 1990, and Peet and Allard, *in press* for more general descriptions of this type of community). Standing fuels reflect the dominant understory vegetation, and consist mostly of herbaceous plants (Glitzenstein et al. 1990, Streng et al., *in press*; see Table 1 for a summary of data for five years). Downed fuels consist mainly of pine needles (often partially burned by past fires) and twigs (Table 1). Due to the history of frequent

TABLE 2. Design of the field experiment within one habitat, indicating treatments (fires) applied over a pretreatment period (P) and four treatment cycles of 2 yr each (1981–1989). Each row in the data field represents one of the 16 plots located in each habitat; the dates in each row indicate years in which the plot was burned.*

Fire regime characteristic			Treatment cycle								
Season	Frequency	P	1		2		3		4		
Late November	Annual	1980	1981	1982	1983	1984	1985	–	1987	–
	Biennial	1980	1981	–	1983	–	1985	–	1987	–
Early January	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Late February	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Early April	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Late May	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Early July	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Late August	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–
Early October	Annual	1980	1982	1983	1984	1985	1986	–	1988	–
	Biennial	1980	1982	–	1984	–	1986	–	1988	–

* Two plots were randomly assigned to each of eight seasons of burn. For each season of burn, plots originally were randomly assigned to either annual or biennial burns. Annual burns were eliminated after 1986; dashes mark the omitted burn years. Tree dynamics data were collected at the end of the third and fourth treatment cycles, just before plots were burned at the start of the fourth and fifth cycles, respectively.

burning, duff, as it is usually defined (see Johnson 1992), is virtually nonexistent in this and other long-leaf-pine-dominated habitats (McKee 1982, Kalisz and Stone 1984, Brown et al. 1990).

Flatwoods.—Pine flatwoods vegetation occurs extensively throughout Florida on sites "characterized by low, flat topography, and relatively poorly drained acidic, sandy soil" (Abrahamson and Hartnett 1990). In the St. Marks Refuge, flatwoods vegetation (see Platt et al. 1991: Fig. 2 for a photograph) is found on lower elevation sites (1–2 m above mean sea level) where the water table is often within a few centimetres of the soil surface for much of the year. Soils typical of such sites are classified as Humaqueptic Psamments or Aquic Quartzipsamments, usually of the Scranton and Ridgewood series (Allen 1991). Except on scattered islands of slightly higher ground, the xerophytic oaks characteristic of sandhills are lacking from flatwoods. The ground cover is dominated by wiregrass, runner oaks (*Q. pumila* and *Q. minima*), gallberry holly (*Ilex glabra*), saw palmetto (*Serenoa repens*) and ericaceous shrubs (e.g., *Gaylussacia dumosa, G. frondosa,* and *Vaccinium myrsinites*). Scattered throughout are patches of slightly lower, even wetter, areas. Shrubs are much reduced in these hydric flatwoods (or "wet savannas"), which are dominated by wiregrass, other grasses (e.g., *Ctenium aromaticum, Sporobolus floridanus*) and sedges (*Rhynchospora* spp.)(see Wells and Shunk 1931, Means and Mohler 1979, Folkerts 1982, Walker and Peet 1983, Taggart 1990, Olson 1992, and Peet and Allard, *in press* for more thorough descriptions of these wet savanna habitats). Pond pine (*Pinus serotina*) or

slash pine (*Pinus elliottii*) may also become prevalent in the hydric flatwoods and along intermittent streams that drain these habitats.

In comparison to the sandhills, fuels in the flatwoods are characterized by greater total live masses and a much greater proportion of live woody plants (Table 1). However, due to a sparser tree canopy and consequent reductions in pine needles and twigs, downed fuels are considerably less in this habitat (Table 1). Thus, total fuel loadings in the two habitats are roughly equivalent ($\approx$0.6 kg/m^2 after 1 yr without burning and 1 kg/m^2 after two fire-free yr, see Table 1).

Experimental design

The study was designed as a randomized-block experiment with three factors (Table 2). Habitat (either sandhills or flatwoods) was the blocking factor. Eight season-of-burn treatments included fires during the following 2-wk periods: (1) 15–30 November, (2) 1–14 January, (3) 15–28 February, (4) 1–14 April, (5) 15–31 May, (6) 1–14 July, (7) 15–31 August, and (8) 1–14 October. Frequency-of-burn treatments were either annual or biennial fires. An unburned control was not included in the experimental design because the effect of not burning is comparatively well established (see citations in *Introduction*); furthermore, the study was designed to compare effects of different burning regimes, not to contrast burning with the absence of burning (Platt et al. 1988a).

In 1980, all sandhills and flatwoods areas ≤2–5 ha in size in the Panacea Unit (see Reinman 1989) of the refuge were located using aerial photos. After exam-

ining each area in the field, 16 areas in each habitat were selected as sites for experimental burning treatments. Sites selected (henceforth referred to as plots) had similar densities of longleaf pine trees, oaks (in the sandhills), and wiregrass. Each combination of season and frequency of burning was randomly assigned to one plot in each habitat.

Before starting the experimental burning treatments, sandhills oaks were thinned to densities and size distributions similar to those found on the Wade Tract, an old-growth longleaf pine savanna in south Georgia (see Platt et al. 1988b). Thinning further standardized densities and size class distributions of these species. In addition, growth of herbaceous species and shrubs was stimulated, thus providing conditions more representative of presettlement vegetation in the area. After the oaks were thinned, all plots were subjected to a pretreatment burn in the winter of 1980 to reduce variation in the times since the last fire, and hence fire intensities, among plots. Cut oak stems and other debris from the thinning operation were burned in a few large piles within each plot to prevent any sort of general enhancement of fire intensity throughout the plot as a whole.

Experimental burning began in November of 1981, and all plots were burned for the first time (after pretreatment burns) over the following 12-mo period (Table 2). Both annual and biennial plots were burned during this first year. The following year (i.e., November 1982 through October 1983) only annual plots were burned. This and subsequent 2-yr periods including one complete set of all burning treatments will henceforth be referred to as a "treatment cycle" (see Table 2). In this paper we will consider data collected before and after the first three treatment cycles, as well as limited data collected after the fourth treatment cycle.

Annual burns tended to be patchy in some plots because of low rates of accumulation of dead vegetation and low flammability of the live vegetation (approximately 60% burned in most cases, according to field observations by M. Davis). Consequently, this treatment was eliminated from the experiment after the second treatment cycle; all plots were switched to a biennial burning schedule, providing replicate plots for analyses of season-of-burn effects (Table 2). Experimental burning has continued beyond the period of time reported here; seven treatment cycles had been completed as of mid-October 1994.

Experimental burns were standardized as much as possible, given our own time constraints and those of the refuge, which provided equipment and most of the field personnel to conduct the burns. Plots were generally burned within 2–3 d after a heavy rain, and exceptionally dry (i.e., relative humidity < 30%) or windy (i.e., gusts > 5 m/s) conditions were avoided. In addition, the plots were nearly always burned using strip headfires, with the width of the strip increasing with the distance from the downwind side of the plot.

To minimize the costs to the refuge, all plots scheduled for burning during any given season (i.e., one or two plots in each habitat) were usually burned on the same day (exceptions occurred in a few cases when fires were postponed due to rain or extreme weather conditions). We recognize that this introduces a certain degree of lack of independence of experimental error (pseudoreplication; see Hurlbert 1984) wherein unique effects of particular fires (or environmental conditions at the time of burning) might be confounded with the seasonal burning treatments. Repeated fires over several years reduce the effects of any such pseudoreplication; in addition, we have employed analytical techniques designed to minimize such effects.

Fire behavior

Data on fire behavior were collected for six of the seasonal burning treatments during the fourth treatment cycle (i.e., fires from February through October 1988). At each of these fires, we measured temperatures, percent of plot area burned, and fuel consumption. These last data were then used to calculate two measures of fire intensity (heat released per unit area and fireline intensity; see Byram 1959, Wade 1986, Johnson 1992).

Field methods.—Fire temperatures were measured using Tempil (Big Three, South Plainfield, New Jersey) heat sensitive tablets. A series of 12 tablets was used, spanning a range of melting temperatures from 52°C to 804°C. Twenty sets of these tablets, each covered in aluminum foil, were placed in random locations prior to each fire. Tablets were collected and scored immediately following the fires (see Platt et al. 1991 for details). An analysis of these fire temperature data, presented in Platt et al. (1991) indicated significant effects of day of burning and proximity of nearby trees (i.e., areas with many large pines had higher fire temperatures), but no significant effect of season of burning.

Fuel consumed by the fires was estimated from four sets of paired (i.e., adjacent) 0.25-m² subplots. Unburned fuels (i.e., standing and downed material, including duff) were collected immediately prior to burning from one subplot in each pair. Following the burn, fuels not consumed by the fire were collected from the adjacent subplot. Fuel consumption (in kilograms per square metre) was then estimated as the average difference in mass per unit area between preburn and post-burn fuels for the four paired subplots.

One hundred permanent sample points are randomly located in each main treatment plot for the purpose of quantifying changes in understory vegetation (Platt et al. 1991, Streng et al., in press). Following experimental burns during the fourth treatment cycle, we checked each point in every plot to determine whether it (i.e., standing vegetation) had burned. The percentage of "burned points" was then used to estimate percentage of area burned in each plot as a whole.

Fire intensity calculations.—Heat released per unit area (in kilojoules per square metre) was calculated by

multiplying fuel consumption (see *Field methods,* above) by low heat of combustion (see Wade 1986, Johnson 1992). Low heat values used in these calculations were based on published values (Hough 1969, Hough and Albini 1978) for herbaceous live fuels, pine needles, and twigs, which together composed the bulk of our fuels (the range of low heat values for these three fuel types is 16 412–19 303 kJ/kg). A low heat value of 17 571 kJ/kg, close to the average value for live herbaceous fuel and pine needles, was used in the sandhill calculations. A slightly greater value (18 408 kJ/kg) was used for the flatwoods, because of the greater proportion of live woody fuel in this habitat. While these estimates may not be precisely correct, error due to this source is generally considered unimportant compared to other sources of variation in fire intensity data (Johnson 1992).

Neither rate of spread nor flame length were measured in the field, and we were therefore unable to calculate fireline intensity from field data alone. However, we did attempt to reconstruct rate of spread (in metres per second), and hence fireline intensity, from available climate data using Nelson and Adkins (1988: Eq. 14) (this equation, which calculates rate of spread from windspeed, fuel consumption, and flame residence time, has been found to work well in vegetation and fuels very similar to those in our study area). Wind data used in these calculations were average daily windspeeds, obtained from the nearest weather station in Tallahassee. The use of these data was justified by a high correlation ($r = 0.83$, $n = 8$, $P = 0.01$, for the eight burning dates in this treatment cycle) between the Tallahassee data and data from Apalachicola, the next closest weather station. Since the distance between Tallahassee and Apalachicola (≈ 110 km) is much greater than that between Tallahassee and the St. Marks Refuge, it is likely that the correlation between Tallahassee windspeeds and windspeeds at the refuge was even higher than the observed correlation between the Tallahassee and Apalachicola data.

Flame residence time, the final variable in Nelson and Adkin's (1988) equation, was assumed to be 5 s in the sandhills and 7 s in the flatwoods (these values appeared reasonable, given data and examples in Nelson and Adkins 1988; again, a slightly greater value was used for the flatwoods because of the somewhat greater proportion of live woody fuels). After reconstructing rate of spread, fireline intensity (in kilowatts per metre) was calculated as the product of heat released per unit area and rate of fire spread (see Wade 1986, Johnson 1992).

Tree population censuses

Prior to the pretreatment burns in 1980 (but after thinning the oaks) all trees >2 cm dbh (diameter at breast height) in a centrally located 1-ha area in each burn plot were tagged with prenumbered aluminum tags, measured for dbh, identified to species, and mapped to the nearest 10 cm (see Platt et al. 1988*b* for a summary of mapping techniques used in this study as well). All stems joined above the ground were considered part of the same tree. If a tree had >1 stem, only the largest stem was tagged, though diameters were measured on all stems >2 cm dbh.

All plots were recensused for the first time in 1987–1988, immediately prior to burns that initiated the fourth treatment cycle. At this time, the former annual-burn plots had burned six times since the start of the study (including the pretreatment fires), while the original biennial-burn plots had burned four times (Table 2). During the recensus each tree was checked for mortality, and dbh was remeasured for all living stems. A tree was considered dead if it had no living branches above breast height. Dead trees were recorded as either topkilled (i.e., with sprouts or with living branches below breast height) or completely killed (i.e., no living sprouts or branches). Some small trees were entirely consumed in the fires and could not be relocated. Longleaf and slash pines that fell in this category were recorded as completely killed because these species do not sprout (at least as trees). Type of death could not, however, be determined for "missing" stems of sprouting species such as pond pine and hardwoods. In addition to checking for mortality and growth on previously tagged trees, we also identified, tagged, measured, and mapped all new recruits (i.e., trees that had grown to >2 cm dbh since the original census). A second recensus for mortality was conducted 2 yr later (prior to the burns that initiated the fifth treatment cycle).

Analyses: dynamics of longleaf pine and sandhills oaks

Of the various trees encountered in the censuses, only longleaf pine and oaks (the latter only in the sandhills) occurred abundantly in all plots (Appendices A, B). Tests for experimental effects on abundance and population dynamics were therefore limited to these two types of trees. All tree species were included in tests for experimental effects on changes in tree species composition. To obtain sufficiently large sample sizes (i.e., $n \geq 10$ trees for each of several size classes, see Appendix A) for analyses of oak dynamics, data were combined for the three most common species of deciduous oaks (*Q. laevis, Q. incana,* and *Q. margaretta*).

Pine dynamics.—Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to test for effects of habitat and the experimental treatments (season and frequency of burning) on longleaf pine population dynamics and changes in abundance. (Plot basal area was included as a covariate in all ANCOVAs to try to control for effects of competition). Several aspects of longleaf pine population dynamics were analyzed, including growth (defined as the average change in dbh between 1980 and 1987 for all living stems in a plot), recruitment, and percent mor-

tality (defined as the percentage of stems in a plot dying since the previous census). To test for effects of treatments on changes in longleaf pine abundance, we analyzed differences in plot basal area and density over the first three treatment cycles. Density and basal area of longleaf pine at the start of the experiment were subtracted from the same quantities determined in 1987 after 6 yr of experimental burning; these differences were then analyzed using ANOVA and ANCOVA. Prior to analysis, mortality and recruitment data were transformed to improve normality [i.e., percent mortality data were corrected for sample size differences and arcsine-transformed as recommended by Snedecor and Cochran (1981); recruit data (count-type data) were square root transformed (see Sokal and Rohlf 1982)]. ANCOVAs were tested for homogeneity of slopes (Snedecor and Cochran 1981) and, if the slopes differed significantly, the analysis was repeated for each level of a factor.

ANOVA and ANCOVA models varied somewhat depending on the date at which the data were collected and the type of data being analyzed. Data collected following the first six years of experimental burning (i.e., data on percent mortality, growth, recruitment, change in density and change in basal area collected during the first recensus in the summer of 1987) were analyzed using three-way ANOVAs and ANCOVAs. Habitat, frequency of burning, and season of burning were each considered fixed treatment effects in these analyses. Because the experimental design lacked true replication (i.e., plots within habitats treated identically) during the period encompassed by these data, the mean square associated with the three-way interaction was used as the error term for testing main effects and lower order interactions. Data on pine mortality collected after the fourth treatment cycle in 1989 were analyzed using two-way ANOVAs with replication, in which the within-cells variance was used as the estimate of experimental error. Because frequency of burning was no longer a factor in the experiment during this treatment cycle it was eliminated from subsequent analyses, and plots within habitats burned in the same season were treated as replicated experimental units regardless of whether they had previously been burned annually or biennially. Fire temperature and intensity measurements obtained during this treatment cycle were not included as additional covariates in the model, though this might seem like a reasonable approach. Fire behavior, like tree dynamics, is potentially dependent on the experimental burning treatments, and cannot, therefore, be considered as an independent effect in the model (S. L. Rathbun, personal communication). Instead, we simply tested for relationships between these variables and tree mortality using product–moment correlations.

Effects of burning often vary with tree size and small trees are usually more vulnerable than large ones (e.g., Abrahamson 1984, Rebertus et al. 1989, Guerin 1993).

To determine whether differently sized trees in our study responded similarly to the experimental burning treatments, analyses of growth and mortality were repeated for each of several dbh-size classes. To maintain adequate sample sizes for the analyses ($n \geq 10$ trees, except in a few cases, see Appendices A, B), size classes were defined slightly differently for different variables and time periods. Mortality data collected after the first three treatment cycles were analyzed using four size classes: 2–4.9, 5–9.9, 10–19.9, and ≥ 20 cm dbh. Size class limits were more narrowly defined for smaller trees to make certain that we would not overlook effects of the experiment on these presumably most vulnerable individuals. After 6 yr of frequent burning, however, sample sizes for small trees were greatly reduced in some plots, and it was therefore necessary to combine the two smallest size classes when analyzing growth, as well as mortality data collected at the end of the fourth treatment cycle.

To take full advantage of the eight different seasonal burning treatments (spaced at roughly equal intervals), we used orthogonal polynomial contrasts to test for seasonal trends (see Snedecor and Cochran 1981, Rosenthal and Rosnow 1985). In these analyses, treatment means were arranged beginning with the January burns and ending with the November burns. Using this arrangement, the two lowest order contrasts (linear and quadratic) allowed us to test previously proposed hypotheses (see the Introduction) about effects of season of burning on dynamics of longleaf pine.

The ambient temperature hypothesis predicts that sensitivity of pines (and other trees) to fires should vary directly with ambient air temperatures. Given the climate in north Florida (Chen and Gerber 1990), this leads to the further prediction that vulnerability of trees to fires should increase from a minimum during the dormant season (when air temperatures are lowest) to a maximum during the middle of the growing season (i.e., June through September in north Florida), when air temperatures are highest. If this prediction is correct most response variables (i.e., the various aspects of longleaf pine demography monitored in this study) should follow either increasing (mortality) or decreasing (growth, recruitment, change in basal area, change in density) quadratic trends. (To simplify the terminology, an "increasing" quadratic trend in the context of this paper will be defined as a curve with a local minimum in the dormant season that rises to a peak during the middle of the growing season, and then declines again at the end of the growing season. In contrast, a "decreasing" quadratic trend will be defined as a curve that begins at a local maximum in the dormant season, decreases to a minimum in midsummer, and then increases once again at the end of the growing season.)

In contrast to the ambient temperature hypothesis, the alternative tree physiology hypothesis predicts that vulnerability of longleaf pine to fires should increase

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TABLE 3. Mean fire behavior measurements for February–October burns in the fourth treatment cycle.

Burn season	Area burned (%)	Tempera-ture (°C)	Fuel consumed (kg/m²)	Fuel consumed (%)
February	97.0	335.3	.4399	45.8
April	100.0	412.5	.6355	60.4
May	98.8	308.1	.4776	53.8
July	100.0	452.4	.8176	61.8
August	100.0	327.5	.4536	42.7
October	96.5	274.8	.5854	48.0

Burn season	Heat per area (kJ/m²)	Rate of fire spread (m/s)	Fireline intensity (kW/m)
February	7921	.1307	1025
April	11440	.1221	1390
May	8564	.2064	1816
July	14650	.1698	2629
August	8175	.1063	881
October	10510	.3358	3744

from a minimum in late winter to a maximum in early autumn. The precise shape of the predicted curve is not at all clear from the available information, but there should at least be a significant linear component (increasing for mortality, decreasing for growth and recruitment). Results of a recent study by Wiese et al. (1989) on two other pine species showed that artificial defoliation in October resulted in much higher mortality, and significantly less growth, than did the same treatment in January, April, or July, suggesting that there also might be a significant quadratic component (decreasing for mortality, increasing for other dependent variables).

The brown-spot control hypothesis predicts that juvenile pines, in particular, may benefit from spring burning (see Maple 1977, Grelen 1983). This effect, if it exists, should primarily influence recruitment, growth, and mortality, of small trees. Like the ambient temperature hypothesis, the brown-spot control hypothesis predicts significant quadratic trends for these three dependent variables. The difference between the two hypotheses is in the direction of the curves: the ambient temperature hypothesis predicts peak mortality

and minimal growth and recruitment following spring and summer burning, while the brown-spot control hypothesis predicts just the opposite.

Some readers may be curious about why we used polynomial contrasts to analyze our data rather than other types of contrasts or paired comparisons. The answer, in part, pertains to the pseudoreplication problem mentioned earlier. Since all replicates of each seasonal burning treatment were burned on the same day, results of these burns do not represent independent determinations of the effect of a particular burning season, but rather reflect in large part conditions prevailing on the day of burning. The consequence of this is that the probability of falsely significant results is enhanced, especially if comparisons involve only a few of the possible seasonal burning treatments. This is especially likely during dry seasons (spring and fall), when burning under more hazardous conditions might tend to be avoided. For example, a significant contrast between October burning and April burning might result if the October plots were burned on a dry windy day and the April plots were burned on a calm humid day, though these conditions might not be generally representative of the prevailing conditions during those two months. Comparisons involving more than two burning seasons are less prone to this problem (i.e., because effects of individual burning days are averaged out), but there is still an enhanced possibility of Type II error (i.e., falsely accepting an untrue hypothesis). We chose to use polynomial contrasts to analyze our data in part because it seemed that this type of contrast would be least vulnerable to this sort of Type II error; that is, it seemed very unlikely that systematic seasonal patterns involving all eight burning dates could arise by chance, even if there might be some problem with pseudoreplication within particular burning seasons.

Sandhills oak dynamics.—Effects of season and frequency of burning on dynamics of sandhill oaks [i.e., on growth, mortality (topkill and complete kill), recruitment, change in basal area, and change in density, as defined previously] were tested using methods similar to those described above for pines. One minor difference was that because oak analyses (i.e., ANOVAs

TABLE 4. Product–moment correlations (r) among selected fire behavior variables and mortality of pines in different diameter (dbh) classes following experimental burns in the fourth treatment cycle. Results for total fuel consumed (not shown) are essentially identical to those for heat per area, since these variables are very highly correlated (r = 0.99).

	Fire temperature	Heat per area	% Fuel consumed	Fireline intensity	Pine mortality 2–9.9 cm dbh	Pine mortality 10–19.9 cm dbh
Heat per area	.47*					
Fuel consumed (%)	.59*	.76*				
Fireline intensity	−.04	.73*	.40*			
Pine mortality:						
2–9.9 cm dbh	.43*	.39*	.40*	.04		
10–19.9 cm dbh	.26	.48*	.23	.10	.18	
≥20 cm dbh	−.16	.21	−.07	.43*	.17	−.07

* Correlation significantly different from zero at $P < 0.05$.

TABLE 5. ANOVA (if the covariate is not significant) or ANCOVA (if the covariate is significant; $P < 0.05$) results of longleaf pine mortality for each of four diameter at breast height (dbh) size classes over the course of three prescribed-burn treatment cycles. Data were corrected for differences in sample size and arcsine transformed before analysis.

Source of variation	Diameter size class (cm dbh)															
	2–4.9				5–9.9				10–19.9				>20			
	df	ss	F	P	df	ss	F	P	df	ss	F	P	df	ss	F	P
Basal area in 1980	1	718.3	8.9	.03*												
Season of burning	7	933.7	1.7	NS	7	523.8	0.6	NS	7	180.5	0.4	NS	7	497.6	1.6	NS
Linear pattern	1	88.9	1.1	NS	1	35.4	0.3	NS	1	25.5	0.4	NS	1	44.3	1.0	NS
Quadratic pattern	1	1.6	<0.1	NS	1	86.5	0.7	NS	1	11.4	0.2	NS	1	<0.1	<0.1	NS
Frequency of burning	1	39.9	0.5	NS	1	166.8	1.3	NS	1	153.5	2.5	NS	1	17.9	0.4	NS
Habitat	1	1241.3	15.3	<.01*	1	82.0	0.6	NS	1	16.9	0.3	NS	1	13.2	0.3	NS
Season × Frequency	7	682.9	1.2	NS	7	546.8	0.6	NS	7	403.0	0.9	NS	7	276.7	0.9	NS
Season × Habitat	7	2215.4	3.9	NS	7	1929.1	3.9	NS	7	669.2	1.6	NS	7	578.9	1.9	NS
Frequency × Habitat	1	147.7	1.8	NS	1	<0.1	<0.1	NS	1	0.1	<0.1	NS	1	66.8	1.5	NS
Error (S × F × H)	6	486.5			7	929.3			7	427.7			7	308.6		

* $P < 0.05$.

and ANCOVAs) were limited to the sandhill plots, habitat was not included as a factor in these analyses. Other minor differences in analytical procedures were as follows: (1) Many oak recruits were observed to originate from stems cut at the start of the study. Thus, density of cut oak stems was included as an additional covariate in the ANCOVA of oak recruitment. (2) Since data on oak growth included observations from several different species, growth data for each species were converted to standard deviates before obtaining plot means; this prevented bias in favor of plots containing more stems of faster growing species. (3) Because the plots contained few oak trees ≥20 cm dbh, the two largest size classes (described above for pines) were combined for analyses of oak mortality data collected during the first recensus. Because of greatly reduced sample sizes in some plots, oak mortality data collected during the second recensus were not analyzed separately for different size classes.

As was done for pines, a priori orthogonal polynomial contrasts were used to test for trends in the effect of season of burning on oak dynamics. Two hypotheses were tested: (1) Negative effects of fire on oaks, as on pines, should be greatest following midsummer burns due to elevated ambient temperatures at this time of year (the ambient temperature hypothesis) and (2) oaks should be most vulnerable to fires in the spring, shortly after leaf expansion, when the trees are thought to be the most vulnerable physiologically (the tree physiology hypothesis). Both of these hypotheses predict significant quadratic contrasts ("increasing" for mortality, "decreasing" for growth, recruitment, and changes over time in basal area and density); they differ, however, in that the tree physiology hypothesis also predicts a significant negative linear trend (i.e., the combination of an increasing quadratic trend and a decreasing linear trend is a curve with the peak shifted somewhat to the left, that is, towards earlier burning dates).

Analyses: community-level changes

In addition to testing for effects of season and frequency of burning on population dynamics of oaks and pines, we also tested for effects of these factors on changes over time in tree species composition. This was accomplished by first converting the basal area and density data for each species into a synthetic "importance value" (IV, = relative basal area + relative density) and then ordinating the IVs using detrended correspondence analysis (DECORANA; see Ter Braak 1987 for a comprehensive discussion of ordination methods). Ordinations were run separately for each habitat due to a large difference in pretreatment species

TABLE 6. ANOVA or ANCOVA results of longleaf pine mortality for three size classes in the fourth prescribed-burn treatment cycle. Data were corrected for differences in sample size and arcsine transformed before analysis.

Source of variation	Diameter size class (cm dbh)											
	2–9.9				10–19.9				>19.9			
	df	ss	F	P	df	ss	F	P	df	ss	F	P
Basal area in 1987	1	184	6.29	.024*								
Season of burning	7	452	2.21	NS	7	116	.59	NS	7	298	3.38	.021*
Linear pattern	1	121	4.15	NS	1	<1	.02	NS	1	42	3.36	NS
Quadratic pattern	1	<1	.02	NS	1	16	.57	NS	1	56	4.47	.051*
Habitat	1	436	14.92	.002*	1	2	.07	NS	1	5	.42	NS
Season × Habitat	7	446	2.18	NS	7	107	.55	NS	7	83	.94	NS
Error (within cells)	15	439			16	444			16	202		

* $P < 0.05$.

TABLE 7. ANOVA or ANCOVA results of longleaf pine growth (measured as increments in diameter at breast height [dbh]) over the course of three treatment cycles. Because of significant habitat × covariate interactions, results are presented separately for sandhills (A) and flatwoods (B). Significant results ($P < 0.05$) are indicated with an asterisk.

| | | Diameter size class (cm dbh) | | | | | | | | |
| | | 2–9.9 | | | 10–19.9 | | | ≥20 | | |
Source of variation	df	ss	F	P	ss	F	P	ss	F	P
A) Sandhills										
1980 basal area	1	2.53		<.01*	2.39	15.8	<.01*	0.82	11.3	.02*
Season of burning	7	1.53	72.9	.02*	2.91	2.8	NS	1.27	2.5	NS
Linear pattern	1	<0.01	6.3	NS	0.29	1.9	NS	0.13	1.8	NS
Quadratic pattern	1	0.74	<0.1	<.01*	<0.01	<0.1	NS	0.19	2.6	NS
Frequency of burning	1	0.06	21.3	NS	0.13	0.9	NS	<0.01	<0.1	NS
Error (Season × Frequency)	6	0.21	1.7		0.91			0.44		
B) Flatwoods										
Season of burning	7	1.26	0.8	NS	2.55	1.1	NS	0.84	1.3	NS
Linear pattern	1	0.73	3.4	NS	0.90	2.7	NS	0.04	0.5	NS
Quadratic pattern	1	0.05	0.2	NS	0.03	0.1	NS	0.02	0.2	NS
Frequency of burning	1	0.16	0.8	NS	0.70	2.0	NS	0.61	6.8	.04*
Error (Season × Frequency)	7	1.52			2.38			0.63		

* $P < 0.05$.

composition. Each plot was entered twice in the ordination for its habitat, once using the pretreatment data and again using the recensus data. After ordinating the data in this way, the change in tree species composition for each plot was determined as the difference in ordination scores at the end of the first three treatment cycles (differences of this sort were calculated for each of the first three ordination axes). Finally, ANOVA and ANCOVA (including contrast analysis as described above) were used to test for effects of season and frequency of burning on species composition changes along each axis (see Bowman et al. 1988 and Wyant et al. 1991 for examples of similar analytical approaches).

RESULTS

Fire descriptions

Our fires (Table 3) were similar to other prescribed burns conducted in frequently burned pine savannas or flatwoods (e.g., Heyward 1938, Williamson and Black 1981, Nelson and Adkins 1988). In general, such fires are restricted to the ground surface and are character-

TABLE 8. ANCOVA results of recruitment of longleaf pine in the sandhills habitat over the course of three treatment cycles. Basal area is included as a covariate based on marginal significance.

Source of variation	df	ss	F	P
1980 basal area	1	12.7	4.3	.08
Season of burning	7	13.9	0.7	NS
Linear pattern	1	2.2	0.7	NS
Quadratic pattern	1	8.1	2.7	NS
Frequency of burning	1	4.4	1.5	NS
Error (Season × Frequency)	6	17.8		

* $P < 0.05$.

ized by low temperatures and intensities, and relatively rapid rates of spread (e.g., compare our results with Johnson 1992: Table 4.2). Like others (e.g., Albini 1976, Andrews and Rothermal 1982, Moreno 1989), we found that our various measures of fire behavior were not entirely independent. Fire temperature, which we measured at ground surface, was significantly correlated with fuel consumed, percent fuel consumed, and heat released per unit area (Table 4). These latter three variables were also highly correlated with fireline intensity, though the latter was not correlated with fire temperature (Table 4).

Despite our efforts to standardize burning conditions, we did detect some variability in both fire temperatures and intensities (Table 3). The data do indicate, however, that, following elimination of the annual burn treatments, almost all the area within a plot was burned during each fire (Table 3).

Dynamics of longleaf pine

Season of burn.—Previous hypotheses (ambient temperature, tree physiology, and brown-spot control hypotheses) regarding effects of season of burn on dynamics of longleaf pine were not well supported by results of this study. Omnibus F tests (i.e., tests of the general hypothesis that significant differences occurred among the means of the eight different season-of-burn treatments) were rarely significant (Tables 5–9), and quadratic and linear trends predicted by the three hypotheses did not materialize (Figs. 1–4). Results of these extensive tests, summarized in Table 10, reveal only two significant comparisons (out of >30 predictions). Thus, season of burning appeared not to influence most aspects of longleaf pine population dynamics.

Though most of the trends predicted by the three

TABLE 9. ANOVA results of changes in longleaf pine density and basal area over the course of three prescribed-burn treatment cycles.

Source of variation	df	Density			Basal area		
		ss	F	P	ss	F	P
Season of burning	7	1107	.76	NS	.90	.71	NS
Linear pattern	1	213	1.02	NS	<.01	<.01	NS
Quadratic pattern	1	7	.03	NS	.09	.49	NS
Frequency of burning	1	18	.09	NS	.16	.90	NS
Habitat	1	5832	28.00	.001*	6.33	34.50	.001*
Season × Frequency	7	5041	3.46	NS	.83	.65	NS
Season × Habitat	7	3514	2.41	NS	2.71	2.14	NS
Error (S × F × H)	7	1459			1.27		

* $P < 0.05$.

hypotheses were not significant (see previous paragraph), two predictions were supported by the data: (1) As predicted by the ambient temperature hypothesis, mortality of large (i.e., ≥20 cm dbh) trees during the fourth treatment cycle did indeed follow an increasing quadratic trend (Fig. 1G), and (2) growth of sandhill pines <10 cm dbh also followed an increasing quadratic trend (Fig. 2A), as predicted by the brown-spot control hypothesis. Upon close inspection, however, it was apparent that neither of these results provided strong support for either hypothesis.

Concerning the increasing quadratic trend in large-tree mortality during the fourth treatment cycle, notice first of all that during this treatment cycle (as in the previous three treatment cycles), mortality of trees in this size class was very low regardless of the season of burning (i.e., even at the highest point on the curve, average mortality was <1%; see Fig. 1G). Thus, despite its statistical significance, this trend was most likely insignificant biologically. Furthermore, this same pattern was not present in the mortality data for this size class collected over the first three treatment cycles (Fig. 1D). [In fact, there were no significant correlations between censuses for any size class in effects of burning season on mortality ($-0.56 < r < 0.47$, $n = 8$ burning seasons, $P > 0.05$)]. Therefore any quadratic relationship between season of burn and mortality of large longleaf would not appear to be a temporally consistent effect of growing-season burns.

A similar observation can be made for the other "confirmed" prediction, i.e., the significant quadratic trend in growth of sandhill pines <10 cm dbh. In this case, the trend was not consistent between habitats (i.e., flatwoods pines in the same size class showed no evidence of such a growth trend; Table 7, Fig. 2d), suggesting that any such trend, if it exists, is unique to the sandhills habitat. Furthermore, other predictions of the brown-spot control hypothesis (e.g., that minimal mortality of small trees should be associated with growing-season burning) were not confirmed for either habitat (Figs. 1a, e). Thus, the actual existence of a brown-spot control effect, even for the sandhills habitat, is doubtful.

Frequency of burn.—Frequency of burning, the other

experimental factor, also appeared to have only a minor influence on longleaf pine demography. Effects of frequency of burn on pine mortality (Fig. 5) were not significant for any size class over the first three treatment cycles (Table 5). Likewise, there were no significant effects of burning frequency on growth of sandhill pines (Table 7A; Fig. 6, left), pine recruitment (Table 8; Fig. 7), or temporal changes in pine densities (Table 9; Fig. 8A) and basal areas (Table 9; Fig. 8B).

The only real effect of frequency of burn was on growth of pines in the flatwoods. For flatwood pines in each of the three size classes, growth was lower in biennially burned than in annually burned plots (Fig. 6D–F). This difference was significant for the largest dbh-size class (Table 7B).

Fire temperature and intensity.—Fire temperature and intensity data were collected (or, in the case of fireline intensity, reconstructed) for six burning dates (24 individual fires) during the fourth treatment cycle. For the period covered by these fires, pine mortality in each size class was significantly correlated with at least one measure of fire behavior (Table 4). Interestingly, however, the size classes differed in the particular fire behavior variables most highly correlated with mortality (Table 4). Mortality in the smallest (2–9.9 cm dbh) size class was most highly correlated with fire temperature, though the correlations with percent fuel consumed and heat per area were also statistically significant. Mortality in the next largest size class (10–19.9 cm dbh) was correlated with total fuel consumed and with heat released per unit area. Finally, mortality in the largest size class (≥20 cm dbh) was significantly correlated only with fireline intensity.

Habitat and competition.—Habitat (i.e., location of longleaf pines in sandhills vs. flatwoods), competition (i.e., stand basal area), and interactions between these two factors, strongly influenced most aspects of longleaf pine dynamics.

The most noticeable effect of competition was on mortality of small trees. In both sandhill and flatwoods habitats, and over both the first three treatment cycles and the fourth treatment cycle, increasing stand basal area was significantly positively associated with mortality of longleaf pine trees in the smallest size class
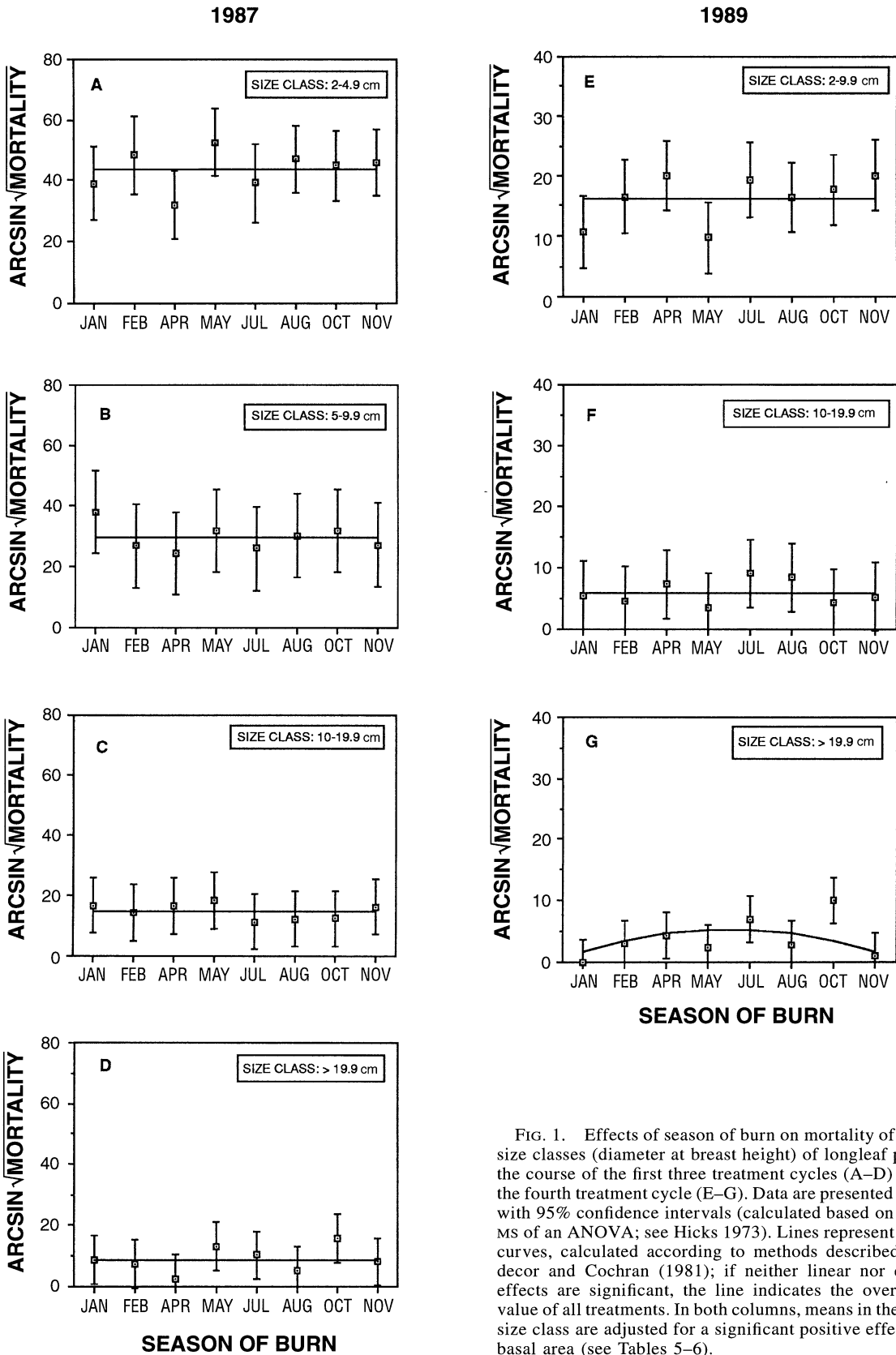
FIG. 1. Effects of season of burn on mortality of different size classes (diameter at breast height) of longleaf pine over the course of the first three treatment cycles (A–D) and over the fourth treatment cycle (E–G). Data are presented as means with 95% confidence intervals (calculated based on the error MS of an ANOVA; see Hicks 1973). Lines represent response curves, calculated according to methods described in Snedecor and Cochran (1981); if neither linear nor quadratic effects are significant, the line indicates the overall mean value of all treatments. In both columns, means in the smallest size class are adjusted for a significant positive effect of plot basal area (see Tables 5–6).

SANDHILLS

FLATWOODS
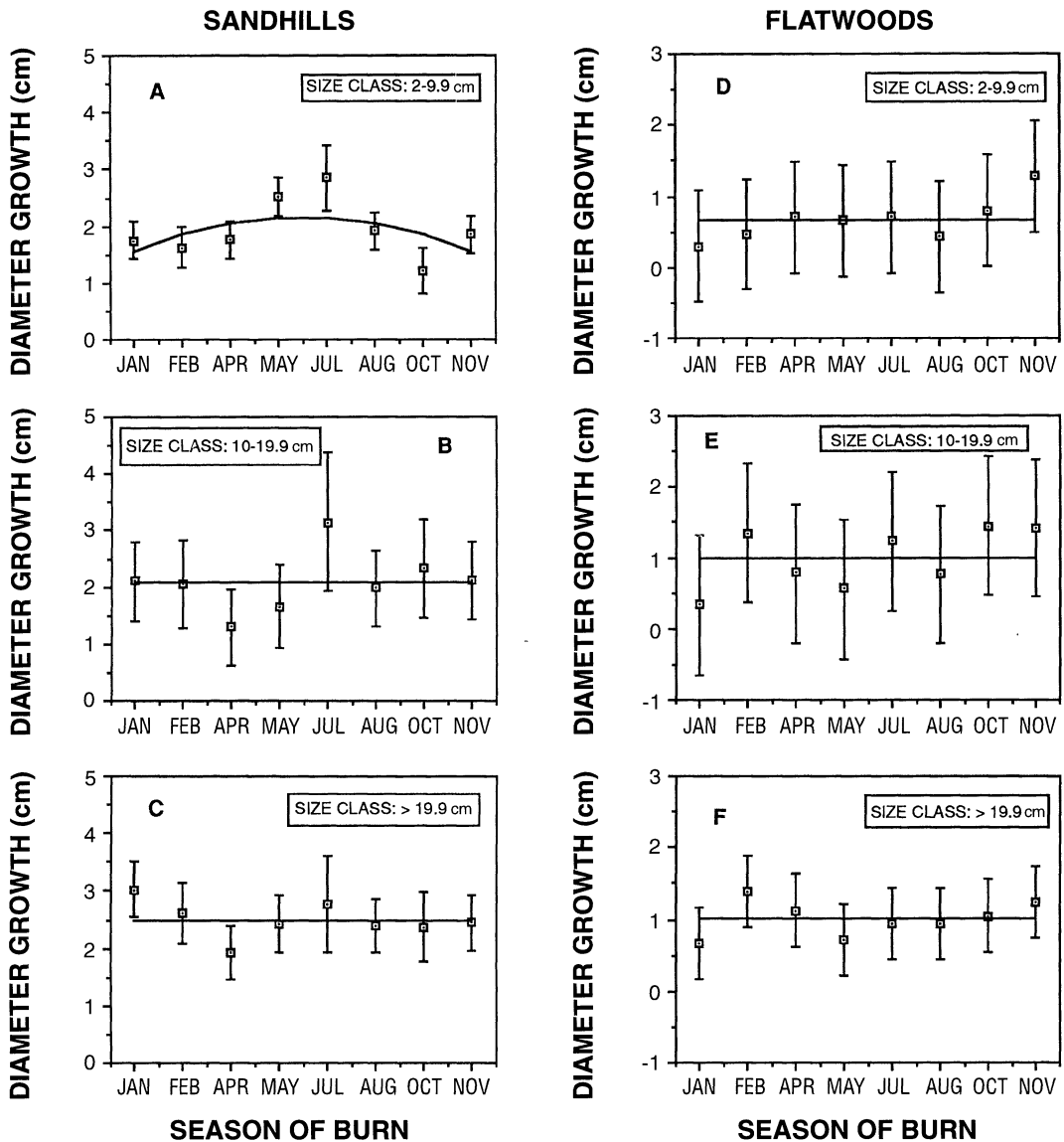
SEASON OF BURN

FIG. 2. Effects of season of burn on diameter growth of different size classes of longleaf pine in the sandhills (A–C) and flatwoods (D–F) over the course of the first three treatment cycles. Sandhills means are adjusted for a significant negative effect of plot basal area (see Table 7). Means, confidence limits, and curves are as described in Fig. 1 legend.

($r = 0.77$ and 0.54 for the two between-census intervals; see Tables 5, 6 for degrees of freedom and F and P values). In the sandhills, increasing competition was also associated with significantly reduced diameter growth (of all size classes; see Table 7 and Fig. 9) and recruitment (Table 8, Fig. 10).

There were two important between-habitat differences in the demography of longleaf pine. First, rates of growth and recruitment were substantially lower in the flatwoods than in the sandhills (especially in plots with low basal areas; Figs. 9, 10). Second, rates of mortality in the smallest size classes, over both the first three treatment cycles (Fig. 11A) and the fourth treatment cycle (Fig. 11E), were significantly higher in flat-

woods than in sandhills (Tables 5, 6). Low recruitment and high rates of small-tree mortality resulted in substantial declines in densities of longleaf pine in the flatwoods plots, while densities of sandhills pines remained essentially unchanged (Fig. 12A). Longleaf pine basal areas increased in both habitats, but the increase was much greater in the sandhills than in the flatwoods (Fig. 12B). Differences between habitats in both density changes and basal area changes were highly significant (Table 9). In general, longleaf pine populations in the sandhills appeared to be constant or increasing in density and to be influenced largely by intraspecific competition despite the regime of frequent burning. In contrast, flatwoods populations appeared in
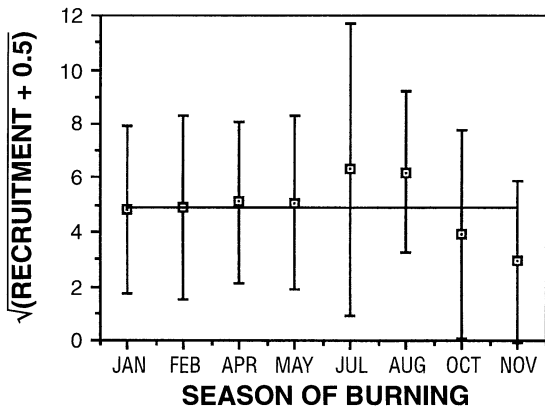
FIG. 3. Effects of season of burn on recruitment of longleaf pine (in stems/ha) into the smallest size class in the sandhills over the course of the first three treatment cycles. Seasonal means are adjusted for a marginally significant negative effect of plot basal area (see Table 8). Means, confidence limits, and curves are as described in Fig. 1 legend.

virtually all cases to be unstable and declining and to be much less affected by intraspecific competition.

Tree size.—Mortality and growth of longleaf pine were also influenced strongly by tree size. Mortality in both census periods declined noticeably with increases
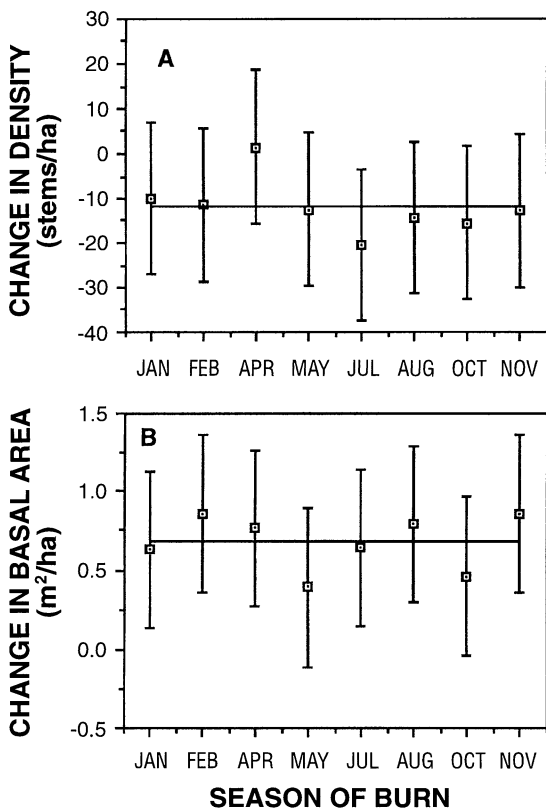
FIG. 4. Effects of season of burn on changes in density (A) and basal area (B) of longleaf pine over the course of the first three prescribed-burning treatment cycles. Means, confidence limits, and curves are as described in Fig. 1 legend.

in tree size (Fig. 11) and larger trees usually grew faster than smaller ones (Fig. 9). In the sandhills, longleaf pine growth appeared to be strongly influenced by an interaction between tree size and level of competition: trees of all sizes grew at approximately equal rates in low-basal-area stands, but small trees grew more slowly than larger trees in stands with high basal areas (Fig. 9).

Dynamics of sandhill oaks

Season of burn.—In contrast to the results presented above for longleaf pine, our data on oak population dynamics generally supported previous hypotheses (Tables 11–14, Figs. 13–16, summary in Table 15). Results on oak mortality in the sandhills habitat, in particular, strongly supported the tree physiology hypothesis. As predicted by this hypothesis, topkill (Figs. 13A–C, 14A) and complete kill (Figs. 13D–F, 14B) of sandhill oaks were highest in plots burned in April and May. Furthermore, increasing quadratic trends were observed for both dependent variables over both the first three treatment cycles and the fourth treatment cycle (Tables 11, 12; the single exception was for complete kill in the smallest size class during the first census interval). Although the linear component was not significant, residuals for the two spring-burning treatments were consistently above predicted means. Thus, the negative effect of burning early in the growing season on oak mortality appeared to be consistent over time, as well as among size classes.

Effects of season of burning on other aspects of the population dynamics of oaks in the sandhills were much less obvious. Oak growth, for example, was clearly not at all related to this factor (Fig. 15A, Table 13A). There was a significant overall effect (i.e., omnibus F test) of season of burning on oak recruitment (Table 13B), and mean oak recruitment in the spring-burned plots (April and May) was generally lower than in the other burning treatments (Fig. 15B). However, quadratic and linear effects were not significant (Table 13B), indicating that effects of burning season on oak recruitment did not vary predictably over the course of the year.

High rates of mortality and low rates of oak recruitment in spring-burned plots resulted in substantial declines in density and basal area of oaks in these plots over the first three treatment cycles (Fig. 16). These changes were reflected in significant quadratic and linear trends in the effect of season of burn on both of these variables (Table 14).

Frequency of burn.—Effects of frequency of burning on oak dynamics were limited largely to topkill and to resultant changes in density and basal area. Topkill of oaks (Fig. 17) in the smallest size class was significantly greater in biennially burned plots than in annually burned plots (Table 11), and a similar, but nonsignificant, tendency occurred for oaks in the next largest size class (Table 11). There was no discernible ef-

TABLE 10. Summary of tests of a-priori predictions of effects of season of burning on dynamics of longleaf pine, St. Marks National Wildlife Refuge, Florida. For details, see Tables 5–9 and Figs. 1–4.

Hypothesis	Response variable	Predicted trend	Result*
Ambient temperature	mortality	increasing quadratic	tc 1–3: sc 1–4 n
			tc 4: sc 1–2 n, sc 3 y
	growth	decreasing quadratic	tc 1–3: sc 1–3 n
	recruitment	decreasing quadratic	tc 1–3: n
	basal area change	decreasing quadratic	tc 1–3: n
	density change	decreasing quadratic	tc 1–3: n
Tree physiology	mortality	linear increase	tc 1–4: all sc n
		decreasing quadratic	tc 1–4: all sc n
	growth	linear decrease	tc 1–3: sc 1–3 n
		increasing quadratic	tc 1–3: sc 1 sh n†, fw n
			sc 2–3 n
	recruitment	linear decrease	tc 1–3: n
		increasing quadratic	tc 1–3: n
	basal area change	linear decrease	tc 1–3: n
		increasing quadratic	tc 1–3: n
	density change	linear decrease	tc 1–3: n
		increasing quadratic	tc 1–3: n
Brown spot control	mortality	decreasing quadratic	tc 1–3: sc 1 n
			tc 4: sc 1 n
	growth	increasing quadratic	tc 1–3: sc 1 sh y, fw n
	recruitment	increasing quadratic	tc 1–3: n

* Key to abbreviations: tc = treatment cycle (see *Methods: Experimental design*); n = predictions not confirmed (i.e., test results not statistically significant, or significant but with the wrong trend); y = prediction confirmed (test result significant, and trend as predicted); sc = size class (see *Analyses: Pine dynamics* for size class definitions during different time periods); sh = sandhill habitat; fw = flatwoods habitat (see *Methods: Study area* for habitat descriptions).

† Note that in the case of the tree physiology hypothesis, a significant quadratic trend is listed as a confirmed prediction only if it is coupled with the appropriate linear trend.
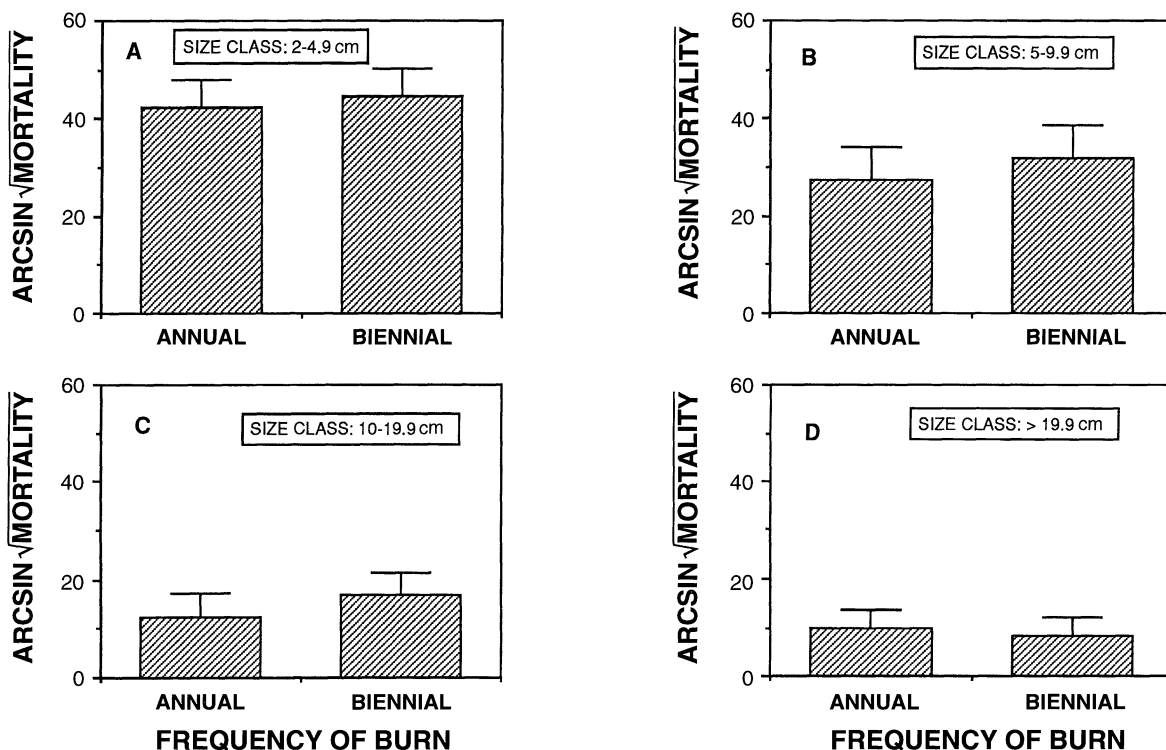

FIG. 5. Effect of frequency of burn on mortality of different size classes of longleaf pine over the course of the first three treatment cycles. Means in the smallest size class are adjusted for a significant positive effect of plot basal area (see Table 5). Means and confidence intervals are as described in Fig. 1 legend.
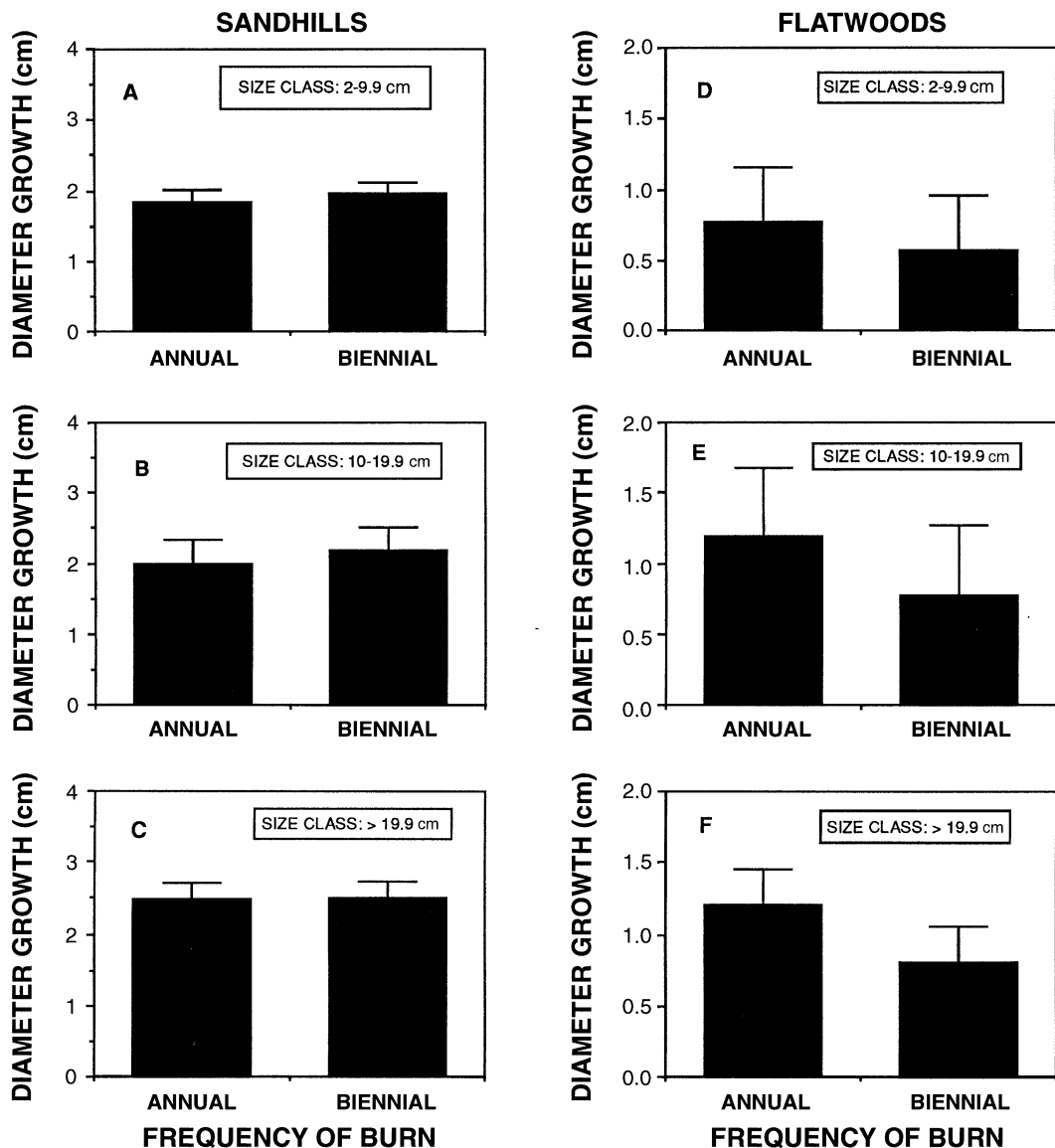
SANDHILLS

FLATWOODS

FIG. 6.   Effect of frequency of burn on growth of different size classes of longleaf pine in the sandhills (A–C) and flatwoods (D–F) over the the course of the first three treatment cycles. Sandhills means are adjusted for a significant negative effect of plot basal area (see Table 7). Means and confidence intervals are as described in Fig. 1 legend.

fect of frequency of burning on topkill in the largest size class (Fig. 17C) or on complete kill in any size class (Fig. 17D–F). Frequency of burning also had no significant effects on growth or recruitment of oaks in the sandhills (Table 13). As a result of greater topkill among smaller size classes, the density of oaks (Fig. 18A) declined significantly (Table 14) in biennially burned plots (an average of >30 stems between 1980 and 1987), while only minor declines occurred in plots burned annually (<5 stems on average over the same time period). There was also a greater decline in oak basal area in the biennially burned plots than in the annually burned plots (Fig. 18B), although this difference was not statistically significant (Table 14).

Fire temperature and intensity.—Oak topkill during the fourth treatment cycle (i.e., February–October burns) was significantly correlated with both fire temperature ($r = 0.71$, $n = 12$ fires, $P < 0.01$, see also Fig. 19A) and percentage of fuel consumed ($r = 0.59$, $n = 12$ fires, $P < 0.05$). Correlations with other measures of fire intensity were not significant ($r < 0.23$, $n = 12$, $P > 0.05$). Correlations were also not significant ($r < 0.26$, $n = 12$, $P > 0.05$) between oak complete kill and any measure of fire behavior (e.g., Fig. 19B).

The relatively high correlation between oak topkill and fire temperature suggests that this latter variable may be responsible for much of the observed effect of burning season on topkill. This conclusion is supported
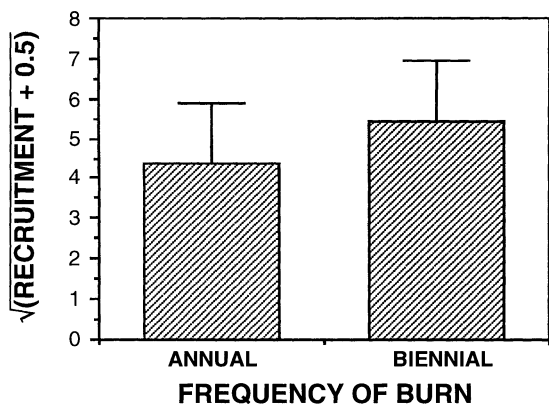
FIG. 7. Effect of frequency of burn on recruitment of longleaf pine (in stems/ha) into the smallest size class in the sandhills over the course of the first three treatment cycles. Seasonal means are adjusted for a marginally significant effect of plot basal area (see Table 8). Means and confidence intervals are as described in Fig. 1 legend.

by a graph of the data showing that even the spring-burned plots fall close to the linear regression of topkill on temperature (Fig. 19A). However, since three of the four spring-burned plots fall above this line, compared to only two of the eight plots burned at other seasons, there may still be some residual effect of spring burning.
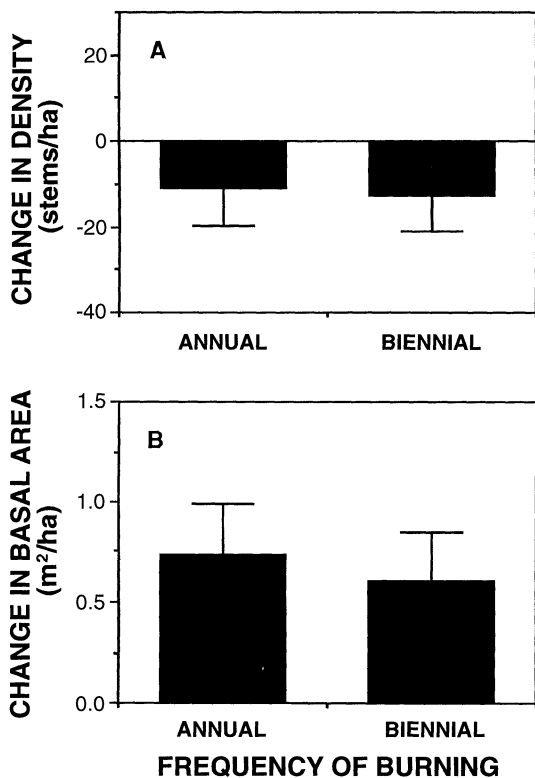
FIG. 8. Effect of frequency of burn on changes in density (A) and basal area (B) of longleaf pine over the course of the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.
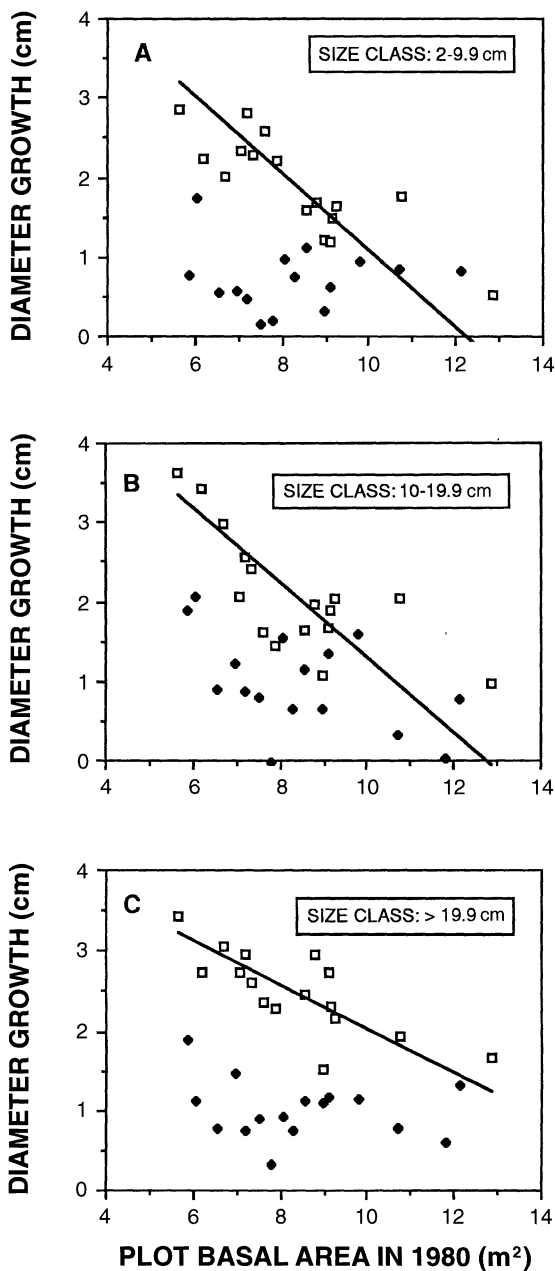

FIG. 9. Effect of plot basal area on diameter growth of longleaf pine in the sandhills (□) and flatwoods (♦) over the the course of the first three treatment cycles. Best fit regression lines for the sandhills were determined from ANCOVA (see Snedecor and Cochran 1981). Regressions for the flatwoods were not statistically significant and are not shown.

Competition.—In general, oaks appeared to be less susceptible than pines to effects of increasing competition. Whereas virtually all aspects of sandhill longleaf pine demography were significantly related to plot basal area, basal area did not significantly affect topkill, complete kill, or growth of the oaks ($F < 3.3$, df = 1, 6, $P > 0.05$). However, there were weak ($0.10 \leq r^2 \leq 0.21$), but significant (Table 13B, Table 14), negative
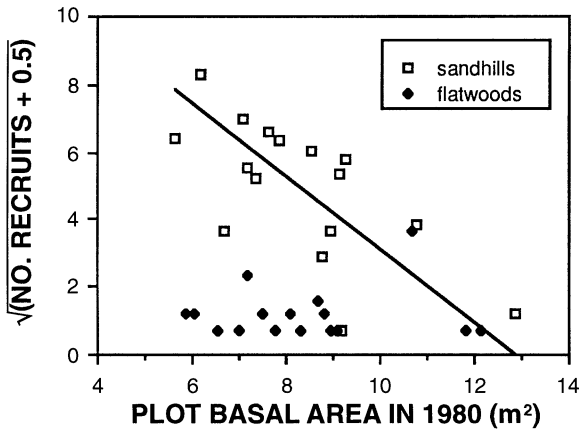
FIG. 10. Effect of plot basal area on recruitment of long-leaf pine (in stems/ha) in sandhills (□) and flatwoods (♦) over the course of the first three treatment cycles. The best fit regression line for the sandhills was determined from AN-COVA (see Snedecor and Cochran 1981). The regression for the flatwoods was not statistically significant and is not shown.

effects of plot basal area on oak recruitment, and on changes over time in oak densities and basal areas.

Tree size.—Unlike pines, which became more resistant to fires as they increased in size, resistance of oaks to burning (or, at least, to the frequent burns in this study) did not increase with tree size (Fig. 17). In fact, because they were less likely to resprout and therefore more likely to be completey killed, larger oak trees, especially during the early growing season, were actually less resistant to fires than were smaller oak trees.

Changes in tree composition

Sandhills.—Plots of scores from the DECORANA ordination (Fig. 20) indicate several weak (i.e., eigenvalues range between 0.081 and 0.016 for the first three axes) gradients in composition of woody species in the sandhills. The first axis (Fig. 20A) represents a gradient from plots distinguished by higher relative abundances of three deciduous oak species (*Quercus margaretta, Q. laevis,* and *Q. incana*) and *P. palustris,* to plots with higher relative abundances of three common species of evergreen oaks (*Q. geminata, Q. hemisphaerica,* and *Q. myrtifolia*). In addition to differences in the relative abundances of deciduous and evergreen oaks, plots were also distinguished by differences in the relative abundances of two species of ericaceous shrubs (Fig. 20A). *Vaccinium arboreum* and *V. stamineum* each had high Axis-1 scores, and were thus associated more closely with evergreen than deciduous oaks.

A second, orthogonal, vegetation gradient was identified by Axis 2 of the ordination. In this case, the gradient extends from plots with greater relative abundances of *Pinus palustris, Q. margaretta,* and *Q. geminata* to plots where these species are somewhat less important relative to *Q. laevis, Q. incana,* and *Q. myrtifolia* (Fig. 20A). Relative abundances of the two *Vac-*

ciniums also change along this indirect gradient; both are associated with *Q. laevis, Q. incana* and *Q. myrtifolia* towards the lower end of the second axis (Fig. 20A).

The third ordination axis (Fig. 20B) illustrates a gradient from plots with high relative abundances of *Q. hemisphaerica, Q. laevis,* and to some extent *P. palustris* to plots where these species are less abundant and several other species of oaks (*Q. margaretta, Q. incana, Q. geminata, Q. falcata, Q. myrtifolia*) and the two species of *Vaccinium* are more abundant (Fig. 20B).

Vegetation gradients along the first (i.e., most important) ordination axis were unrelated to the experimental burning treatments. The average plot score along Axis 1 did not change significantly over time (i.e., a paired *t* test found no significant change between 1980 plot scores and 1987 plot scores: df = 1, 7; *F* = 0.50, *P* > 0.05) as would have been expected if the burning treatments were having an effect. Furthermore, neither season (Fig. 21A) nor frequency (Fig. 21D) of burn had significant effects on differences in individual plot scores over the first three treatment cycles (Table 16). Instead, site scores along Axis 1 appeared to be related mostly to a subtle difference in physical environments between two parts of the study area. Plots with low Axis 1 scores occurred relatively close to one another in compartment 11 of the refuge, while plots with high Axis-1 scores occurred farther away in compartment 7 (Fig. 20C).

Though the first axis of the ordination appeared unrelated to the experimental burning treatments, this was not true of the other two axes. Plot scores along the Axis 2 increased in a highly significant fashion between 1980 and 1987 (paired *t* test: df = 1, 7, *F* = 56.54, *P* < 0.001). Furthermore, these changes were significantly related to season of burning (Table 16). The effect of season of burning on vegetation change along this axis followed a quadratic trend with the greatest change observed after spring burning (Fig. 21B). Since this change was towards higher Axis-2 scores, it suggests that the effect of spring burning is to increase the abundances of longleaf pine, *Q. margaretta,* and *Q. geminata* relative to the abundances of *Q. incana, Q. laevis, Q. hemisphaerica, Q. myrtifolia,* and the two species of *Vaccinium.*

Increases in plot scores along the second axis occurred both for annually and biennially burned plots (Fig. 21E) and frequency of burn had no significant effects on plot scores along this axis (Table 16). However, changes in vegetation along the third ordination axis were significantly related to frequency (Fig. 21F), but not season (Fig. 21C), of burn (Table 16). Biennial burning resulted in a positive change along this ordination axis, indicating a shift toward higher relative abundances of longleaf pine, *Q. laevis,* and *Q. hemisphaerica,* and reduced relative abundances of *Q. incana, Q. margaretta, Q. geminata, Q. myrtifolia,* and
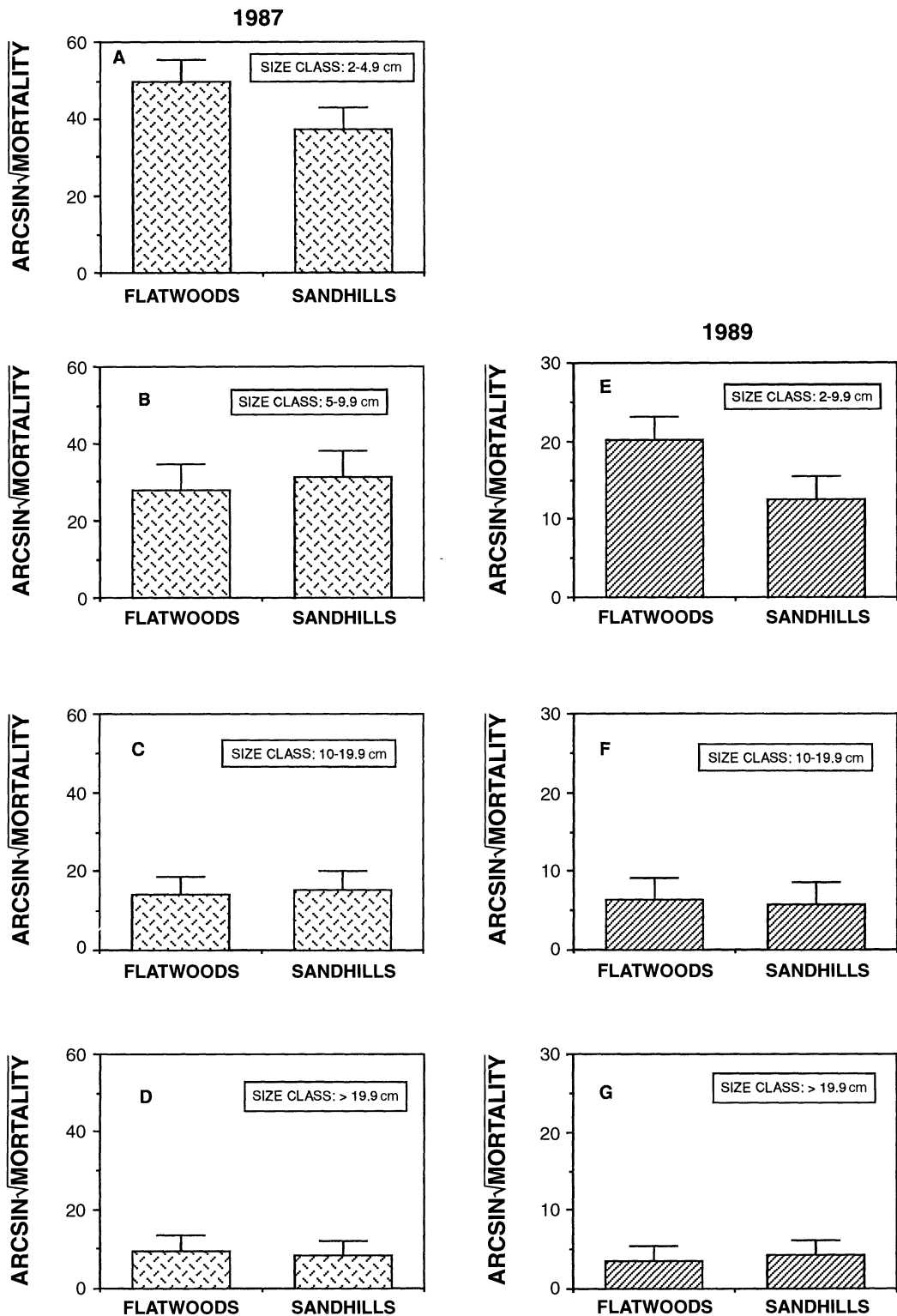
FIG. 11. Mortality of different size classes of longleaf pine in sandhills and flatwoods over the course of the first three treatment cycles (A–D) and over the fourth treatment cycle (E–G). Means in the smallest size class are adjusted for a significant positive effect of plot basal area (see Tables 5–6). Means and confidence intervals are as described in Fig. 1 legend.
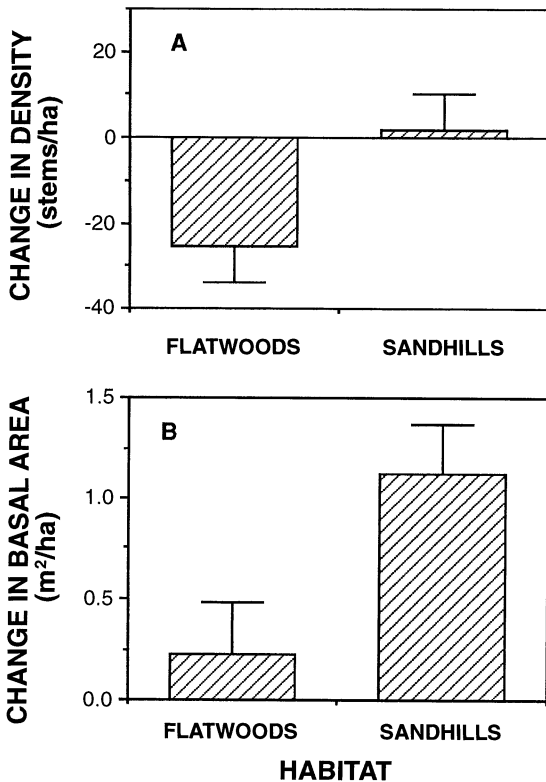
FIG. 12. Changes in density (A) and basal area (B) of longleaf pine in sandhills and flatwoods over the course of the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

TABLE 12. ANOVA results of sandhill oak (*Quercus laevis, Q. incana, Q. margaretta*) topkill (A) and complete kill (B) in the fourth prescribed-burn treatment cycle. Data were corrected for sample size differences and arcsine transformed prior to analysis.

Source of variation	df	SS	F	P
A) Topkill				
Season of burning	7	2334	3.5	.05*
Linear pattern	1	163	1.7	NS
Quadratic pattern	1	1485	15.5	<.01*
Error (within cells)	8	769		
B) Complete kill				
Season of burning	7	1044	3.5	.05*
Linear pattern	1	137	3.2	NS
Quadratic pattern	1	389	9.0	.02*
Error (within cells)	8	346		

*P < 0.05.

(eigenvalue = 0.06 for the second axis). Species separation along the remaining axes was so minor as to preclude meaningful interpretation (eigenvalues ≤0.01). Based on the plot of species scores (not shown, but available on request), the strong gradient was characterized as a transition from wet flatwoods codominated by slash or pond pine to dry flatwoods with longleaf the only pine present, along with a significant oak component. Tree species composition averaged across all plots did not change significantly along either of the first two axes during the first three treatment cycles (F ≤ 1.99, df = 1, 7, P > 0.05). Neither season nor frequency of burn had significant effects on changes over time in individual plot scores (Table 17).

DISCUSSION

Population dynamics of longleaf pine

Season of burn.—Results of our study did not support previous hypotheses regarding effects of seasonality of fire on population dynamics of southern pines.

the species of *Vaccinium.* Annual burning resulted in reduced third axis scores, indicating changes in vegetation composition in the opposite direction.

Flatwoods.—The DECORANA ordination of the flatwoods tree data identified one comparatively strong vegetation gradient (eigenvalue = 0.34 for the first axis) and one weak but possibly meaningful gradient

TABLE 11. ANOVA results of sandhill oak (*Quercus laevis, Q. margaretta, Q. incana*) topkill (A) and complete kill (B) over the course of the first three prescribed-burn treatment cycles. Data were corrected for differences in sample size and arcsine transformed prior to analysis.

Source of variation	df	Diameter size class (cm dbh)								
		2–4.9			5–9.9			>9.9		
		SS	F	P	SS	F	P	SS	F	P
A) Topkill										
Season of burning	7	3553	12.2	<.01*	2553	3.8	.05*	3875	3.6	.06
Linear pattern	1	150	3.6	NS	171	1.8	NS	44	0.3	NS
Quadratic pattern	1	458	11.0	.01*	901	9.4	.02*	1729	11.3	.01*
Frequency of burning	1	326	7.8	.03*	399	4.2	NS	7	<0.1	NS
Error (S × F)	7	292			673			1070		
B) Complete kill										
Season of burning	7	1040	1.5	NS	2085	3.5	NS	3948	2.5	NS
Linear pattern	1	14	0.1	NS	14	0.2	NS	9	<0.1	NS
Quadratic pattern	1	477	4.7	NS	1273	15.0	<.01*	1669	7.4	.03*
Frequency of burning	1	8	0.1	NS	84	1.0	NS	19	0.1	NS
Error (S × F)	7	711			595			1590		

*P < 0.05.

TABLE 13. ANOVA and ANCOVA results of sandhill oak (*Quercus laevis, Q. incana, Q. margaretta*) growth (measured as increments in dbh) and recruitment over the course of three prescribed-burn treatment cycles.

Source of variation	df	ss	F	P
A) Growth				
Season of burning	7	1.72	.38	NS
Linear pattern	1	.43	2.21	NS
Quadratic pattern	1	.15	.78	NS
Frequency of burning	1	.01	.01	NS
Error (S × F)	7	1.36		
B) Recruitment				
1980 basal area	1	39.57	20.08	.004*
Season of burning	7	73.60	5.33	.029*
Linear pattern	1	9.47	4.81	NS
Quadratic pattern	1	0.05	0.03	NS
Frequency of burning	1	2.22	1.13	NS
Error (S × F)	6	11.83		

* $P < 0.05$.

All of these hypotheses (the "ambient temperature hypothesis," the "tree physiology hypothesis," and the "brown-spot control hypothesis") predict that fire effects will vary with the season of burn. No such effects were evident as clear, consistent trends for any size class of pines in either sandhill or flatwoods habitats.

We suggest three reasons why results of our study are not consistent with data and ideas used to develop these prior hypotheses. (1) Longleaf pine, widely acknowledged as the most fire resistant of the southern pines (see review of Landers 1991) may be particularly tolerant of fires regardless of when they occur (see also Ferguson 1955 and *Discussion: Fire behavior*). Longleaf pine, therefore, may be resistant to detrimental effects of late growing season burning or experimental defoliation documented for other southern pines (e.g., Ferguson 1961, Weise et al. 1989). (2) Though high ambient temperatures are sometimes mentioned as one possible cause for high levels of observed crown scorch (e.g., Cooper and Altobelli 1969, Villarubia and Chambers 1978), Van Wagner's (1973) theoretical relationship between ambient temperature and crown scorch has never been thoroughly validated. Van Wagner's (1973) own attempt at verification was unsuccessful, and he concluded that, at least within the range of temperatures included in his study, fireline intensity alone could account for most of the observed variation. Our results suggest that for longleaf pine as well, variation in fire behavior (temperature or intensity) may be much more important than ambient temperature or season of burning for predicting population dynamics. Considered within this context, isolated observations of elevated mortality or reduced growth following growing-season fires (e.g., Cary 1932, Boyer 1990) appear to be largely coincidental and do not constitute strong evidence for detrimental effects of growing season fires. Boyer's (1987) study, which documented slightly (but significantly) higher levels of longleaf pine mor-

tality following summer burning (8.0% compared to 4.3% for burns conducted in winter and spring), continues to provide the only truly reliable evidence for the possible existence of an ambient-temperature effect on longleaf pine. It is important to note, however, that the negative effect of summer burning in this study was confined to only one of three summer burn treatments (i.e., the study was a factorial design with varying methods of supplemental understory control) suggesting that even in this case the effect of season of burning was probably rather minor compared to other influences on fire behavior. (3) Prior studies supporting the brown-spot control hypothesis were conducted mainly on "grass stage" seedlings, while our results were limited to stems ≥2 cm dbh. Thus, we cannot state unequivocally that this effect did not occur in our study; we can, however, conclude that even if there were some such effect it apparently had little impact on sapling recruitment or on the overall dynamics of longleaf pine populations.

Based on our evaluation of the literature (Streng et al., *in press*) and analyses of our data, we conclude that there is no *consistent* seasonal pattern to the vulnerability of longleaf pine to fire damage in frequently burned sandhill or flatwood habitats. We emphasize the word "consistent" because there may well be seasonal effects in any given year resulting from droughts, unusually hot or intense fires, or other exceptional conditions, but such effects are not likely to be constant from one year to the next. This conclusion helps to explain the widespread dominance of longleaf pine in original old growth savannas and woodlands of the southeastern Coastal Plain. Indeed, if longleaf pine were highly vulnerable to summer burning, as has been suggested, it could not have dominated vast areas of presettlement forest under a natural regime of frequent summer burning. There is also an important implication for habitat management: as long as fuel accumulations

TABLE 14. ANCOVA results of changes in density (A) and basal area (B) of sandhill oaks (*Quercus laevis, Q. incana, Q. margaretta*) over the course of three treatment cycles.

Source of variation	df	ss	F	P
A) Density				
Basal area in 1980	1	3140	14.1	.009*
Season of burning	7	21307	13.7	.003*
Linear pattern	1	4011	18.0	.005*
Quadratic pattern	1	1890	8.5	.027*
Frequency of burning	1	3144	14.1	.009*
Error (S × F)	6	1336		
B) Basal area				
Basal area in 1980	1	.094	18.6	.005*
Season of burning	7	.337	9.5	.007*
Linear pattern	1	.046	9.0	.024*
Quadratic pattern	1	.032	6.2	.047*
Frequency of burning	1	.008	1.5	NS
Error (S × F)	6	.031		

* $P < 0.05$.

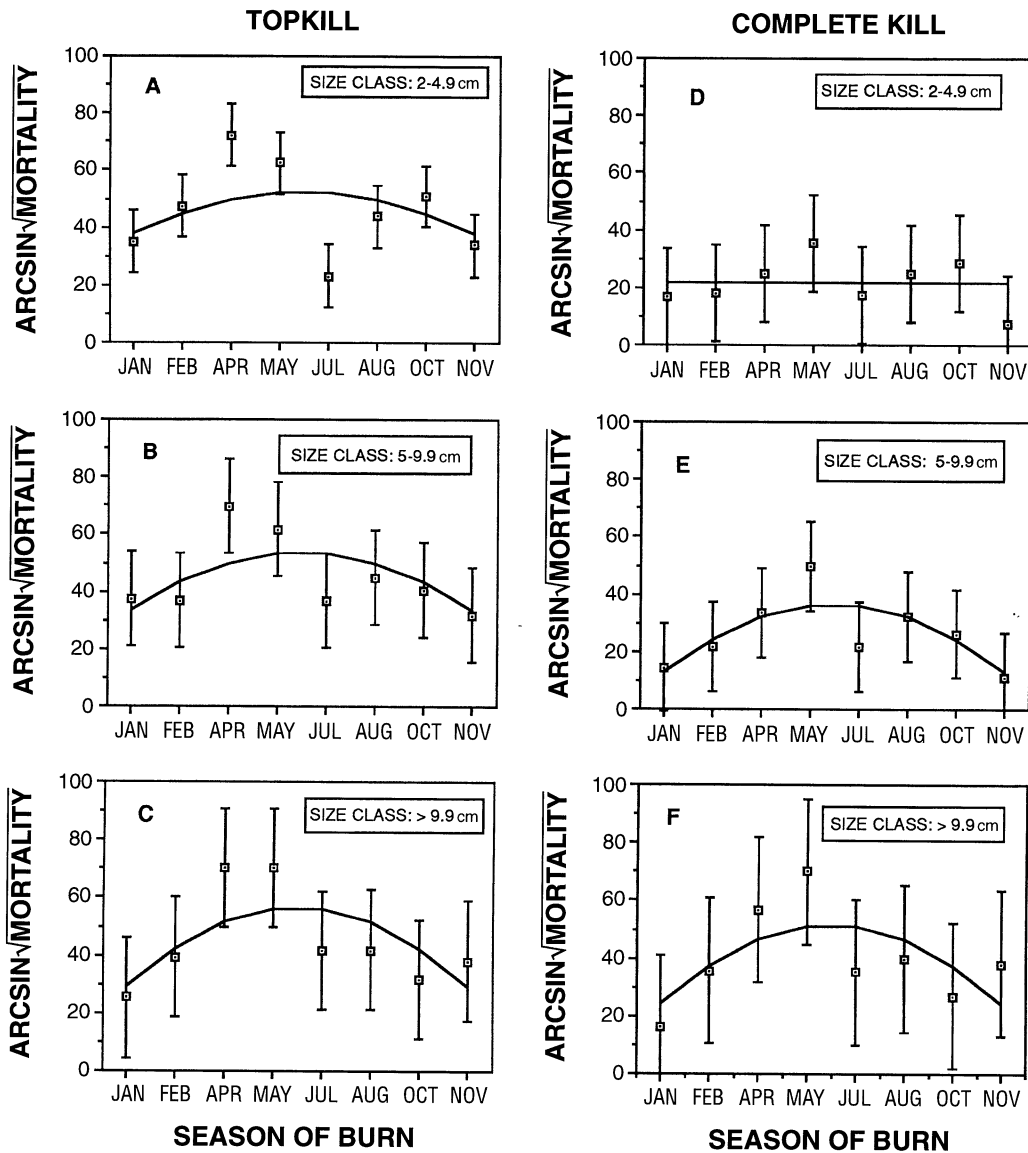## TOPKILL

COMPLETE KILL

FIG. 13.   Effect of season of burn on topkill (A–C) and complete kill (D–F) of oaks in sandhills over the course of the first three treatment cycles. Means, confidence intervals, and curves are as described in Fig. 1 legend.

are low and dangerous fire weather conditions are avoided (see also Bradshaw et al. 1983), prescribed (i.e., managed) burning can occur at any season without excessive risk to either canopy pines or new regeneration.

Frequency of burn.—Like season of burn, frequency of burn (i.e., the contrast between annual and biennial burning) had little impact on longleaf pine population dynamics. This suggests, as did our results on season of burning (see previous section) that longleaf pine is rather insensitive to minor fluctuations in the regime of frequent burning once characteristic of old growth forests in the region. One significant result was that growth of pines in the flatwoods, but not the sandhills, was significantly reduced by biennial burning (i.e.,

compared to the annually burned plots). This effect was most likely a result of greater fuel accumulations (see Table 1), and hence greater crown scorch (fire related defoliation), in the less frequently burned plots. [In woodlands/savannas of the Coastal Plain of the southeastern USA, there is ordinarily a strong relationship between accumulated fuel and fire temperatures/intensities (see e.g., Heyward 1938, Hare 1961, Williamson and Black 1981, and Platt et al. 1991).]

Fire behavior.—We have already noted that fire behavior may be a more important influence on population dynamics of longleaf pine than either season or frequency of burning. This finding is consistent with the results from a number of other studies which also emphasize the importance of fire intensity and related

variables (e.g., crown scorch) for predicting tree growth or mortality (Gruschow 1952, Cooper and Altobellis 1969, Van Wagner 1973, Villarubia and Chambers 1978, Greene 1987, Ryan and Reinhardt 1988). Our results do, however, demonstrate the extreme tolerance of longleaf pine, even to relatively intense surface fires. For example, Ryan and Reinhardt (1988), documented post-fire tree mortalities in the western USA ranging from 16% to 88%, depending on the species. Mortality rates for longleaf pine documented in the present study were considerably lower than this (except in the smallest size classes), even though burning techniques and the range of fireline intensities were comparable between the studies.

Another interesting feature of our results was the suggestion that effects of the different fire behavior variables might vary with tree size. The smallest trees appeared most vulnerable to high fire temperatures and other indicators of heat flux directly at the ground surface (e.g., percent fuel consumption, heat released per unit area). This may indicate that girdling (i.e., complete cambial death around the entire circumference of the stem), rather than crown scorch, may have been mostly responsible for killing these trees. Larger pine trees have thicker bark than smaller trees and are generally more resistent to girdling (Wade 1986, Wade and Johansen 1986b, Greene 1987). In our study, large

FIG. 15. Effect of season of burn on growth (A) and recruitment (B) of oaks in sandhills over the course of the first three treatment cycles. Data shown in (A) were derived by converting growth of each oak species to standard deviation units (SDUs) for that species and then averaging across species to obtain plot means (see Analyses: Sandhills oak dynamics). Means, confidence intervals, and curves are as described in Fig. 1 legend.
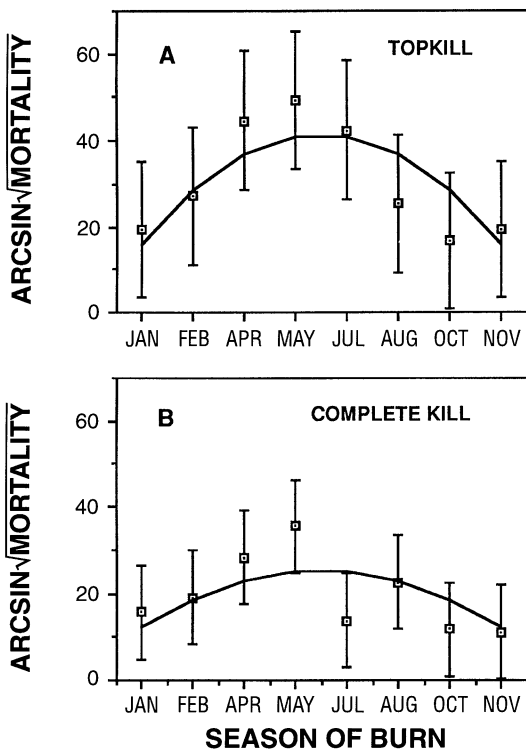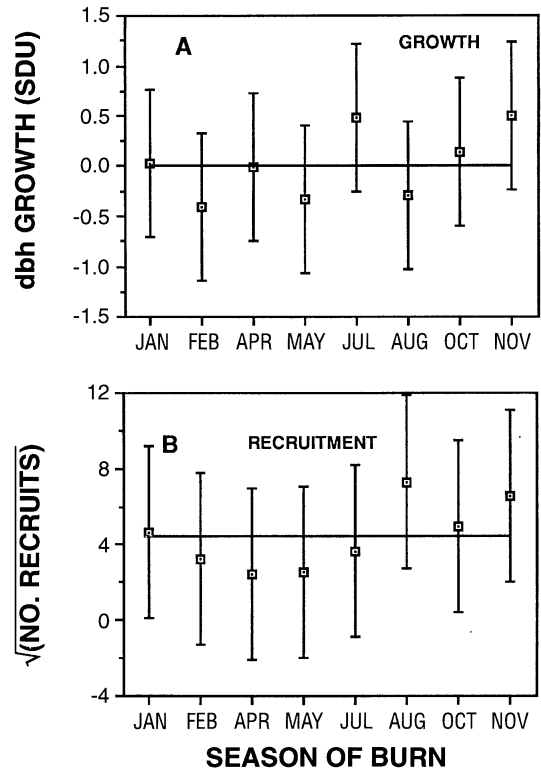
FIG. 14. Effect of season of burn on topkill (A) and complete kill (B) of oaks in sandhills over the fourth treatment cycle. Means, confidence intervals, and curves are as described in Fig. 1 legend.

longleaf pine trees appeared relatively insensitive to fire temperatures and other measures of heat flux near the ground surface. Instead, mortality of these trees was related mostly to fireline intensity. Since fireline intensity is generally correlated mostly with crown scorch or other canopy effects (Van Wagner 1973, Wade 1986, Ryan and Reinhardt 1988), it appears likely that high levels of crown scorch may have been responsible for killing the few large pine trees that died during our study.

Habitat.—In addition to the above-mentioned differences between habitats in the effect of frequency of burning on pine growth, there were several other important differences between sandhill and flatwoods habitats in the population dynamics of longleaf pine. These differences, including less recruitment, as well as much higher mortality rates for small trees, consistently suggested that the flatwoods were a more stressful environment than the sandhills for longleaf pine. In fact, declining densities in all flatwoods plots suggest that the combination of a stressful environment and frequent fires could (if the experiment is continued),
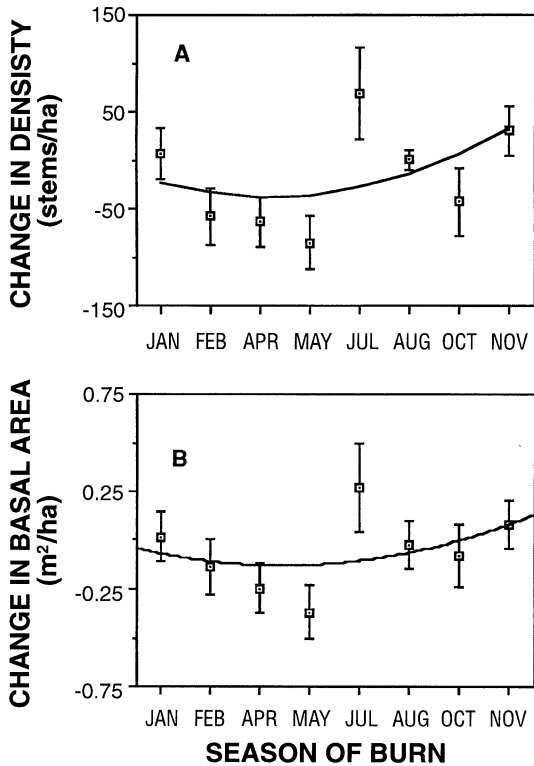
FIG. 16. Effect of season of burn on changes in density (A) and basal area (B) of oaks in sandhills over the course of the first three treatment cycles. Means, confidence intervals, and curves are as described in Fig. 1 legend.

eventually result in almost complete disappearance of longleaf pine from these plots.

It may be instructive to consider in more detail the reasons for declining longleaf pine populations in the flatwoods habitat. Prior studies (Wahlenberg 1946, Ferguson 1961, Maple 1975), and the results of our own study, emphasize that vulnerability of longleaf pine to fire generally declines with increasing size. An exception occurs during height growth (the transition between the grass and small sapling stages), when a secondary peak in post-fire mortality sometimes occurs (see Maple 1975, Rebertus et al., *in press*). Because we have shown (see also Bruce 1951) that juvenile growth rates, and in fact tree growth rates generally, are much lower in the flatwoods (presumably because of harsher environmental conditions, such as waterlogged soils, but possibly also because of more intense competition from groundcover vegetation) it follows that longleaf pines in the flatwoods spend more time in these vulnerable juvenile life stages than do longleaf pines in the sandhills. Juvenile longleaf pine in more stressful flatwoods (such as those that flood frequently) may even grow so slowly that, under a regime of frequent fire, they are unable to reach a fire-resistant size before being killed.

We suggest that this restriction on regeneration, produced by the interaction between juvenile life history attributes, burning regime, and environmental characteristics, may have produced very low densities of

TABLE 15. Summary of tests of a-priori predictions concerning effects of season of burning on dynamics of sandhill oaks (*Quercus laevis, Q. incana, Q. margaretta*), St. Marks National Wildlife Refuge, Florida. For details, see Tables 11–14 and Figs. 13–16.

Hypothesis	Response variable	Predicted trend	Result*
Ambient temperature	topkill	increasing quadratic	tc 1–3: sc 1–3 y tc 4: y
	complete kill	increasing quadratic	tc 1–3: sc 1 n, sc 2–3 y tc 4: y
	growth	decreasing quadratic	tc 1–3: n
	recruitment	decreasing quadratic	tc 1–3: n
	basal area change	decreasing quadratic	tc 1–3: y
	density change	decreasing quadratic	tc 1–3: y
Tree physiology	topkill	increasing quadratic	tc 1–3: sc 1–3 y tc 4: y
		decreasing linear	tc 1–3: sc 1–3 n tc 4: n
	complete kill	increasing quadratic	tc 1–3: sc 1 n, sc 2–3 y tc 4: y
		decreasing linear	tc 1–3: sc 1–3 n tc 4: n
	growth	decreasing quadratic	tc 1–3: n
		increasing linear	tc 1–3: n
	recruitment	decreasing quadratic	tc 1–3: n
		increasing linear	tc 1–3: n
	basal area change	decreasing quadratic	tc 1–3: y
		increasing linear	tc 1–3: y
	density change	decreasing quadratic	tc 1–3: y
		increasing linear	tc 1–3: y

* Key to abbreviations: tc = treatment cycle (see *Methods: Experimental design*); n = prediction not confirmed (i.e., test result not statistically significant, or significant but with the wrong trend); y = prediction confirmed (test result significant and trend as predicted); sc = size class (see *Analyses: Sandhills oak dynamics* for size class definitions during different time periods).

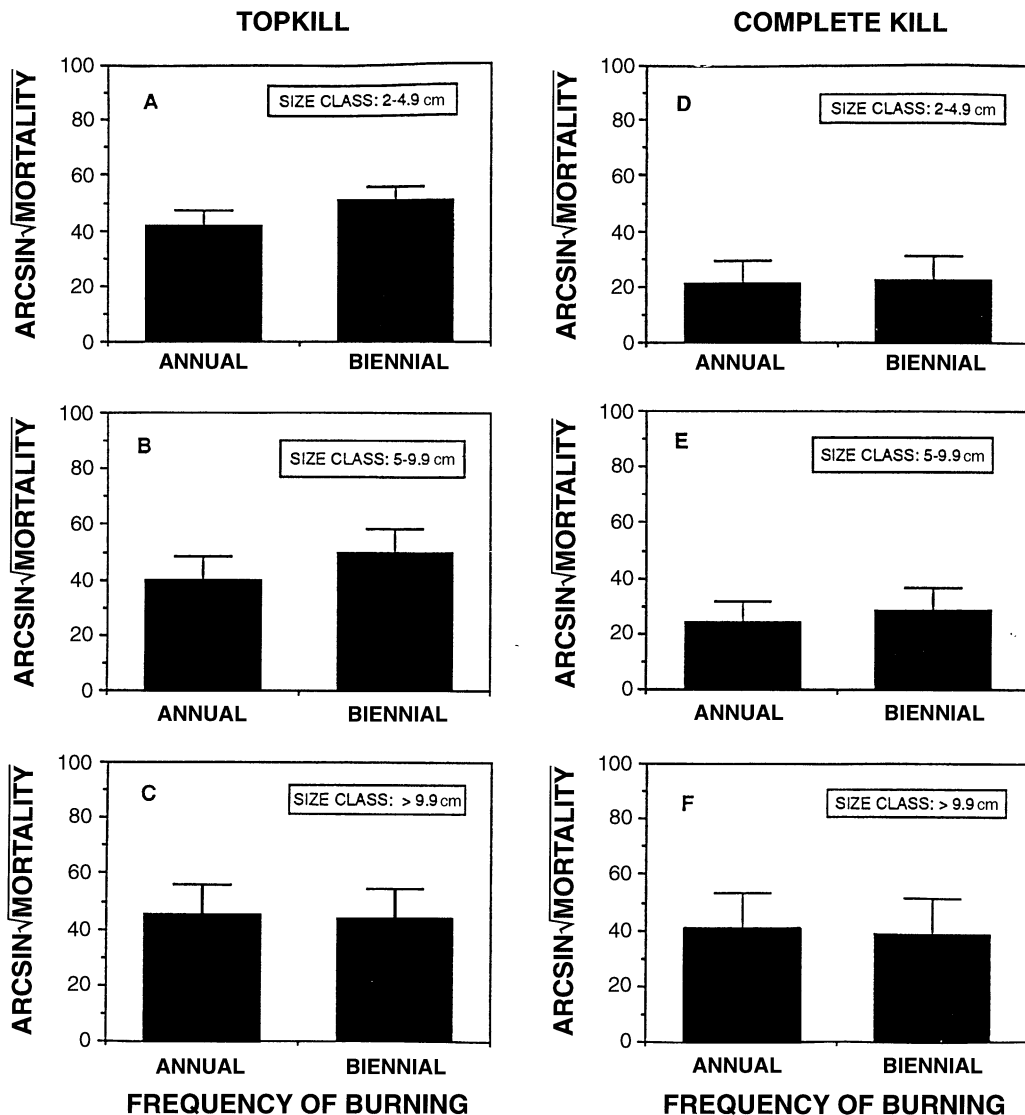**TOPKILL** **COMPLETE KILL**

FIG. 17. Effects of frequency of burn on topkill (A–C) and complete kill (D–F) in three size classes of oaks in sandhills over the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

longleaf pine in presettlement flatwoods. Variable fire frequencies that included periodic longer fire-free intervals probably enabled longleaf pine to invade and persist in flatwoods habitats. While others have emphasized the potential importance of interactions between disturbance regime and plant life history characteristics (e.g., Noble and Slatyer 1980, Keeley 1981, Keeley and Keeley 1988, Rebertus et al., *in press*), we note here that the local environment can strongly modify such interactions. [For a similar example of the interacting effects of environment and fire limiting the distribution of trees in a different habitat, see Barton (1993).]

In addition to the above theoretical considerations, our results on habitat related differences in dynamics of longleaf pine also have important practical implications. Of fundamental importance is the suggestion

that techniques or practices developed for one habitat or environment may produce very different effects in another, even superficially rather similar, habitat. In the present case, it is quite clear that annual or biennial burning would maintain or even enhance longleaf pine populations in the sandhills, but would not accomplish the same objective in the flatwoods. Lower fire frequencies or, at the least, occasional extended fire-free intervals would be necessary for recruitment of longleaf pines in the flatwoods.

Competition.—Competition strongly influenced the population dynamics of longleaf pine (especially in the sandhills, where regeneration was not limited environmentally). This finding is consistent with results from the forestry literature (Wahlenberg 1946, Farrar, *in press,* and references therein) and with a recent model for the patch structure of old-growth longleaf pine for-
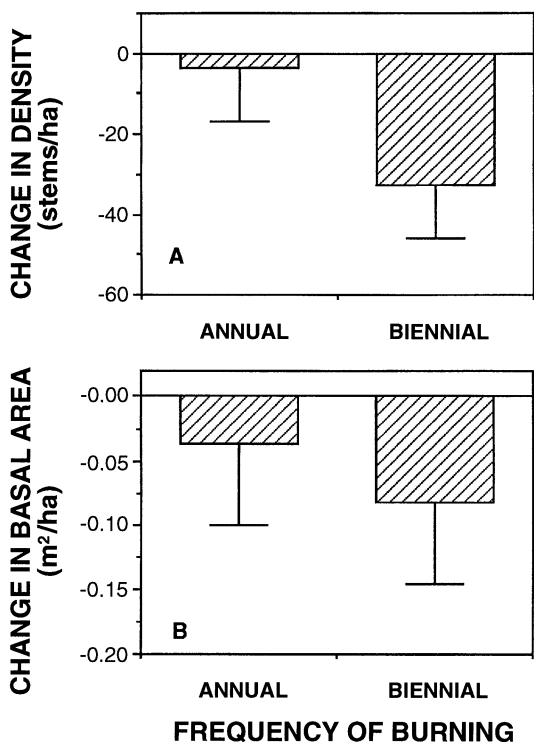
FIG. 18. Effects of frequency of burn on changes in density (A) and basal area (B) of oaks in sandhills over the first three treatment cycles. Means and confidence intervals are as described in Fig. 1 legend.

est developed for the Wade Tract, southeastern Georgia (see Platt and Rathbun, *in press*). When this model is applied to field data, significant effects of competition occur over distances up to 30 m from large trees. Moreover, as distances between neighbors decrease and the sizes of those neighbors increase, growth and survival of juveniles decreases markedly. Our current study demonstrates clearly that competition has much greater effects on pine dynamics (at least in the sandhills) than do seasonal and other minor differences in fire regimes. By comparison, the relative insensitivity of oaks to competition emphasizes the critical role of fire, especially during the spring, in limiting population sizes of these species.

Population dynamics of sandhill oaks

Though our results did not support previous hypotheses about effects of burning season on the population dynamics of longleaf pine, the results did tend to confirm the tree physiology hypothesis in the case of sandhill oaks. There was consistent evidence (especially from tree mortality patterns and consequent effects on basal areas and densities) that oaks were negatively affected by fires during the early growing season. This result supports findings of prior studies based on physiological data (Woods et al. 1959) and is consistent with other research demonstrating increased rates of hardwood topkill or complete kill after spring or summer burning (Hodgkins 1958 and references therein,
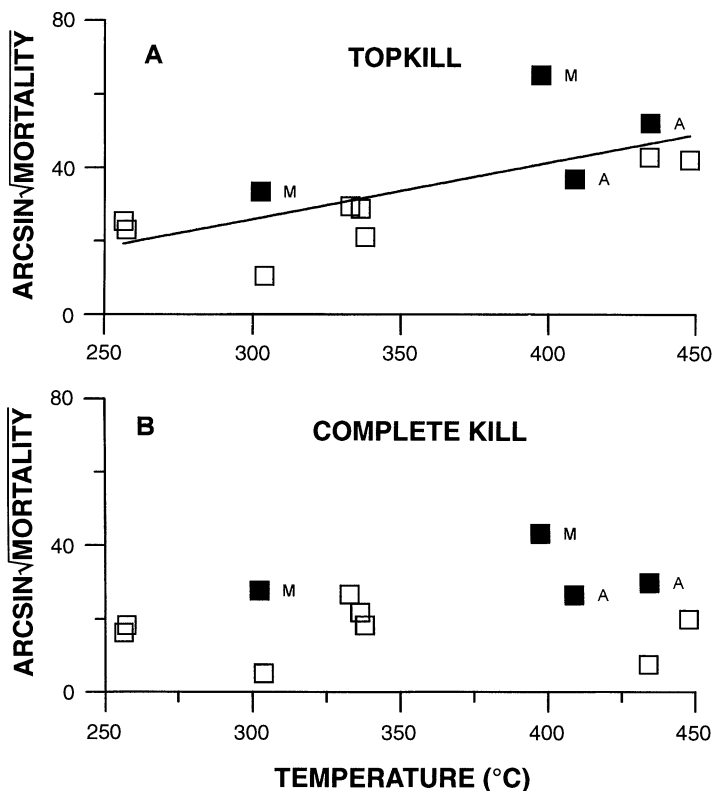

FIG. 19. Effects of fire temperatures on (A) topkill and (B) complete kill of oaks (*Q. laevis, Q. incana, Q. margaretta*) in the sandhills. ■ spring-burned plots (A=April, M=May); □ plots burned at other seasons. The correlation between temperature and complete kill was not significant ($P < 0.05$), so a line was not fitted to these data.
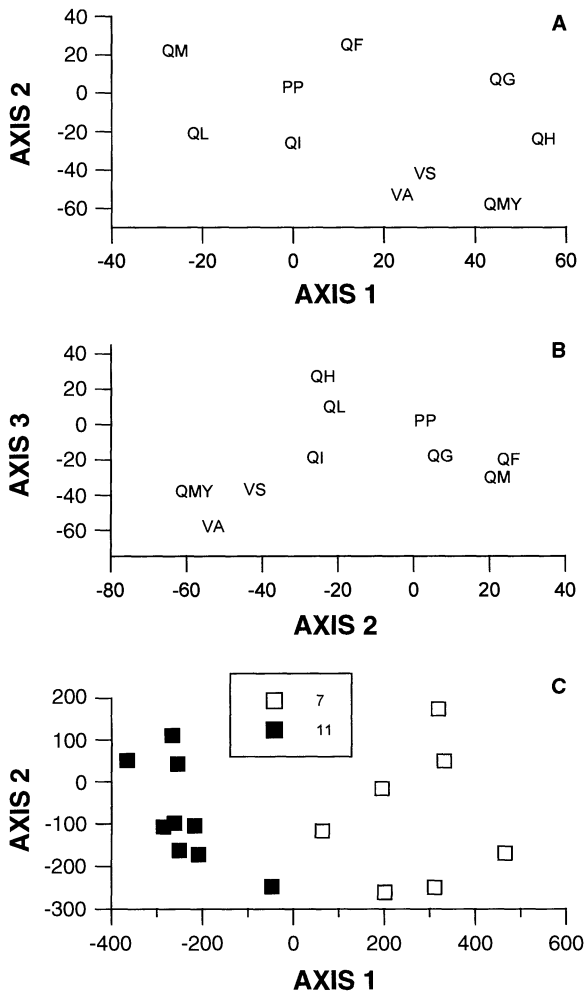
FIG. 20. DECORANA ordination results of woody species composition of sandhills. Species codes: PP=*Pinus palustris*, QF=*Quercus falcata*, QG=*Q. geminata*, QH=*Q. hemisphaerica*, QI=*Q. incana*, QL=*Q. laevis*, QM=*Q. margaretta*, QMY=*Q. myrtifolia*, VA=*Vaccinium arboreum*, VS=*V. stamineum*. In part C, plots located in compartments 7 and 11 of the St. Marks Wildlife Refuge are distinguished by □ and ■, respectively.

Ferguson 1961, Brender and Cooper 1968, Boyer 1990, 1993, Waldrop et al. 1992 and references therein).

The relatively strong correlation of oak topkill with fire temperature and intensity does implicate these variables as potentially important causes of the observed effect of season of burning on oak mortality. In north Florida, those environmental conditions that produce drier fuels and higher fire intensities are more likely to occur early in the growing season (Chen and Gerber 1990). However, the lack of fire behavior effects on oak complete kill suggests an important additional effect of tree physiology, particularly on the capacity of oaks to resprout after fires.

Community dynamics

Effects of seasonality of fire.—Results of the season-of-burn component of our long-term study have at least

two important implications for understanding composition of longleaf pine savannas, at least as they existed prior to settlement. The first such implication concerns the role of spring fires in maintaining the dominance of longleaf pine over oaks. Presettlement fire regimes in the southeastern Coastal Plain probably were characterized by frequent spring fires, as suggested by evidence from lightning frequencies (Maier et al. 1979) and wildfire patterns (Komarek 1964, Robbins and Myers 1992). Our results showing sharp declines in densities of oaks in the sandhills following repeated spring burning thus strongly suggest that tree-sized oaks were a minor component (at best) of the vegetation in presettlement upland savannas. Longleaf pine would have comprised essentially monospecific stands of trees in any of these habitats where spring fires occurred frequently.

The second implication concerns the effect of temporal variability in seasonality of fire on maintenance of tree species diversity in longleaf pine savannas. Not all presettlement fires occurred in the spring. A significant proportion occurred later in the summer; data in Komarek (1964) suggest that any given area had a likelihood of burning in July and August about one-third as great as that in May and June. Occasional fires may also have occurred in the fall or winter as a result of rare thunderstorms or burning by Native Americans [Pyne 1982, e.g., Lawson 1709 (1967 edition):215]. Our results show clearly that oaks were much less susceptible to fires occurring outside of the early growing season. By reducing the frequency of fires to which oaks were susceptible, variability in fire season may have contributed to the persistence of oaks as trees in savannas dominated by longleaf pine (cf. Rebertus et al., *in press*).

Our finding of consistently lower sandhill oak mortality following non-spring fires also supports the hypothesis that a shift from growing- to dormant-season burning over the last several centuries (along with clear-cutting of large pines) has transformed many savannnas formerly dominated (in the canopy) almost entirely by longleaf pine into more or less closed woodlands or forests dominated largely by turkey and bluejack oaks (Means and Grow 1985, Myers 1990, Platt et al. 1991, Gilliam et al. 1993). This transformation has resulted in pronounced ecological changes, not only in the relative abundances of trees, but also in the diversity of understory herbs, which declines rapidly under an oak canopy (Lemon 1949, Vogl 1973, Streng 1979, Myers 1990).

Results of our study also suggest, however, that high oak densities may be rapidly reduced by frequent spring burning (if the ground cover is capable of carrying a fire). As few as three biennial fires in the spring greatly reduced the densities and basal areas of oaks in the sandhill plots. Such fires also enhanced flowering by a number of late-season flowering grasses and forbs (Platt et al. 1988a, 1991, Streng et al., *in press*). Fire-
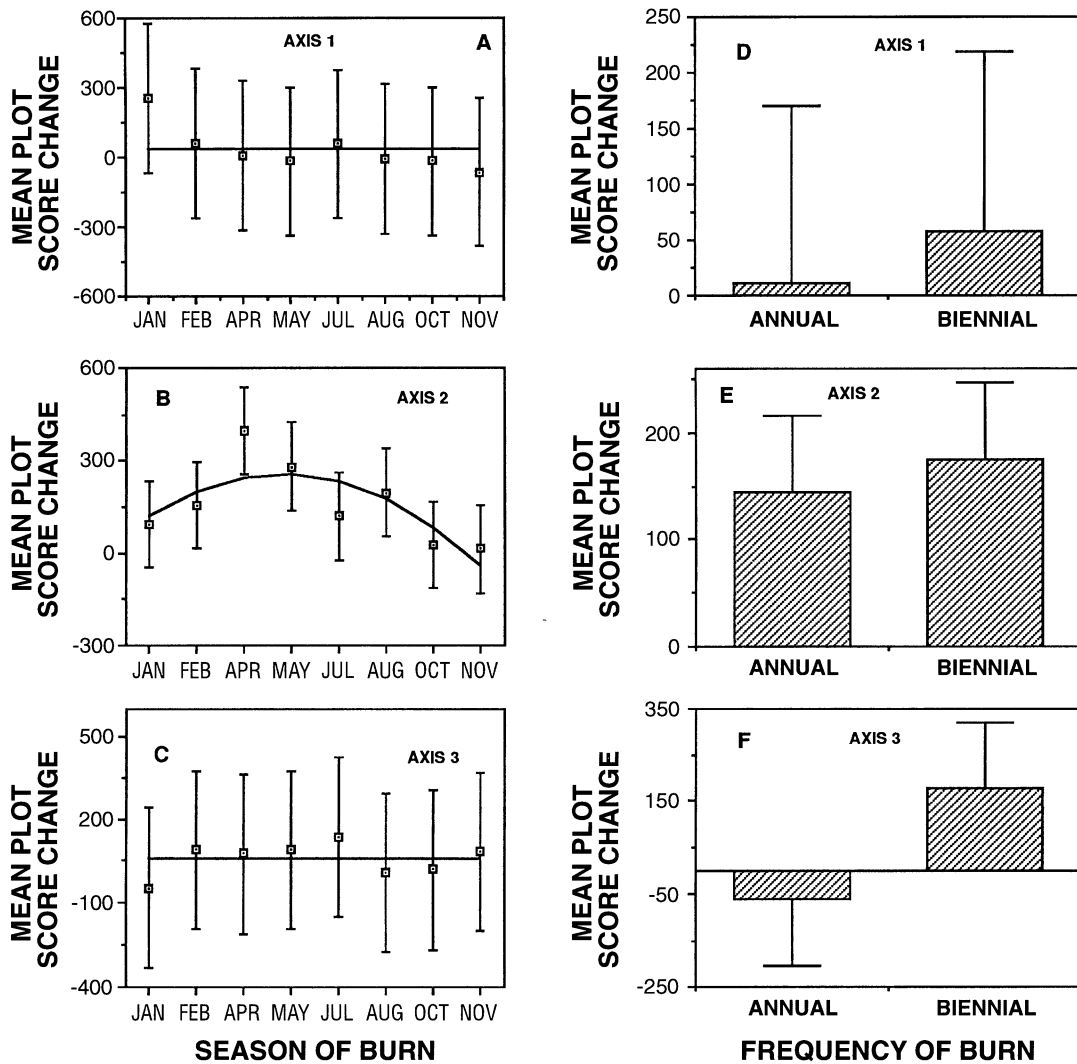
FIG. 21. Effects of season of burn (A–C) and frequency of burn (D–F) on changes in DECORANA ordination plot scores in the sandhills over the course of the first three treatment cycles. A,D: Axis 1; B,E: Axis 2; C,F: Axis 3. Means, confidence intervals, and curves are as described in Fig. 1.

stimulated flowering and/or reduced densities of mid-canopy oaks may also be responsible for recently observed increases in the abundance of the dominant forb, *Pityopsis graminifolia,* in the spring-burned sandhill plots (Brewer and Platt 1994a, b).

For the most part, ordination analyses indicated that spring burning significantly influenced tree species composition in the sandhills by increasing relative abundance of longleaf pine over oaks. However, one unexpected finding was the suggestion that sandhill oak species might differ in their tolerance to spring burning. In particular, it appeared that *Q. margaretta* and *Q. geminata* might be more tolerant of spring fires than other species of hardwoods. In the case of *Q. geminata,* this apparent resistance was most likely due not so much to greater fire tolerance per se, as it was to the tendency of this species to grow in dense clumps not often penetrated by fires (see Rebertus 1988, Guerin

1993). In contrast, high relative tolerance of *Q. margaretta* to fires in the spring may be a function of seasonal phenology. While *Q. laevis* and *Q. incana* leaf out in early spring and are therefore highly susceptible to both April and May burns, *Q. margaretta* often does not break dormancy until late April (J. S. Glitzenstein, *personal observation*). Consequently, this species may suffer less damage from early spring fires.

Effects of fire frequency and intensity.—Current theories suggest a rather straightforward relationship between fire frequency and tree species composition in upland habitats of the Southeastern Coastal Plain (Heyward 1939, Garren 1943, Komarek 1974, Veno 1976, Christensen 1981, Myers 1985, 1990, Myers and White 1987, Platt and Schwartz 1990, Platt et al. 1991, Rebertus et al., *in press*; however, see also Menges et al. 1993 for a somewhat more complex picture of long-term trends in the absence of fire). Highest fire fre-

TABLE 16. ANOVA results of changes in DECORANA ordination scores for the sandhill plots over the course of three prescribed-burning treatment cycles.

Source of variation	df	ss	F	P
Axis 1				
Season of burning	7	133691	0.52	NS
Linear pattern	1	80198	2.17	NS
Quadratic pattern	1	16144	0.44	NS
Frequency of burning	1	8978	0.24	NS
Error (S × F)	7	58130		
Axis 2				
Season of burning	7	235821	4.61	0.03*
Linear pattern	1	46295	6.33	0.04*
Quadratic pattern	1	97717	13.36	0.01*
Frequency of burning	1	3844	0.53	NS
Error (S × F)	7	51186		
Axis 3				
Season of burning	7	48206	0.24	NS
Linear pattern	1	1857	0.06	NS
Quadratic pattern	1	11881	0.41	NS
Frequency of burning	1	228484	7.88	0.03*
Error (S × F)	7	203046		

quencies are predicted to favor longleaf pine over all other tree species; somewhat less frequent fires are predicted to favor mixtures of pines and the more fire tolerant hardwoods (e.g., sandhill oaks on dry sites); and complete fire suppression is predicted to produce a major shift in dominance toward fire intolerant, but more shade tolerant vegetation. While our comparisons of effects of annual and biennial burning did not test the complete range of fire frequencies that are covered by this hypothesis, they suggested that, at least toward the high end of the fire frequency spectrum, relationships between fire frequency and woody species dominance may be more complicated than previously hypothesized. Such complications appear to result from differences in fire intensities produced by variations in fuel loads at different fire frequencies.

In contradiction to the prevailing hypothesis, results of our ordination analyses indicated that increasing the fire return interval slightly at the high frequency end of the fire frequency gradient increased the abundance of pines relative to hardwoods. This is because oak trees in the sandhills experienced greater topkill, and hence greater declines in density, from biennial than from annual burns. In addition, mortality was lower for tree-sized pines than tree-sized oaks under regimes of biennial compared to annual fires. In southeastern pine forests, longer intervals between fires typically result in greater fuel accumulations (Table 1; Sackett 1975) and hotter and more intense fires (e.g., compare results of Heyward 1938, Hare 1961, and Williamson and Black 1981). Tree-sized pines are more tolerant of intense fires than are tree-sized hardwoods (Greene 1987; also our own *Results*). More intense fires associated with slightly less frequent burns thus favor pines over oaks by selectively eliminating the latter.

We note that increased abundances of pines relative

to oaks resulting from increased fire return times (and hence more intense fires) are a result of increases in the topkill of oaks. Biennial burns did not result in increased complete kill of sandhill oaks relative to annual burns. As a result of their clonal nature, sandhill oaks might be considered more tolerant than pines of high intensity fires. The ability of oaks to remain as shrubs in the ground cover and grow into trees during long intervals free of growing-season fires was used to suggest mechanisms whereby clonal oaks could persist in a fire regime involving frequent fires, but variable return times (Rebertus et al., *in press*). We also note that hardwood sprouts are favored by the same burning regime that reduces densities of tree-sized individuals of these same species (Waldrop et al. 1992 and earlier papers, cited therein, describing the long-term burning study at the Santee Experimental Forest, near Charleston, South Carolina). Increased topkill and increased regeneration can only occur in stands characterized by fires erratic over space and/or time, where tree-sized hardwoods are able to become established in the first place (Rebertus et al., *in press*). Such patterns, characteristic of oaks in the sandhills, increase the difficulty of predicting changes in vegetation composition given complicated spatio-temporal variability in fire regimes (see also Noble and Slatyer 1980, Keeley 1981, Streng and Harcombe 1982, Rebertus et al., *in press*).

Relationships between pines and oaks.—Longleaf pines and sandhill oaks respond to the same aspects of the upland Southeastern Coastal Plain environment, but in different ways. Fires are essential for persistence of both longleaf pines and sandhill oaks, which tend to be replaced by less fire tolerant species of hardwoods if fire exclusion occurs. Very different attributes enhance survival of fires by pines and oaks, however

TABLE 17. ANOVA results of changes in DECORANA ordination scores for the flatwoods plots over the course of three prescribed-burning treatment cycles (between 1980 and 1987).

Source of variation	df	ss	F	P
Axis 1				
Season of burning	7	97.8	0.38	NS
Linear pattern	1	0.3	0.01	NS
Quadratic pattern	1	3.4	0.10	NS
Frequency of burning	1	6.2	0.17	NS
Error (S × F)	7	253.8		
Axis 2				
Season of burning	7	4947.8	0.93	NS
Linear pattern	1	289.7	0.38	NS
Quadratic pattern	1	407.4	0.54	NS
Frequency of burning	1	576.0	0.76	NS
Error (S × F)	7	5304.0		
Axis 3				
Season of burning	7	1601.9	3.17	NS
Linear pattern	1	1.1	0.01	NS
Quadratic pattern	1	12.6	0.17	NS
Frequency of burning	1	10.6	0.15	NS
Error (S × F)	7	505.9		

(Rebertus et al., *in press*). In addition, there are strong suggestions of fire facilitation in pines (see Williamson and Black 1981, Platt et al. 1988*b*, 1991). Thus, the dynamics of tree populations in upland longleaf pine savannas might reflect interactions among trees that have a long evolutionary history involving frequent fire, but that are sensitive to different aspects of the environment.

Results of our study suggest, however, that stable mixtures of longleaf pines and sandhill oaks are unlikely. If fires occur frequently early in the growing season, the relative abundance of trees shifts rapidly toward longleaf pine, to the virtual exclusion of oaks. The oaks persist in the ground cover, however, as clonal shrubs, perhaps indefinitely (especially if there are spatial or temporal irregularities in the fire regimes). If fires occur frequently later in the growing season, the relative abundance shifts toward oaks. Although longleaf pine is not directly excluded, the formation of closed oak woodlands depresses longleaf recruitment and growth; the density of longleaf pine decreases very slowly (because the longevity of established longleaf is several hundred years; Platt et al. 1988*b*). Complete exclusion of longleaf pine from such a system, therefore, is probably not likely (see Williamson and Black 1981, Platt et al. 1991, Gilliam et al. 1993), given variability in fire regimes and other disturbances that might open space for regeneration of pines (e.g., hurricanes; see Platt and Rathbun, *in press*). Shifts over long periods of time ($\geqslant 10^6$ yr) in the seasonality of thunderstorms and accompanying lightning-initiated fires could result in shifts in relative abundances of pines and oaks in the southeastern U.S. such as those noted in palynological studies (see Watts 1980, Platt and Schwarz 1990). Predicted future changes in regional climate (e.g., drier summers, changes in the seasonal distribution of precipitation; see Smith and Tirpak 1990) are also likely to alter fire regimes (even under managed conditions), thus altering once again the balance between pines and oaks in upland habitats of the southeastern U.S.

ACKNOWLEDGMENTS

LITERATURE CITED

Abrahamson, W. G. 1984. Post-fire recovery of Florida Lake Wales Ridge vegetation. American Journal of Botany **71**: 9–21.

Abrahamson, W. G., and D. C. Hartnett. 1990. Pine flatwoods and dry prairies. Pages 103–149 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Albini, F. A. 1976. Estimating wildfire behavior and effects. United States Department of Agriculture Forest Service General Technical Report **INT-30**.

Allen, W. J. 1991. Soil survey of Wakulla County, Florida. United States Department of Agriculture Soil Conservation Service.

Andrews, P. L., and R. C. Rothermal. 1982. Charts for interpreting wildland fire behavior characteristics. United States Department of Agriculture Forest Service General Technical Report **INT-131**.

Baldwin, W. 1811. Letter to H. E. Muhlenberg (dated 6 December). *In* W. Darlington, editor. 1843. Reliquae Baldwinianae: selections from the correspondence of the late William Baldwin. Hafner, New York, New York, USA (1969 edition).

Bartram, W. 1791. The travels of William Bartram. James and Johnson, Philadelphia, Pennsylvania, USA.

Barton, A. M. 1993. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. Ecological Monographs **63**:367–398.

Bowman, D. M. J. S., B. A. Wilson, and R. J. Hooper. 1988. Responses of eucalyptus forest and woodland to four fire regimes at Munmarlary, Northern Territory, Australia. Journal of Ecology **76**:215–232.

Boyer, W. D. 1987. Volume growth loss: a hidden cost of periodic prescribed burning in longleaf pine. Southern Journal of Applied Forestry **11**:154–157.

———. 1990. Growing-season burns for control of hardwoods in longleaf pine stands. United States Department of Agriculture Forest Service Research Paper **SO-256**.

———. 1993. Season of burn and hardwood development in young longleaf pine stands. Pages 511–515 *in* J. C. Brissette, editor. Proceedings of the Seventh Biennial Southern Silviculture Research Conference (November 17–19, Mobile, Alabama, USA). United States Department of Agriculture Forest Service General Technical Report **SO-93**.

Bradshaw, L. S., J. E. Deeming, R. E. Burgan, and J. D. Cohen. The 1978 national fire-danger rating system: technical documentation. United States Department of Agriculture Forest Service General Technical Report **INT-169**.

Brender, E. V., and R. W. Cooper. 1968. Prescribed burning in Georgia's Piedmont loblolly pine stands. Journal of Forestry **66**:31–36.

Brewer, J. S., and W. J. Platt. 1994*a*. Effects of fire season and herbivory on reproductive success in a clonal forb, *Pityopsis graminifolia* (Michx.) Nutt. Journal of Ecology **82**:665–675.

Brewer, J. S., and W. J. Platt. 1994*b*. Effects of fire season and soil fertility on clonal growth in a pyrophilic forb, *Pityopsis graminifolia* (Asteraceae). American Journal of Botany **81**:805–814.

Bridges, E. L., and S. L. Orzell. 1989. Longleaf pine com-

munities of the West Gulf Coastal Plain. Natural Areas Journal 9:246–253.

Brown, R. B., E. L. Stone, and V. W. Carlisle. 1990. Soils. Pages 35–69 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Bruce, D. 1951. Fire, site and longleaf height growth. Journal of Forestry 49:25–28.

Byram, G. M. 1959. Combustion of forest fuels. Pages 61–89 in K. P. Davis, editor. Forest fire: control and use. McGraw-Hill, New York, New York, USA.

Cary, A. 1932. Some relations of fire to longleaf pine. Journal of Forestry 30:594–601.

Chapman, H. H. 1932. Is the longleaf type a climax? Ecology 13:328–334.

Chen, E., and J. F. Gerber. 1990. Climate. Pages 11–34 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Christensen, N. L. 1981. Fire regimes in southeastern ecosystems. Pages 112–136 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. Proceedings of a Conference: fire regimes and ecosystem properties. (December 1978, Honolulu, Hawaii, USA). United States Department of Agriculture Forest Service, General Technical Report WO-26.

———. 1988. Vegetation of the Southeastern Coastal Plain. Pages 317–363 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.

Clewell, A. F. 1985. Guide to the vascular plants of the Florida panhandle. University of Florida Presses, Gainesville, Florida, USA.

Collins, S. L., and D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. Pages 81–98 in S. L. Collins and L. L. Wallace, editors. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, Oklahoma, USA.

Cooper, R. W., and A. T. Altobellis. 1969. Fire kill in young loblolly pine. United States Department of Agriculture Forest Service Fire Control Notes 30:14–15.

Crawley, M. J. 1986. Life history and environment. Pages 253–290 in M. J. Crawley, editor. Plant ecology. Blackwell Scientific, Oxford, UK.

Farrar, R. M. In press. Growth and yield in naturally regenerated longleaf pine stands. Proceedings of the Tall Timbers Fire Ecology Conference 18.

Fensham, R. J. 1990. Interactive effects of fire frequency and site factors in tropical eucalyptus forest. Australian Journal of Ecology 15:255–266.

Ferguson, E. R. 1955. Fire-scorched trees—will they live or die? Pages 102–113 in Modern forest fire management in the South. Proceedings of the Fourth Annual Forestry Symposium. Louisiana State University, Baton Rouge, Louisiana, USA.

———. 1961. Effects of prescribed fires on understory stems in pine–hardwood stands of Texas. Journal of Forestry 59:356–359.

Folkerts, G. W. 1982. The Gulf Coast pitcher plant bogs. American Scientist 70:260–267.

Fox, M. D., and B. J. Fox. 1987. The role of fire in the scleromorphic forests and shrublands of eastern Australia. Pages 23–48 in L. T. Trabaud, editor. The role of fire in ecological systems. SPB Academic Publishing, The Hague, The Netherlands.

Frost, C. C., J. Walker, and R. K. Peet. 1986. Fire dependent savannas and prairies of the southeast: original extent, preservation status and management problems. Pages 348–357 in D. L. Kulhavy and R. N. Conner, editors. Proceedings of a symposium: wilderness and natural areas in the eastern United States (13 May, 1985, Nacogdoches). Center for

Applied Studies, School of Forestry, Stephen F. Austin State University, Nacogdoches, Texas, USA.

Garren, K. H. 1943. Effects of fire on vegetation of the southeastern United States. Botanical Review 9:617–654.

Gill, A. M., R. H. Groves, and I. R. Noble, editors. 1981. Proceedings of a symposium: fire and the Australian biota (9 October 1978, Canberra). Australian Academy of Science, Canberra, Australia.

Gilliam, F. S., B. M. Yurish, and L. M. Goodwin. 1993. Community composition of an old growth longleaf pine forest: relationship to soil texture. Bulletin of the Torrey Botanical Club 120:287–294.

Glitzenstein, J. S., D. R. Streng, and W. J. Platt. 1990. Evaluating effects of season of burn on vegetation in longleaf pine savannas. Florida Game and Freshwater Fish Commission Final Report. Tallahassee, Florida, USA.

Greene, T. A. 1987. Mortality and growth responses of juvenile pines and hardwoods to various fire intensities. Dissertation. Louisiana State University, Baton Rouge, Louisiana, USA.

Grelen, H. E. 1983. May burning favors survival and early height growth of longleaf pine seedlings. Southern Journal of Applied Forestry 7:16–20.

Gruschow, G. F. 1952. Effect of winter burning on growth of slash pine in the flatwoods. Journal of Forestry 50:515–517.

Guerin, D. N. 1993. Oak dome clonal structure and fire ecology in a Florida longleaf pine dominated community. Bulletin of the Torrey Botanical Club 120:107–114.

Harcombe, P. A., J. S. Glitzenstein, R. G. Knox, S. L. Orzell, and E. L. Bridges. In press. Vegetation of the longleaf pine region of the west Gulf Coastal Plain. Proceedings of the Tall Timbers Fire Ecology Conference 18.

Hare, R. C. 1961. Heat effects on living plants. United States Department of Agriculture Forest Service Occasional Paper SO-183.

Harper, R. M. 1911. The relation of climax vegetation to islands and peninsulas. Bulletin of the Torrey Botanical Club 38:515–525.

———. 1962. Historical notes on the relation of fires to forests. Proceedings of the Tall Timbers Fire Ecology Conference 1:11–29.

Hepting, G. H. 1945. Reserve food storage in shortleaf pine in relation to little-leaf disease. Phytopathology 35:106–119.

Heyward, F. 1938. Soil temperatures during forest fires in the longleaf pine region. Journal of Forestry 36:478–491.

———. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20:287–304.

Hicks, C. R. 1973. Fundamental concepts in the design of experiments. Holt, Rinehart, and Winston, New York, New York, USA.

Hobbs, R. J. 1984. Length of burning rotation and community composition in high-level Calluna–Eriophorum bog in N. England. Vegetatio 57:129–136.

Hobbs, R. J., and R. J. Gimingham. 1987. Vegetation, fire and herbivore interactions in heathland. Advances in Ecological Research 16:87–173.

Hodgkins, E. J. 1958. Effects of fire on undergrowth vegetation in upland southern pine forests. Ecology 39:36–46.

Hough, W. A. 1969. Caloric value of some forest fuels of the southern United States. United States Department of Agriculture Forest Service Research Note SE-120.

Hough, W. A., and F. A. Albini. 1978. Predicting fire behavior in palmetto–gallberry fuel complexes. United States Department of Agriculture Forest Service Research Paper SE-174.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Johnson, E. A. 1992. Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, New York, New York, USA.

Kalisz, P. J., and E. L. Stone. 1984. The longleaf pine islands of the Ocala National Forest, Florida: a soil study. Ecology 65:1743–1754.

Keeley, J. E. 1981. Reproductive cycles and fire regimes. Pages 231–277 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. Proceedings of a conference: fire regimes and ecosystem properties (December 1978, Honolulu, Hawaii, USA). United States Department of Agriculture Forest Service, General Technical Report WO-26.

Keeley, J. E., and S. C. Keeley. 1988. Chapparal. Pages 165–207 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.

Komarek, E. V., Sr. 1964. The natural history of lightning. Proceedings of the Tall Timbers Fire Ecology Conference 3:139–183.

———. 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States. Pages 251–278 in T. T. Kozlowski and C. E. Ahlgren, editors. Fire and ecosystems. Academic Press, New York, New York, USA.

Kozlowski, T. T., and C. E. Ahlgren, editors. 1974. Fire and ecosystems. Academic Press, New York, New York, USA.

Krueger, F. J. 1984. Effects of fire on vegetation structure and dynamics. Pages 219–243 in P. de J. Booysen and N. M. Tainton, editors. Ecological effects of fire in South African ecosystems. Springer-Verlag, Berlin-Heidelberg, Germany.

Landers, L. L. 1991. Disturbance influences on pine traits in the southeastern United States. Proceedings of the Tall Timbers Fire Ecology Conference 17:61–98.

Lawson, J. 1709. A new voyage to Carolina; containing an exact description and natural history of that country: together with the present state thereof. And a journal of a thousand miles, travelled through several nations of Indians, giving a particular account of their customs, manners etc. 1967 edition. University of North Carolina Press, Chapel Hill, North Carolina, USA.

Le Maitre, D. C. 1987. Effects of season of burn on species populations and composition of fynbos in the Jonkershoek valley. South African Journal of Botany 53:284–292.

Lemon, P. C. 1949. Successional responses of herbs in the longleaf–slash pine forest after fire. Ecology 30:135–145.

Lonsdale, W. M., and R. W. Braithwaite. 1991. Assessing the effects of fire on vegetation in tropical savannas. Australian Journal of Ecology 16:363–374.

Maier, M. W., A. G. Boulanger, and R. I. Sax. 1979. An initial assessment of flash density and peak current characteristics of lightning flashes to ground in south Florida. U.S. Nuclear Regulatory Commission Report CR-1024.

Malanson, G. P. 1987. Diversity, stability and resilience: effects of fire regime. Pages 49–63 in L. Trabaud, editor. The role of fire in ecological systems. Academic Publishing, The Hague, The Netherlands.

Malanson, G. P., and L. Trabaud. 1988. Vigour of post-fire resprouting by Quercus coccifera L. Journal of Ecology 76: 351–365.

Maple, W. R. 1975. Mortality of longleaf pine seedlings following a winter burn against brown-spot needle blight. United States Department of Agriculture Forest Service Southern Forest Experiment Station Research Note SO-195.

———. 1977. Spring burn aids longleaf pine seedling height growth. United States Department of Agriculture Forest Service Southern Forest Experiment Station Research Note SO-228.

McKee, W. H. 1982. Changes in soil fertility following pre-scribed burning on Coastal Plain sites. United States Department of Agriculture Forest Service Research Paper SE-234.

Means, D. B., and G. Grow. 1985. The endangered longleaf pine community. ENFO (Environmental Information Center) 85:1–12. Florida Conservation Foundation, Winter Park, Florida, USA.

Means, D. B., and P. E. Mohler. 1979. The pine barrens treefrog: fire, seepage bogs, and management implications. Pages 77–83 in R. R. Odum and L. Landers, editors. Proceedings of rare and endangered wildlife symposium. Georgia Department of Natural Resources, Game and Fish Division Technical Bulletin WL4.

Menges, E. S., W. G. Abrahamson, K. T. Givens, N. P. Gallo, and J. N. Layne. 1993. Twenty years of vegetation change in five long unburned Florida plant communities. Journal of Vegetation Science 4:375–394.

Midgley, J. J. 1989. Season of burn of serotinous fynbos Proteaceae: a critical review and further data. South African Journal of Botany 55:165–170.

Moreno, J. M. 1989. A simple method for estimating fire intensity after a burn in California chaparral. Acta Oecologica Oecologica Plantarum 10:57–68.

Moreno, J. M., and W. C. Oechel. 1991a. Fire intensity effects on germination of shrubs and herbs in southern Californian chaparral. Ecology 72:1993–2004.

Moreno, J. M., and W. C. Oechel. 1991b. Fire intensity and herbivory effects on postfire resprouting of Adenostoma fasciculatum in southern California chaparral. Oecologia 85:429–433.

Myers, R. L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bulletin of the Torrey Botanical Club 112:241–252.

———. 1990. Scrub and high pine. Pages 150–193 in R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Myers, R. L., and D. L. White. 1987. Landscape history and changes in sandhill vegetation in north-central and south-central Florida. Bulletin of the Torrey Botanical Club 114: 21–32.

Nelson, R. M., and C. W. Adkins. 1988. A dimensionless correlation for the spread of wind-driven fires. Canadian Journal of Forest Research 18:391–397.

Nieuwenhuis, A. 1987. The effect of fire frequency on the sclerophyll vegetation of the West Head, New South Wales. Australian Journal of Ecology 12:373–385.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in communities subject to recurrent disturbances. Vegetatio 43:5–21.

Olson, M. S. 1992. Effects of early and late growing season fires on resprouting of shrubs in upland longleaf pine savannas and embedded seepage savannas. Thesis. Lousiana State University, Baton Rouge, Louisiana, USA.

Peet, R. K. 1993. A taxonomic study of Aristida stricta and A. beyrichiana. Rhodora 95:25–37.

Peet, R. K., and D. J. Allard. In press. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Proceedings of the Tall Timbers Fire Ecology Conference 18.

Platt, W. J., and S. L. Rathbun. In press. Population dyanmics of an old-growth population of longleaf pine (Pinus palustris). Proceedings of the Tall Timbers Fire Ecology Conference 18.

Platt, W. J., G. W. Evans, and M. M. Davis. 1988a. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76:353–363.

Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988b. The population dynamics of a long lived conifer (Pinus palustris). American Naturalist 131:491–525.

Platt, W. J., J. S. Glitzenstein, and D. R. Streng. 1991. Eval-

uating pyrogenicity and its effects on vegetation in longleaf pine savannas. Proceedings of the Tall Timbers Fire Ecology Conference **17**:143–162.

Platt, W. J., and M. W. Schwartz. 1990. Temperate hardwood forests. Pages 194–229 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, USA.

Pyne, S. J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton University Press, Princeton, New Jersey, USA.

Rebertus, A. J. 1988. The effects of fire on forest community composition, structure, and pattern in Florida sandhills. Dissertation. Louisiana State University, Baton Rouge, Louisiana, USA.

Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989. Longleaf pine pyrogencity and turkey oak mortality in Florida xeric sandhills. Ecology **70**:60–70.

Rebertus, A. J., G. B. Williamson, and W. J. Platt. *In press.* Impacts of temporal variation in fire regime on savanna oaks and pines. Proceedings of the Tall Timbers Fire Ecology Conference **18**.

Reinman, J. 1989. A wildlife management plan for the forested uplands of the St. Marks national wildlife refuge. U.S. Department of the Interior Fish and Wildlife Service, unpublished report.

Robbins, L. E., and R. L. Myers. 1992. Seasonal effects of prescribed burning in Florida: a review. Tall Timbers Research Station Miscellaneous Publication No. 8.

Rose-Innes, R. 1972. Fire in West African vegetation. Proceedings of the Tall Timbers Fire Ecology Conference **11**: 147–173.

Rosenthal, R., and R. L. Rosnow. 1985. Contrast analysis: focused comparisons in the analysis of variance. Cambridge University Press, Cambridge, UK.

Ruffin, Edmund. 1843. The private diary of Edmund Ruffin. William M. Mathew, editor. University of Georgia Press, Athens, Georgia, USA (1992 edition).

Ryan, K. C., and E. D. Reinhardt. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research **18**:1291–1297.

Sackett, S. S. 1975. Scheduling prescribed burns for hazard reduction in the Southeast. Journal of Forestry **73**:143–147.

Schwarz, G. F. 1907. The longleaf pine in virgin forest. John Wiley and Sons, New York, New York, USA.

Schwartz, M. W. 1994. Estimating 19th-century abundances of trees in northern Florida. Ecology **75**:687–705.

Silver, T. 1990. A new face on the countryside: indians, colonists and slaves in South Atlantic forests, 1500–1800. Cambridge University Press, Cambridge, UK.

Smith, J. B., and D. A. Tirpak, editors. 1990. The potential effects of global climate change on the United States. Hemisphere, New York, New York, USA.

Snedecor, G. W., and W. G. Cochran. 1981. Statistical methods. Iowa University Press, Ames, Iowa, USA.

Sokal, R. R., and F. J. Rohlf. 1982. Biometry. Freeman, San Francisco, California, USA.

Streng, D. R. 1979. Edaphic and pyric influences on two contiguous East Texas savannas. Thesis. Rice University, Houston, Texas, USA.

Streng, D. R., and P. A. Harcombe. 1982. Why don't east Texas savannas grow up to forest? American Midland Naturalist **108**:278–294.

Streng, D. R., J. S. Glitzenstein, and W. J. Platt. *In press.* Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing study. Proceedings of the Tall Timbers Fire Ecology Conference **18**.

Swezy, D. M., and J. K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research **21**:626–634.

Taggart, J. B. 1990. Inventory, classification and preservation of Coastal Plain savannas in the Carolinas. Dissertation. The University of North Carolina, Chapel Hill, North Carolina, USA.

Ter Braak, C. J. F. 1987. Ordination. Pages 91–173 *in* R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. van Tongeren, editors. Data analysis in community and landscape ecology. Pudoc (Center for Agricultural Publishing and Documentation), Wageningen, The Netherlands.

Trabaud, L., editor. 1987. The role of fire in ecological systems. SPB Academic Publishing, The Hague, The Netherlands.

Trabaud, L., and J. Lepart. 1981. Changes in the floristic composition of a *Quercus coccifera* L. garrigue in relation to different fire regimes. Vegetatio **46**:105–116.

Trapnell, C. G. 1959. Ecological results of woodland burning experiments in Northern Rhodesia. Journal of Ecology **47**: 129–168.

Van Wagner, C. E. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research **3**:373–378.

Veno, P. A. 1976. Successional relationships of five Florida plant communities. Ecology **57**:498–508.

Villarubia, C. R., and J. L. Chambers. 1978. Fire: its effects on growth and survival of loblolly pine, *Pinus taeda* L. Louisiana Academy of Science **41**:85–93.

Vogl, R. J. 1973. Fire in the southeastern grasslands. Proceedings of the Tall Timbers Fire Ecology Conference **12**: 175–198.

Wade, D. D. 1986. Linking fire behavior to its effects on living plant tissue. Pages 112–116 *in* Proceedings of the Society of American Foresters National Convention (5–8 October, 1986 Birmingham, Alabama, USA). Society of American Foresters, Bethesda, Maryland, USA.

Wade, D. D., and R. W. Johansen. 1986*a*. Relating wildland fire to defoliation and mortality in pine. Pages 107–110 *in* Proceedings of the Fourth Biennial Southern Silvicultural Research Conference (4–6 November 1986, Atlanta, Georgia, USA). United States Department of Agriculture Forest Service General Technical Report **SE-42**.

Wade, D. D., and R. W. Johansen. 1986*b*. Effects of fire on southern pine: observations and recommendations. United States Department of Agriculture Forest Service General Technical Report **SE-41**.

Wahlenberg, W. G. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth and management. Charles Lathrop Pack Forestry Foundation, Washington, D.C., USA.

Waldrop T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine–grassland communities in the southeastern United States. Forest Ecology and Management **47**: 195–210.

Walker, J., and R. K. Peet. 1983. Composition and species diversity of pine–wiregrass savannas of the Green Swamp, North Carolina. Vegetatio **55**:163–179.

Ware, S., C. Frost, and P. D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pages 447–493 *in* W. H. Martin, editor. Biodiversity of the southeastern United States: I. upland communities. John Wiley and Sons, New York, New York, USA.

Watts, W. A. 1980. The late quaternary vegetation history of the southeastern United States. Annual Review of Ecology and Systematics **11**:387–409.

Wells, B. W. 1942. Ecological problems of the southeastern United States Coastal Plain. Botanical Review **8**:533–561.

Wells, B. W., and I. V. Shunk. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina Coastal Plain: an ecological study. Ecological Monographs **1**:465–521.

Weise, D. R., D. D. Wade, and R. W. Johansen. 1989. Survival and growth of young southern pine after simulated

crown scorch. Pages 161–168 *in* D. C. MacIver, H. Auld, and R. Whitewood, editors. Proceedings of the 10th Conference on Fire and Forest Meteorology (17–21 April 1989, Ottawa, Canada).

Williamson, G. B., and E. M. Black. 1981. High temperature of forest fires under pines as a selective advantage over oaks. Nature **293**:643–644.

Woods, F. W., H. C. Harris, and R. E. Caldwell. 1959. Monthly variations of carbohydrates and nitrogen in roots of sandhill oaks and wiregrass. Ecology **40**:292–295.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology. John Wiley and Sons, New York, New York, USA.

Wyant, J. G., R. J. Alig, and W. A. Bechtold. 1991. Physiographic position, disturbance and species composition in North Carolina Coastal Plain forests. Forest Ecology and Management **41**:1–19.

Zontek, F. 1966. Prescribed burning on the St. Marks National Wildlife Refuge. Proceedings of the Tall Timbers Fire Ecology Conference **5**:195–201.

APPENDIX A

Stem densities of tree species in 1-ha sandhills plots in 1980, after thinning the oaks but before starting the experimental burning treatments. Plots are identified by season and frequency (A—annual, B—biennial) of burn. Size classes (SC) are as follows: (1) 2–4.9 cm dbh, (2) 5–9.9 cm dbh, (3) 10–19.9 cm dbh, (4) $\geq$20 cm dbh.

Species	SC	JAN		FEB		APR		MAY		JUL		AUG		OCT		NOV	
		A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Diospyros virginiana	(1)			1					3								
	(2)								1			1	1				
Ilex vomitoria	(1)	6						2									
	(2)	5															
Pinus palustris	(1)	12	15	90	50	8	9	33	72	11	10	48	43	10	61	25	7
	(2)	21	33	25	26	18	15	27	25	66	41	35	47	29	35	28	32
	(3)	44	53	36	38	29	38	43	54	40	35	51	43	33	48	53	26
	(4)	108	108	64	94	100	90	91	83	145	108	89	112	66	75	86	106
Quercus falcata	(1)									1							
	(2)			1			1			1				1			
	(3)						2										
	(4)													1			
Q. geminata	(1)	7	2	4		10	1	27		23	4		2	10			15
	(2)	8			3	2		5	1	13	1			8			6
	(3)						1	1						2			
	(4)	1															
Q. hemisphaerica	(1)	3	1	3	1					2	4						
	(2)	1												1			
	(3)																
	(4)	1			1												
Q. incana	(1)	10	20	17	29	15	23	30	26	3	36	24	12	8	9	19	12
	(2)	15	19	8	19	19	16	22	11	5	9	11	17	7	5	17	7
	(3)	2	4	1	3	6	3	3	2	7	4	1		5	3	1	6
	(4)	1	1			3	3		1	2			1		1	1	
Q. laevis	(1)		38	39	27	10	25	13	18	1	3	35	29	4	39	33	4
	(2)	1	16	20	16	3	17	5	16	1	2	23	14	1	26	17	3
	(3)	4	2	4	2		3	1	4			5	3		2	6	
	(4)		2	2	1		2		2	1	1	2	1		2	1	2
Q. margaretta	(1)		4	6	3		16	1	19	8	6	21		19	10		
	(2)		5	4			7	2	14		7	6	11		7	3	1
	(3)			1	1			1					2	1	4		
	(4)								1						1		
Q. myrtifolia	(1)	2				5											
	(2)					2											
Vaccinium arboreum	(1)	1			2	2	1	6					2			1	3
	(2)								1				2	1			
V. stamineum	(1)	4			2	2		16					6	1	2	1	1
	(2)								1	1							

APPENDIX B

Stem densities of tree species in 1-ha flatwoods plots in 1980, before the experimental burning treatments were begun. Plots are identified by season and frequency (A—annual, B—biennial) of burn. Size classes (SC) are as follows: (1) 2–4.9 cm dbh, (2) 5–9.9 cm dbh, (3) 10–19.9 cm dbh, (4) ≥20 cm dbh.

| | | Month of experimental burns | | | | | | | | | | | | | | | |
| | | JAN | | FEB | | APR | | MAY | | JUL | | AUG | | OCT | | NOV | |
Species	SC	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Pinus elliottii	(1)	2	6	1	6	2		1	1	3						9	1
	(2)	7	6	2	11	5		8	1	4	1			5		5	
	(3)	14	2	1	2	3		43		11				17		6	1
	(4)	31	9	2	1			93	47				18	1	1		
P. palustris	(1)	6	4	52	26	9	25	3	8	36	17	48	23	29	14	6	14
	(2)	21	17	41	50	62	25	23	14	88	23	41	85	111	27	20	21
	(3)	18	47	41	134	134	37	33	52	102	20	49	155	91	15	71	13
	(4)	79	165	60	80	76	154	33	108	58	92	81	109	77	105	181	81
P. serotina	(1)		11				3										
	(2)		5	1			1										
	(3)		9				1										
	(4)		1	1													
P. taeda	(1)			3													
	(2)			2													
	(3)			1													
	(4)			1													
Quercus geminata	(1)				2					25							
	(2)		2							34							
	(3)									17							
	(4)				1					1							
Q. hemisphaerica	(1)						2										
Q. incana	(1)		2	15	41		1			12							
	(2)		2	6	4					8							
	(3)		3	2	1					1							
	(4)								2								
Q. laevis	(1)	1			1		1			47				2			
	(2)				1					35				5			
Q. margaretta	(1)				2					12							
	(2)		2		2												