

Impact of Temporal Variation in Fire Regime on Savanna Oaks and Pines

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ABSTRACT

Variation in fire regimes in upland Southeastern Coastal Plain habitats occurs on three progressively finer time scales: (1) variation in the occurrence of fire over millennia that results from long-term climatic changes, (2) variation in the occurrence of fire over the decades to centuries that comprise the life spans of dominant plants in the flora, and (3) variation in the times at which fires occur within any single growing season. Each of these three forms of variation uniquely affects the trees, longleaf pine (*Pinus palustris*) and oaks (e.g., *Quercus laevis*, *Q. incana*, *Q. geminata*) indigenous to upland xeric sandhill and clayhill habitats of the Southeastern United States.

The data available at the current time can be used to construct a general hypothesis that relates the relative abundances of longleaf pine and oaks to variations that occur in fire regimes. In upland habitats of the Southeastern Coastal Plain, both longleaf pine and oaks are dependent on frequent fires—on the order of at least once a decade. Within that time span, as the frequency of fire increases and as recurrent early growing-season fires started by lightning become more common, the importance of longleaf pine is increased relative to the oaks. The greater the variance in the fire regimes, both within season and among years within decades, whether caused by the erratic nature of lightning or by anthropogenic manipulations, the greater will be the importance of oaks relative to longleaf pine.

INTRODUCTION

Recurrent natural disturbance is recognized as an integral part of the dynamics of many communities (White 1979, Sousa 1984, White and Pickett 1985). The concept of "disturbance regime," the sum of disturbances operating in a given landscape (White 1979), has emerged as a conceptual framework for describing the characteristics of habitats. The key parameters of the disturbance regime include (1) type of disturbance, (2) size and spatial distribution, (3) frequency (including return interval, rotation period, cycles, turnover times), (4) intensity, (5) predictability, and (6) synergistic interactions of different types of disturbances (White and Pickett 1985).

Disturbance predictability, both spatial and temporal, is an important element of the disturbance regime that rarely has been investigated

(Pickett and White 1985). Disturbance predictability has been defined as "a scaled inverse function of variance in the return interval" (White 1979, Sousa 1984, White and Pickett 1985); however, this appears to be a better definition for disturbance "periodicity," which is defined as the "quality, state, or fact of being regularly recurrent" (Webster's Third New International Dictionary). Based on this definition, periodicity would be some measure of the regularity in the occurrence of a disturbance—e.g., variance about a mean fire frequency. Nevertheless, a fire history terminology workshop found no consensus in the meaning of "periodicity" and failed to come up with even a tentative definition (Romme 1980). At least part of the confusion regarding the meaning of "periodicity" and "predictability" arises because variability of disturbance occurs over a temporal and spatial continuum (see Allen and Starr 1982, White and Pickett 1985).

Life history attributes of many plants (growth patterns, maturation, reproduction, and longevity) have evolved in response to relatively predictable, periodic intervals between disturbances (see Pickett and White 1985). If we assume that disturbance frequency is normally distributed, plants of some species will have higher fitness in narrow bands around the mean frequency, while plants of other species may have higher fitness in wider bands around the mean frequency. The latter may be capable of surviving extremes in the disturbance regime, for example, by persisting vegetatively when disturbances are very frequent, then maturing and reproducing when the disturbance regime is more favorable (e.g., longer fire-free intervals that may or may not be periodic). Finally, fugitive species may thrive only when extremes in the disturbance regime create favorable openings. Clearly some species are opportunistic, highly responsive to the environment, and may have higher fitness when disturbances are less periodic.

Harper (1977) proposed a distinction between disasters and catastrophes, the latter not occurring frequently enough to be a selective force on the plant's life history. Yet, for long-lived plants and even plants with shorter lifespans, rare disturbances may cause significant changes in the gene pool, and thus act as potent selective forces (Sousa 1984). Rare disturbances, which may be necessary for regeneration, have some degree of certainty for trees that may live for centuries or millennia. In this case, the scale of variability relative to the lifespan of the species is most relevant. Great longevity in some tree species results in opportunities for regeneration during their lifespans that would be spatially and/or temporally limited over shorter time intervals (Ogden 1985, Platt et al. 1988b).

In this paper we focus on the temporal variability of fire in upland sandhill habitats of the southeastern coastal plain of the United States. We examine temporal variation in fire regimes over three hierarchical time frames: (1) variation in the occurrence of fire over millennia, which usually results from long-term climatic change, (2) variation in the occurrence of fire over the decades to centuries that comprise the lifespans of dominant plants in the flora, and (3) variation in the seasons at which fires occur. In the sections that follow we will discuss how each of these scales of variability is likely to affect the relative dominance of the predominant trees: savanna oaks, particularly turkey oak (*Quercus laevis* Walt.), and longleaf pine (*Pinus palustris* Mill.).

LONG-TERM VARIABILITY IN THE FIRE REGIME

Over millennia, changes in the fire regime of longleaf pine savannas resulted initially from variations in climate and more recently from variations in both climate and human activity (Kalisz 1982, Myers and White 1987, Robbins and Myers 1989, Platt et al. 1991). The effects of long-term climatic changes on fire frequency and vegetation are not well known, but short-term studies of fire exclusion indicate that longleaf pine savannas persist only if fires occur very frequently. Several fire-free decades may be sufficient for less pyrophilic species of trees to invade and suppress flammable graminoids, as well as small longleaf pines and oaks (Heyward 1939, Veno 1976). Sandhill vegetation is gradually invaded by scrub and/or hardwood tree species, depending on the site conditions, length of fire suppression, and availability of seed source (Monk 1960, 1968; Snedaker 1963; Laessle 1968; Veno 1976; Myers 1985; Myers and White 1987; Platt and Schwartz 1990).

The relationship between sandhill and scrub communities in the Florida peninsula appears to be dynamic and to depend on intervals between successive fires. Evidence from soil phytoliths suggests that boundaries between sandhill and scrub habitats in the Ocala National Forest have fluctuated considerably in the past, perhaps in response to fire (Kalisz and Stone 1984). Myers (1985) has suggested that changes in the fire frequency could lead to shifts in sandhill vegetation towards scrub and vice versa. In the absence of fire, sand pine (*Pinus clausa* Vasey ex Sarg.), along with several xeric hardwood species, tend to invade the sandhills from adjacent scrub and form a mixed pine-xeric hardwood forest within 50 years (Myers 1985). In the continued absence of fire, the pines would be unable to regenerate, and eventually the site would develop a xeric hardwood forest. However, changes in fuel composition and structure could result not only in low likelihood of fire (as might occur with moist compacted hardwood litter), but also in high intensity crown fires during drought conditions (Streng and Harcombe 1982). If a high-intensity fire occurred before the pines died out, scrub species would tend to replace sandhill species. Both pine species would be killed, but sand pine would reseed from serotinous cones, and scrub hardwoods would resprout. This incipient scrub community could then be maintained by periodic long-interval, high intensity fires, although a rare, short-interval fire might have dramatic ef-

fects, such as removing sand pine from the developing scrub habitat. The fire regime would eventually become somewhat stabilized by vegetation of the developing scrub (e.g., the size and spacing of sand pines, as well as dead fuel accumulation; Myers 1985, 1990). Scrub vegetation would tend to resist short-interval fires due to the allelopathic influence of several shrubs (Williamson 1990). However, if fires repeatedly crossed the sandhill-scrub ecotone, sandhill species would gradually invade scrub and the patterns of vegetation change would be reversed (Myers 1985, 1990).

This general paradigm for fire-mediated relationships between sandhill, scrub, and hardwood hammock vegetation has not been tested. Analogous changes have been documented, however, in chaparral vegetation following single fires. Zedler (1983) documented a rare short-interval fire across chaparral and coastal sage scrub communities which caused sudden and relatively permanent changes in species composition. Two dominant chaparral species were largely eliminated by the short-interval fire, and Zedler speculated that coastal sage scrub would likely expand as a result. Rare, intense fires are thought to have a major impact on the boundaries of many hardwood-pineland communities in the Southeast (Platt and Schwartz 1990). With long-term changes in climate, extreme events might become more common or involve more extensive areas, hastening shifts in community boundaries.

The universal similarity of the results of fire exclusion, even in the most xeric habitats, argues strongly for a continued presence of frequent fire in at least some coastal plain regions for millions of years (Platt et al. 1991). Given the periodic occurrence of fire on the order of at least every few decades, the relative frequency within that time scale probably influenced the extent of longleaf pine savannas relative to adjacent, less pyrogenic communities (Platt and Schwartz 1990; Harcombe et al., 1993). The boundaries between longleaf pine savannas and xeric scrub or hammock, as well as ecotones between these savannas and downslope mesic hardwood hammocks or seepage habitats, probably were to at least some extent dynamic, changing with the frequency of fire. Some of the surrounding habitats may owe their existence--and even the evolution of component species--to the periodic spread of fires from the pyrogenic longleaf pine savannas (Platt and Schwartz 1990).

VARIATION IN FIRE FREQUENCY OVER A SPECIES' LIFESPAN

Life history traits, such as seedling development, reproductive age, and longevity are often timed to the predictability of disturbances over the lifespans of individuals in plant populations. Serotinous pines, for example, typically produce open cones at an early age, when the young stands lack enough fuel to carry a crown fire. Serotiny tends to increase as the tree becomes older, fuel in the stand accumulates, and the likelihood of wildfire increases (Crossley 1956, Sutton 1979). It is equally plausible that certain attributes may also have evolved in response to inherent variability in the fire regime. If two species are potential competitors, and one is not well adapted to short- or long-interval fires, individuals of the other species that can survive such fires and/or reproduce successfully in the intervals between such fires might have higher fitness. Resprouting, for example, would favor persistence during extremes in the fire regime (Lamont et al. 1991).

Adverse effects of irregular fire intervals on plant survival have been considered in studies in other habitats. Short-interval fires may preempt maturation of a post-fire cohort and lead to complete regeneration failure (Keeley 1981, Zedler 1983, Whelan and Muston 1991). Long-interval fires may lead to unusually intense fires that kill adults capable of surviving less intense fires (Heinselman 1973). If a species requires fire for successful regeneration, the fire-free interval may exceed the longevity of a plant or its seed pool (Keeley 1981, Lamont et al. 1991).

Life history attributes, particularly of the regeneration niche, become paramount to a plant's response to variable disturbance intervals (Noble and Slatyer 1980, Noble 1981). This appears to be particularly true for trees in sandhills. Platt et al. (1991) and Christensen (1981) hypothesized that the natural fire frequency in longleaf pine savannas ranged from 1-10 years and 3-8 years, respectively. Both longleaf pine and oaks can withstand this high fire frequency by remaining in the ground cover (via different mechanisms) for many years, then exhibiting rapid growth (following fire) to sizes that can survive subsequent low-intensity fires.

The growth characteristics of longleaf pine juveniles are fairly well known. Production of sec-

ondary needles that surround the terminal bud results in juveniles becoming fire resistant within two years after germination (Huberman 1940; Bruce 1951; Boyer 1974). While in this "grass-stage," annual increments occur in basal diameter, but stem elongation occurs very slowly (Platt et al. 1988b). In the old-growth stand on the Wade Tract in Thomas County, Georgia, the timing of entry into a "height-growth" phase of the life cycle is highly variable within a cohort and even within the same clump of juveniles. Some juveniles in a cohort that germinated in 1978 began to elongate within 3-4 years after germination, while others have not yet exhibited stem elongation after thirteen years (Fig. 1). Stem elongation may be delayed up to 15-20 years in the absence of fire (Crocker and Boyer 1975). Long-suppressed juveniles eventually die from brown-spot disease or competition (Bruce 1958, Grelen 1983).

Above some size, longleaf pine appears not to be affected by low-intensity ground cover fires unless trees are damaged by some other agent (Wahlenberg 1946, Chapman 1947, Platt et al. 1988b, Platt and Rathbun 1993). On the Wade

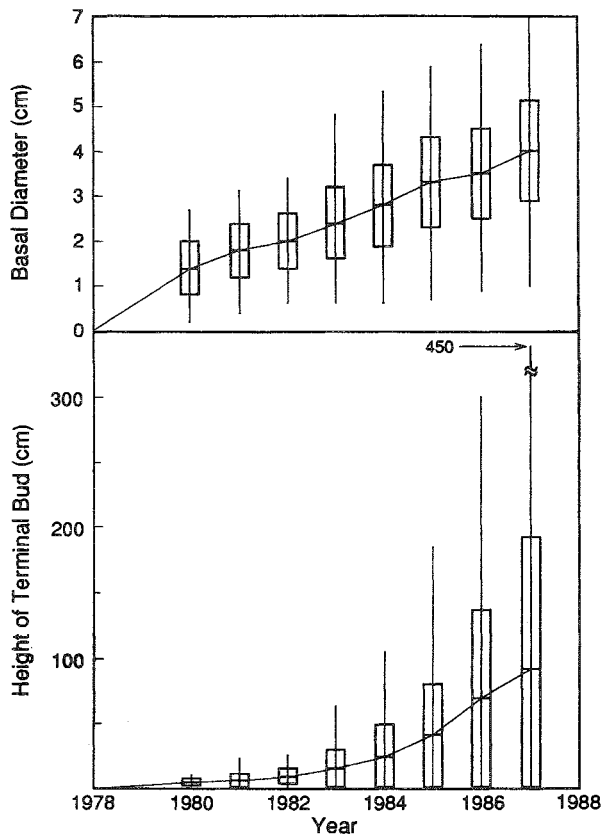


Figure 1. Basal diameter (upper) and height of terminal bud (lower) of 80 juvenile longleaf pines that germinated on the Wade Tract in 1978. Horizontal bars denote means \pm standard deviation. Vertical bars denote ranges. The sample of 80 individuals represents those trees in a cohort that germinated within 4 randomly selected hectares of the mapped plot and survived for 10 years (until 1987).

Tract, trees that have elongated rapidly for 3-5 years, are above 5 m tall, and approach 10 cm or more in dbh, also have thickened bark capable of resisting even fairly intense fires. The only time that surface fires have been observed to damage large trees is when large amounts of flammable fuels are present at the bases of trees; then fires may smolder, girdling the trunk and/or killing surface roots (W.J. Platt, personal observation).

Less is known regarding the growth characteristics of sandhill oaks, but there are some similarities to longleaf pine. Turkey oak juveniles sometimes display a shrub stage. As a result, there is a sigmoidal height-growth pattern involving initial slow growth, 6-10 years of more rapid stem elongation, and a gradual slowing of the rates of height growth (Fig. 2). Small turkey oaks (<5 cm dbh) are vulnerable to crown mortality, but resprout vigorously even with repeated spring burns (Rebertus et al. 1989a). Other "juveniles," which probably are basal resprouts, lack the initial shrub stage (Fig. 2). Data from the University of South Florida Study Area (Hillsborough County, Florida) indicate that crown survival increases as

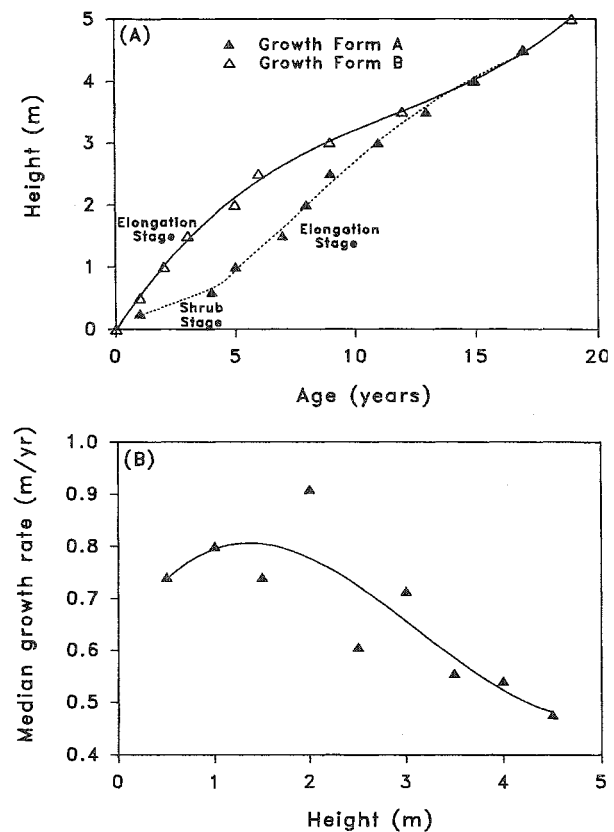


Figure 2. Upper: Height vs. age growth patterns for turkey oaks in sandhills, University of South Florida Ecological Study Area. Two representative trees are shown: growth form "A" displays a typical sigmoidal pattern, whereas "B" lacks a shrub stage. Lower: Median growth rate vs. height for turkey oaks ($n=6-9$) in sandhill, University of South Florida Ecological Study Area, Tampa. Trees were sectioned at ca. 0.5-m intervals (\blacktriangle).

a function of the size of the turkey oak (Fig. 3), but the height growth of juvenile turkey oaks is clearly less than that of at least some juvenile pines (cf. Figs. 1 and 2), and thus turkey oaks probably require a longer fire-free interval to reach sufficient size to survive surface fires. Data from the USF plots suggest that turkey oaks require at least 6-9 fire-free years to survive spring sandhill fires, although this undoubtedly varies depending on fire intensity.

Given these key differences between the juvenile stages of longleaf pines and turkey oaks, characteristics of fire regimes should influence relative dominance. In Fig. 4 we illustrate how effects of differences in the mean intervals between successive fires and the variance in the return intervals between fires are predicted to alter relative dominance of longleaf pine and turkey oaks. For longleaf pine, a mean fire frequency of ca. 3-6 years with low variance is predicted to facilitate regeneration, because seedlings pass through the grass and elongation stages with maximum development and attain sufficient size to survive light surface fires (Fig. 4A). The range of favorable frequencies undoubtedly varies somewhat among habitats, however, depending on growing conditions and fuel loads. As the variance in fire frequency increases, seedlings are vulnerable to short-interval fires during the elongation stage and vulnerable to brown spot disease and competition during the longer fire-free intervals. As the variance in fire frequency increases further, long fire-free intervals would lead to excessive fuel accumulation, and the likelihood of longleaf pine experiencing mortality,

particularly in the elongation and seedling stage, is predicted to increase (Fig. 4A).

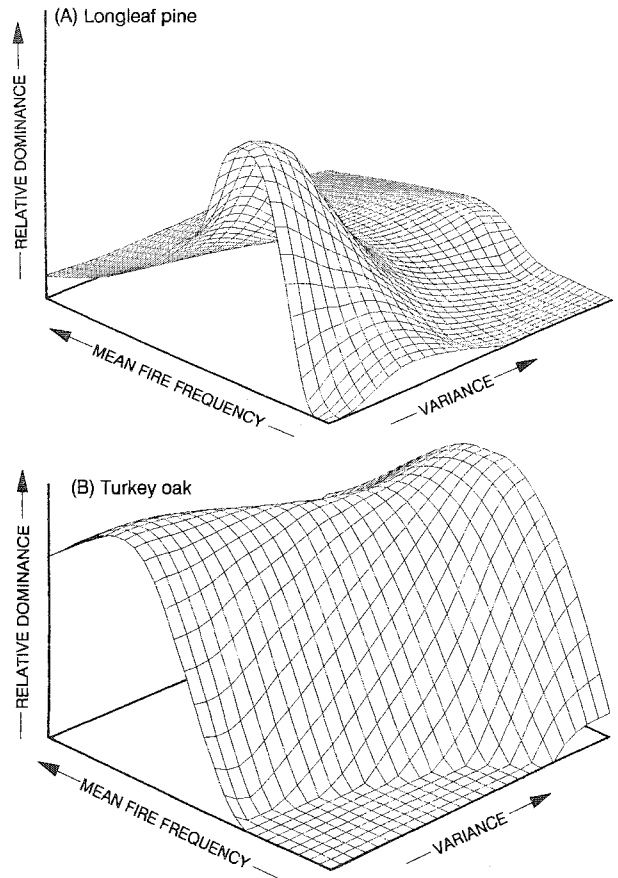


Figure 4. Hypothetical model depicting the relative success (e.g., dominance, recruitment into adult size-classes, fitness) of longleaf pine (A) and turkey oak (B) as a function of long-term mean and standard deviation in the fire frequency, measured as return interval in years.

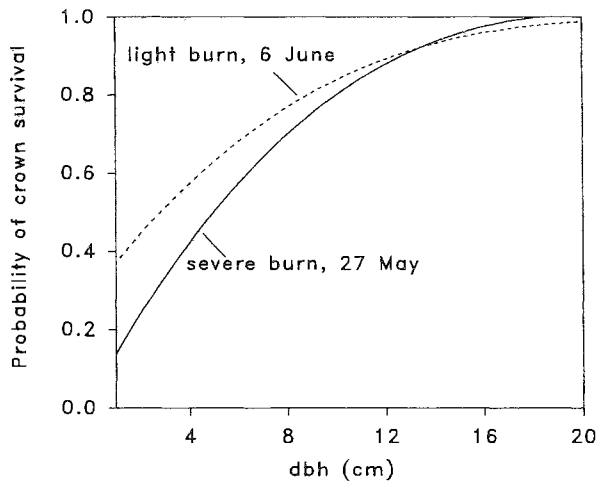


Figure 3. Probability of turkey oak crown survival as a function of dbh in two spring fires, University of South Florida Ecological Study Area. The fitted logistic model for the light burn was: $\underline{Y} = 1 / [1 + e^{(0.706 - 0.240 \cdot \text{DBH})}]$, ($n=458$; $P < .01$); and for the severe burn, $\underline{Y} = 1 / [1 + e^{(1.791 - 0.333 \cdot \text{DBH})}]$, ($n=500$; $P < .01$); where \underline{Y} is the probability of crown survival.

Growth during the "height-growth" phase of the life cycle is also variable. On the Wade Tract, the majority of individuals in clumps grow slowly, but there are some trees in most clumps that elongate rapidly, over a meter per year (Fig. 1). As a result of such differential growth, clumps of juveniles become divided into eventual "winners" and "losers." The latter appear to be especially sensitive to competition with neighboring trees (see Platt and Rathbun, 1993). Juveniles are more vulnerable to fire during this elongation stage, but the critical factor for survival is the intensity of the burn (Mattoon 1922; Bruce and Bickford 1950; Bruce 1951; Williamson, unpublished). In areas that are annually or biennially burned, low intensity fires appear to have little effect on survival or growth of longleaf pine (Platt et al. 1991, Streg et al. 1993). The timing of fires also may be important for juvenile growth. Spring fires have been reported to stimulate elongation (Grelen 1983). Data from the Wade Tract, which has been burned biennially in

the spring, indicate that not all juveniles in a cohort respond to repeated low-intensity spring fires with stem elongation (Fig. 1).

In contrast, turkey oaks rarely reach maturity with fires occurring more than once a decade (Fig. 4B). However, given the same mean return interval, the likelihood that turkey oaks will reach a "survivable size" increases as the variance between fires increases. Given long-term averages in mean fire frequency and variance, turkey oaks should be favored by increased variance in fire frequency until long fire-free intervals lead to competition by less pyrophilic species, or eventual fires become too severe for any turkey oaks to survive (Fig. 4B). If at any stage turkey oaks are top-killed by fire, they may resprout, unlike longleaf pine. Hence, they may persist vegetatively until longer fire-free intervals allow maturation. Sprout clumps have high resprouting rates (>90%) even after eight annual spring burns (Rebertus et al. 1989a), and oaks forming extensive clones (e.g., *Quercus geminata*) also vigorously resprout and may be able to maintain themselves indefinitely when fires are too frequent for maturation. Large underground stems may accumulate reserves that enable oaks to produce stems that reproduce sexually in the longer intervals between fires. Mast production by turkey oaks

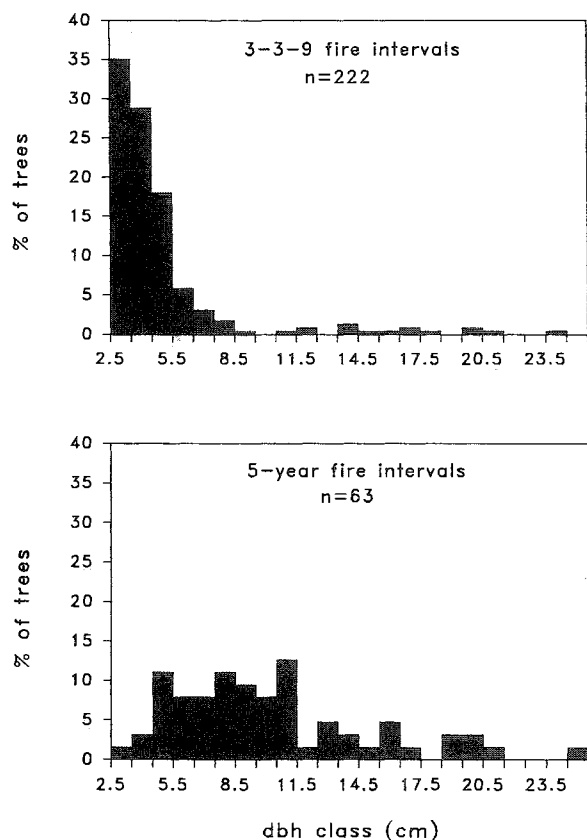


Figure 5. Comparison of diameter-class distributions of turkey oaks in plots burned at 3-3-9 and 5-year intervals (see text for further explanation).

and sand post oaks (*Q. margaretta*) on the Wade Tract occurs only in areas that have not burned for at least eight years. The presence in longleaf pine savannas of oak species that have essentially abandoned the tree form of growth (i.e., the "runner oaks" *Q. pumila* and *Q. minima*) further suggests that there may be a range of adaptations within this genus for inhabitation of areas that burn at different frequencies.

We have some experimental evidence that turkey oaks are favored by increased variance in fire frequency. At the University of South Florida Ecological Study Area, a 0.34-ha plot burned four times (one cycle) on a 3-3-9 (years between fires) schedule has 570 turkey oaks >2.5 cm dbh per hectare, compared to 120 per hectare for an adjacent 0.37-ha plot burned three times at 5-year intervals. All fires were in late spring (May-June), except the first fire in the 3-3-9, which was a January wildfire. Initial oak densities in these plots are unknown, but the current densities of trees and clumps of sprouts combined are very similar (ca. 2900/ha), probably a reflection of past tree densities. The diameter-class distributions illustrated in Fig. 5 are even more revealing. Eighty-two percent of the trees in the 3-3-9 plot are in the 2.5-5.5 cm dbh-class, which are trees that had elongated just enough in the 9-year fire-free period to survive the next fire; whereas, only 16% of the trees in the 5-year plot are in the 2.5-5.5 cm dbh-class. In the 3-3-9 plot, crown mortality in the intense 9-year fire was 55.6% (n=500), including 67% crown mortality (n=242) in the 2.5-3.5 cm dbh-class. Nevertheless, a significant spurt of recruitment followed the 9-year fire interval. This was not observed after any of the shorter-interval fires in either plot. A long-term study is needed to confirm these preliminary results.

Regardless of the tendency for pines or oaks to be aspect dominants in sandhill habitat, both are potentially long-lived. This longevity may result in persistence of individuals of each species until spatially and temporally limited regeneration opportunities occur. Genetic individuals of both longleaf pines and turkey oaks may persist for centuries, reproducing successfully at rare intervals, depending on the nature of the disturbance regimes.

VARIATION IN SEASONAL OCCURRENCE OF FIRE

When fires occur frequently, variation in the season at which fire occurs might influence growth

and survival of longleaf pines and oaks. Survival and growth of longleaf pines and oaks located within 1-ha study plots in sandhill and flatwoods habitats on the St. Marks National Wildlife Refuge (Wakulla County, Florida) were measured over the period from 1981-1988. Trees in plots burned at eight different times of the year (every six weeks beginning in the first two weeks in November) and at two different frequencies (annual, biennial) were mapped, tagged, and measured (dbh) in 1981 and then resampled after three (biennial) or six (annual) fires. Descriptions of habitats and the long-term experimental design are presented in Platt et al. (1988a, 1991) and Streng et al. (1993).

Variation in fire regime characteristics had little impact on the demography of longleaf pine. There were almost no effects of season of burn on the survival and growth of longleaf pines in either sandhills or flatwoods habitats (Platt et al. 1991, Streng et al. 1993). There also were no direct effects of annual or biennial fires on growth and survival of longleaf pine (Streng et al. 1993).

Variation in fire regime characteristics produced one striking effect on the demography of oaks. Although top-kill was greater for oaks than pines under both 1 and 2-year frequencies and all seasons of burn, varying the season of burn produced large differences in the survival of oaks. The top-kill of oaks was about twice as great in plots burned during the early growing season compared to plots burned at other times of the year (Platt et al. 1991, Streng et al. 1993). This increased top-kill was evident in all size classes of oaks (Streng et al. 1993). Because resprouting following fire decreased as oak size increased, the increased top-kill of oaks in spring-burned plots resulted in increased oak mortality (Streng et al. 1993). Also, no effects of small variations in fire frequency on survival of oaks were noted (Streng et al. 1993).

At the same time that the effects of season of burn were assessed, the effects of differences in maximum fire temperature were examined. Initial results indicated no significant effects of variation in maximum fire temperatures on survival of either pines or oaks, indicating that the seasonal timing was more important than fire intensity or small-scale variations in frequent fires (Platt et al. 1991).

Data from the St. Marks fire plots, where the variations in the characteristics of frequently occurring fires have been controlled, support the hypothesis that pines are favored over oaks when fires occur frequently. In addition, pines are especially

favored by a regime of frequent early growing season fires, such as would result during the transition from long dry periods that occur commonly during the spring to daily thunderstorms that characterize southeastern coastal plain summers (Chen and Gerber 1990). Thus frequent, early growing season lightning-initiated fires, such as those documented by Komarek (1964) for northern Florida, are likely to produce open pine savannas in which the oaks are restricted to sites that burn less frequently. The extent to which increases in intervals between successive fires, especially at different seasons of burn, might change relative survival and growth of oaks and pines, remains to be determined. In addition, the role of fire intensity at all seasons and frequencies has not yet been explored sufficiently to determine if there are differences in responses of trees (especially the oaks).

INTERACTION OF SPATIAL AND TEMPORAL VARIATION

Although the emphasis in this paper has been on temporal variation in fire, there is an obvious link between temporal and spatial variation in disturbance (Pickett and White 1985). Prior to European settlement, upland habitats in the Southeast often were interconnected; hence fire frequencies may have been higher than at the current time. After settlement, fragmentation of the landscape resulted in smaller fires, and a more heterogeneous fuel mosaic probably occurred as a result of different patterns of land use. This increased spatial variability, coupled with variation in patterns of anthropogenic ignitions, almost certainly has resulted in less periodic fires, both over the entire landscape and within any single site (see Christensen 1981).

Oaks and juvenile pines are more likely to survive fires if they are located away from the pyrogenic influence of large pines (Williamson and Black 1981, Platt et al. 1988b, Rebertus et al. 1989b, Platt et al. 1991). In these small patches, trees may have sufficient time to reach a size such that they can survive subsequent fires. We note, however, that the location of these patches changes with the characteristics of fire regimes. For example, switching from February-March fires to May-June fires on the Wade Tract has changed the locations of patches that do not burn regularly (W.J. Platt, personal observation). When the Wade Tract was burned in the late winter, patches in open areas in the sandy upland ridge tops sometimes did not burn, creating sites where tree seedlings and/or hardwood resprouts survived. The shift to early

growing season fires, however, stimulated the growth of wiregrass (*Aristida stricta*) and these ridge sites tended to burn more frequently. Other sites that previously burned regularly, such as seepage areas and along lower slopes, then began to escape the early growing season fires. These observations suggest that in presettlement habitats, fire regimes variable with respect to both fire frequency and seasonal timing might have produced spatio-temporal mosaics that favored the survival of small patches of hardwoods.

CONCLUSIONS

The data available at the current time can be used to construct a general hypothesis relating the relative abundance of longleaf pine and oaks to spatio-temporal variations that occur in fire regimes. In upland habitats of the southeastern coastal plain, both longleaf pine and oaks are dependent on frequent fires at least once a decade. Within that timespan, as the periodicity of fire increases and as recurrent early growing season fires started by lightning become more common, the importance of longleaf pine increases relative to oaks. The greater the variance in the fire regime, both within seasons and among years within decades, whether caused by the erratic nature of lightning, or by anthropogenic manipulations, the greater will be the importance of oaks relative to longleaf pine.

We hope the ideas presented here will serve as a framework for more detailed, and possibly long-term experimentation that will include one or more components of spatial and temporal fire variabil-

ity. Prescribed burning at regular intervals has been fine-tuned on managed lands in the South to produce desirable effects, yet the natural fire regime undoubtedly was more variable. At the other extreme, we are increasingly faced with the unknown effects of highly erratic, accidental, or poorly planned fires on the biota now present in many southeastern sandhill landscapes. Recently, Robbins and Myers (1989) proposed a burning schedule for natural areas in Florida that is based on weighted fire return-intervals between 1 and 10 years, the hypothesized range of natural variation. In terms of enhancing biodiversity, this may be an improvement over artificially uniform schedules, but probably still is insufficient for management of natural areas because we lack basic information regarding the effects of natural variability in the fire regime on sandhill habitats.

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LITERATURE CITED

- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University of Chicago Press, Chicago, Illinois.
- Boyer, W. D. 1974. Impact of prescribed fires on mortality of released and unreleased longleaf pine seedlings. U.S.D.A. Forest Service Research Note SO-182.
- Bruce, D. 1951. Fire, site, and longleaf height growth. *Journal of Forestry* 52:442-443.
- Bruce, D. 1958. Effect of low competition on longleaf pine seedling growth. Pages 151-153 in *Proceedings of the Society of American Foresters, 1958*, Salt Lake City, Utah.
- Bruce, D., and C. A. Bickford. 1950. Use of fire in natural regeneration of longleaf pine. *Journal of Forestry* 48:114-117.
- Chapman, H. H. 1947. Results of a prescribed fire at Urania, La., on longleaf pine land. *Journal of Forestry* 45:121-123.
- Chen, E., and J. F. Gerber. 1990. Climate. Pages 11-34 in R. Myers and J. Ewel, eds. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida.
- Christensen, N. L. 1981. Fire regimes in southeastern ecosystems. Pages 112-136 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. A. Lotan, and W. A. Reiners, eds. *Fire regimes and ecosystem properties*. U.S.D.A. Forest Service General Technical Report WO-26.
- Crocker, T. C. Jr., and W. D. Boyer. 1975. Regenerating longleaf pine naturally. U.S.D.A. Forest Service Research Paper SO-105.
- Crossley, D. I. 1956. Fruiting habits of lodgepole pine. Canadian Department of Northern Affairs and Natural Resources, Forest Service Research Division Technical Note 35.
- Grelen, H. E. 1983. May burning favors survival and early height growth of longleaf pine seedlings. *Southern Journal of Applied Forestry* 7:16-20.
- Harcombe, P. A., J. S. Glitzenstein, R. G. Knox, S. L. Orzell, and E. L. Bridges. 1993. Vegetation of the longleaf pine region of the west Gulf coastal plain. (this volume).
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329-382.
- Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. *Ecology* 20:287-304.
- Huberman, M. A. 1940. Normal growth and development of southern pine seedlings in the nursery. *Ecology* 21:323-334.
- Kalisz, P. J. 1982. *The longleaf pine islands of the Ocala National Forest*. Doctoral dissertation, University of Florida, Gainesville, Florida.
- 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. A. Lotan, and W. A. Reiners, eds. *Fire regimes and ecosystem properties*. U.S.D.A. Forest Service General Technical Report WO-26.
- Komarek, E. V., Sr. 1964. The natural history of lightning. Pages 139-183 in *Proceedings of the Third Annual Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, Florida.
- Laessle, A. M. 1968. Relationships of sand pine scrub to former shore lines. *Quarterly Journal of the Florida Academy of Science* 30:269-286.
- Lamont, B. B., D. C. LeMaitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. *Botanical Review* 57:277-317.
- Mattoon, W. R. 1922. Longleaf pine. U.S.D.A. Bulletin 1061.
- Monk, C. D. 1960. A preliminary study on the relationships between the vegetation of a mesic hammock community and a sandhill community. *Quarterly Journal of the Florida Academy of Sciences* 23:1-12.
- Monk, C. D. 1968. Successional and environmental relationships of the forest vegetation of north central Florida. *American Midland Naturalist* 79:441-457.

- 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.
- Myers, R. L. 1990. Scrub and high pine. Pages 150-193 in R. Myers and J. Ewel, eds. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida.
- 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.
- Noble, I. R. 1981. Predicting successional change. Pages 278-300 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. A. Lotan, and W. A. Reiners, eds. *Fire regimes and ecosystem properties*. U.S.D.A. Forest Service General Technical Report WO-26.
- Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional change in plant communities subject to recurrent disturbances. *Vegetatio* 43:5-21.
- Ogden, J. 1985. An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany* 23:751-772.
- Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: a synthesis. Pages 371-384 in S. T. A. Pickett and P. S. White, eds. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando.
- Platt, W. J., and M. W. Schwartz. 1990. Temperate Hardwood Forests. Pages 194-229 in R. Myers and J. Ewel, eds. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Florida.
- Platt, W. J., and S. L. Rathbun. 1993. Population dynamics of longleaf pine (*Pinus palustris* Mill.). (this volume).
- 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. J. 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. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. Pages 143-161 in *Proceedings of the 17th Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, Florida.
- Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989a. Longleaf pine pyrogenicity and turkey oak mortality in Florida xeric sandhills. *Ecology* 70:60-70.
- Rebertus, A. J., G. B. Williamson, and E. B. Moser. 1989b. Fire-induced changes in *Quercus laevis* spatial pattern in Florida sandhills. *Journal of Ecology* 77:638-650.
- Robbins, L. E., and R. L. Myers. 1989. Seasonal effects of prescribed burning in Florida: a review. Report to Nongame Wildlife Program of Florida Game and Freshwater Fish Commission. The Nature Conservancy Fire Management and Research Program, Tallahassee, Florida.
- Romme, W. 1980. Fire history terminology: report of the ad hoc committee. Pages 135-137 in M. A. Stokes and J. H. Dietrich, technical coordinators. *Proceedings of the fire history workshop, October 20-24, Tucson, Arizona*. U.S.D.A. Forest Service General Technical Report RM-81.
- Snedaker, S. C. 1963. Some aspects of the ecology of the Florida sandhills. Masters thesis, University of Florida, Gainesville, Florida.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Streng, D. R., J. S. Glitzenstein, and W. J. Platt. 1993. Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. (this volume).
- Streng, D. R., and P. A. Harcombe. 1982. Why don't east Texas savannas grow up to be forest? *American Midland Naturalist* 108:278-294.
- Sutton, R. F. 1979. Young planted jack pine as a seed source for supplementary natural regeneration. *Forestry Chronicle* 55:198-199.
- Veno, P. A. 1976. Successional relationships of five Florida plant communities. *Ecology* 57:498-508.

- Wahlenberg, W. G. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth and management. Charles Lathrup Pack Forestry Foundation, Washington, D.C..
- Whelan, R. J., and R. M. Muston. 1991. Fire regimes and management in southeastern Australia. Pages 235-258 *in* Proceedings of the 17th Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in* S. T. A. Pickett and P. S. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.
- Williamson, G. B. 1990. Allelopathy, Koch's postulates, and the neck riddle. Pages 143-162 *in* J. B. Grace and D. Tilman, eds. Perspectives on plant competition. Academic Press, New York.
- Williamson, G.B. and E.M. Black. 1981. High temperature of forest fires under pines as a selective advantage over oaks. *Nature (London)* 293:643-644.
- Zedler, P. H. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809-818.

