Effects of fire season on flowering of forbs and shrubs in longleaf pine forests

William J. Platt*, Gregory W. Evans**, and Mary M. Davis***
Tall Timbers Research Station, Route 1, Box 678, Tallahassee, FL 32312, USA and Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA

Summary. Effects of variation in fire season on flowering of forbs and shrubs were studied experimentally in two longleaf pine forest habitats in northern Florida, USA. Large, replicated plots were burned at different times of the year, and flowering on each plot was measured over the twelve months following fire. While fire season had little effect on the number of species flowering during the year following fire, fires during the growing season decreased average flowering duration per species and increased synchronization of peak flowering times within species relative to fires between growing seasons. Fires during the growing season also increased the dominance of fall flowering forbs and delayed peak fall flowering. Differences in flowering resulting from variation in fire season were related to seasonal changes in the morphology of clonal forbs, especially fall-flowering composites. Community level differences in flowering phenologies indicated that timing of fire relative to environmental cues that induced flowering was important in determining flowering synchrony among species within the ground cover of longleaf pine forests. Differences in fire season produced qualitatively similar effects on flowering phenologies in both habitats, indicating plant responses to variation in the timing of fires were not habitat specific.

Key words: Flowering phenology – Fire season – Longleaf pine forests – Synchronization of flowering – Clonal growth

Ground cover vegetation containing large numbers of flowering plants typically is present in habitats in which fires occur frequently. Fire affects flowering in these habitats (e.g. Daubenmire 1968; Vogl 1973; Rowley 1970; Dickson and Dodd 1976; Christensen 1981; Gill 1981b; Gunderson et al. 1983; Whelan 1986). Within species, both the timing of flowering (Curtis and Partch 1950; Gill and Ingwerson 1976; Abrahamson 1984) and numbers of flowering stems produced (Burton 1944; Stone 1951; Kucera and Ehrenreich 1962) change following fire. Effects vary with season of fire (Gill 1981a; Henderson et al. 1983; Lovell et al. 1983; Snyder 1986). While there have been studies of flowering phenologies in fire-dominated habitats (e.g., Parrish and Bazzaz 1979; Anderson and Schelfhout 1980; Tepedino and Stanton 1980; Rabinowitz et al. 1981), the effects of fire upon flowering phenologies of coexisting species have received little attention.

In this study, we experimentally manipulated fire season in longleaf pine forests of northern Florida, USA, and measured characteristics of flowering by forbs and shrubs in the ground cover during the year following fire. We addressed three questions. First, did season of fire affect numbers of species that flowered and/or species-specific characteristics of flowering (i.e., numbers of flowering stems per species or the duration of flowering per species)? Second, were effects of fire season on flowering similar in different habitats within longleaf pine forests? Third, did changing the season of fire alter characteristics of flowering by the flora in the ground cover of longleaf pine forests (i.e., the evenness and synchronization of flowering among species, or the timing of peak flowering)?

Methods

Study area. This study was conducted in second growth longleaf pine (Pinus palustris) forests in the St. Marks National Wildlife Refuge, Wakulla County, Florida. Old river bars and stream channels, once part of an old (Pleistocene) delta of the Ochlockonee River, constitute two distinct habitats that represent extremes of a local moisture gradient within the study area. Sandhills (old river bars) are xeric and are located on deep, well drained, layered sands. In contrast, flatwoods (old stream channels) are located on shallow layers of sand and clay above limerock. The water table is usually just below the soil surface, and lowest areas may be seasonally inundated. Within each habitat, the topography is generally flat, with slight slopes toward drainages.

Although the entire refuge was timbered in the early 1900s, the presence of ground cover species typical of old-growth longleaf forests that have not been cleared and plowed (see Wells and Shunk 1931; Hebb 1957) indicates human disturbance of the soil has been minimal. Aristida stricta dominates the ground cover in both habitats. A number of other species of grasses, as well as numerous forbs and shrubs, are present in the ground cover of both sandhills and flatwoods. Vegetation is more dense in the latter habitat (Davis 1985). Virtually all species in the
ground cover are long-lived perennials that resprout following fire.

The ground cover of longleaf pine forests burns frequently (every 1–5 yrs) as a result of lightning strikes (Chapman 1932a, b, 1950; Christensen 1981) igniting pyrogenic vegetation (Platt et al. 1988). Prior to European settlement, fires occurred mainly between April and October (Komarek 1964, 1974). Settlers also burned the pine forests frequently, but altered the natural fire regime by burning between growing seasons. Over the past 30 years prescribed burning by the refuge staff has occurred 2–3 times a decade, mostly during the winter.

**Experimental design.** In 1980, seventeen 2–5 ha plots were established in both sandhill and flatwoods habitats within a 10 square kilometer area of the Panacea unit of the refuge. Plots were selected that had similar densities of *P. palustris, A. stricta,* and *Quercus sp.* To reduce edge effects, sampling was restricted to a one hectare area centered within each plot. In the sandhills, large oaks that had entered the overstory as a result of fire suppression after logging earlier in the century were cut at the base of the tree during the winter of 1980–1981. Most of these trees resprouted, forming shrubs in the ground cover. A pretreatment burn was applied to all plots in the winter of 1980–1981 to establish similar times since the last burn for all plots.

The design of the study involved two treatments. Season of burn (eight different times during the year) and habitat (sandhills and flatwoods) were considered random and fixed effects, respectively. Times of burning were randomly assigned to plots within habitats. Beginning in November, 1981, two plots in each habitat (i.e., replicated experimental units) were burned during each of the following two-week periods: late November, early January, late February, early April, late May, early July, late August, and early October. Within each two-week period, plots were burned on the first day suitable for backfires and stripfires.

True controls do not exist for this study. We note specifically that fire exclusion (e.g., see Lewis and Harshbarger 1976; Towne and Owensby 1984) is not a control for studies of fire regimes anymore than lack of rainfall is a control for variation in precipitation. The absence of fire in pyrogenic habitats is unnatural and fundamentally alters relationships between organisms and their environments (Henselman 1981). Inferences made in this study rely upon comparisons among treatments, the null hypothesis being that variation in fire season had no effect upon flowering of forbs and shrubs in the ground cover during the year following fire. For comparison with other studies, after the pre-treatment burn, one plot in each habitat was left unburned to serve as a reference. Throughout the study, fewer species and fewer individual stems flowered on reference than on burned plots. All species flowering on the reference plots also flowered on at least one burned plot during the year following fire (Davis 1985).

**Flowering phenologies.** In each plot, flowering was censused using a permanent 200 × 2.5 meter (500 m²) transect randomly located except that equivalent portions of each transect occurred under trees and in the open. In this way, microhabitat differences within plots were controlled. In both habitats areas of 30–40 m² were adequate to encounter the majority of species present (Davis 1985).

After experimental treatments began, 45 censuses were made over a two year period from October 27, 1981, to September 25, 1983. Counts of flowering stems of the different species were recorded along each transect at approximately two week intervals. A stem was recorded as flowering if at least one flower had a receptive stigma and/or anthers shedding pollen. Rosettes flowering without stems present were counted as one stem.

Six pre-treatment censuses were made in each plot from August 3 to October 12, 1981. Chi-square goodness of fit tests (Sokal and Rohlf 1969) indicated no significant differences in the average numbers of species flowering per census for the 17 plots in each habitat (Davis 1985). Thus, plots within habitats were considered sufficiently homogeneous experimental units for the experimental design used in this study.

Forbs and those shrubs restricted to the ground cover were included in this study. Nomenclature followed Clewell (1985). Voucher specimens have been placed in herbaria at Tall Timbers Research Station and Florida State University. Trees, which included pines (*P. palustris, P. elliottii, P. serotina*) and seven oaks (*Q. incana, Q. laevis, Q. margaratta, Q. geminata, Q. falcata, Q. hemisphaerica, Q. myrtifolia*) were excluded. Grasses (Gramineae), sedges (Cyperaceae), rushes (Juncaceae), and ferns (i.e., *Pteridium aquilinum*) also were not censused.

**Statistical analyses.** Controlled burns applied as treatments in this study were staggered over a 12 month period (November 1981 to October 1982). We conducted statistical analyses on data collected during the first year following fire on each plot. Therefore, we made inferences regarding the effects of fire only during the first complete growing season following fire. A confounding effect of the study was that, depending on when plots were burned, different portions of the growing seasons of two years (1982 and 1983) were included in the first year following fire. To minimize this confounding effect, we eliminated from further consideration any census in either year for which there was no census on a corresponding date in the other year. Data used in statistical analyses thus were those from a subset of 18 census dates that occurred within the first year following fire. These dates represented a total of 35 different censuses (Table 1).

We used multivariate analysis of variance (MANOVA) to examine effects of habitat and season of burn on total number of species that flowered, total number of stems that flowered, and mean duration of flowering (number of census dates that each species was in flower). Distributions of all three dependent variables were right skewed, and thus data were log transformed for analysis. (These transformations also reduced heterogeneity that resulted from unequal abundances of ubiquitous species among plots within habitats.) Reference plots were not included in these analyses.

The linear combination of the dependent variables which maximally discriminated among treatments was represented by the first discriminant function, and was used to test for significant treatment effects. Correlations between the discriminant function score for each observation and the dependent variables were used to assess the relative importance of the dependent variables in distinguishing among treatments. These correlations are less sensitive to differences in the magnitude and variance of the dependent variables than are discriminant function coefficients (Timm 1975; Morin 1983).