Fire in the Southeastern Grasslands

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INTRODUCTION

There has been more research on the effects of fire in the southeastern United States than in any region of North America. Most studies have been concerned with the effects of fire on the trees, including the role of fire in controlling hardwood succession, fire damage to trees, the effects of fire on soils and litter, the influence of fire on conifer growth and reproduction, and the relationships of fire to tree diseases (Garren 1943; Ahlgren and Ahlgren 1960; Cushwa 1968). A lesser, but still substantial number of studies have been focused on the effects of fire on forage yields and livestock production (Wahlenberg et al. 1939), and the use of fire in wildlife management in the Southeast. But academic or phytosociological studies of the vegetational composition and of the effects of fire on the understory vegetation are generally lacking.

Except for some range and wildlife research and several general studies (Wells and Shunk 1931; Leukel and Stokes 1939; Biswell and Lemon 1943; Burton 1944; Lemon 1949, 1967; Campbell 1955; Biswell 1958; Hodgkins 1958; Arata 1959; Cushwa et al. 1966, 1970; Wolters 1972), most investigators have ignored the herbaceous cover or grassland vegetation under southeastern trees. Even early botanists often became more interested in the unusual botanical features such as the southern extent of Appalachian tree species (Harper 1943, 1952), the description of the silaceous dunes of the

Gulf Coast (Kurz 1942), the habits of eastern red cedar (Harper 1912), the vegetation of the Okefenokee Swamp (Wright and Wright 1932), or why the Black Belt Prairie of Alabama was treeless (Ranking and Davis 1971), thereby neglecting the widespread and common grassland vegetation and its relationship to fire.

This lack of recognition of the grassland understory still exists for most current texts on biology, botany, and ecology emphasize southeast forests, at best, relegating grasslands to old fields or to early stages of forest succession.

HISTORICAL ACCOUNTS

Historical accounts of early explorers, travelers, and botanists show conclusively that most upland areas of the Southeast were occupied by a pine savanna rather than a forest, scattered stately pines occuring on extensive and rich grassland or prairie understories (Fig. 1) that stretched across the level Coastal Plains and the rolling Piedmont hills from the Atlantic to the Gulf of Mexico. On the Coastal Plains or "flatwoods", this grassland understory dominated wet or wet-mesic sites, grading sometimes into open prairies, treeless marshes, and often into a variety of wooded or thicketed swamps, or giving way to dry prairies and pine savannas on the sugar-white sand ridges, old beach lines, and coastal strands. In the Piedmont sections, upland prairies, and savannas dissected by streams or "branches" and hardwood swamps, were common, grading from xeric to mesic sites on the red lateritic soils. Except for locations that were extremely wet or dry, or fluctuated seasonally from wet to dry, sites with atypical soil-parent materials, or unburned "islands" (Harper 1911), the southeastern grassland ground cover was overshadowed by pine trees, whose species, densities, and compositions were determined largely by site conditions, locations, fire histories, and burning regimes. This pine savanna was contiguous with the coastal prairies of Alabama, Louisiana, and Texas, continued beyond the "pineywoods" and Big Thicket of Texas into the tallgrass prairies of the Great Plains, and shared species with the prairies of the Middlewest, the Appalachian balds, and the eastern grassland relics of the Prairie Penninsula.

FIG. 1. Most southeastern uplands were once occupied by pine savannas. The widely-spaced pines allowed adequate light to reach the sun-loving tall-grass prairie plants. This savanna on the Tall Timbers Research Station, Tallahassee, Florida has been maintained by annual winter burning.

Some of the best accounts of the pristine vegetation are to be found in the writings of botanist William Bartram (VanDoren 1940; Harper 1942), who traveled and collected plants extensively in the Southeast in 1773. His frequent references to the upland vegetation generally describe a pine savanna, a lush green grassland understory with a widely-spaced overstory of tall pines. A few quotes that summarize what he recorded follow:

> I rode several miles through a high forest of pines, thinly growing on a level plain, which admitted an ample view, and a free circulation of air, to another swamp: (p. 38—near Darien, Ga.)
>
> Being safely landed on the opposite bank, I mounted my horse, and followed the high road to the ferry on St. Ille, about sixty miles south of Alatamaha, passing through an uninhabited wilderness. The sudden transition from rich cultivated settlements, to

high pine forest, dark and grassy savannas, forms in my opinion no disagreeable contrasts; (p. 42—St. Ille, Ga.)

. . . . . high open forests of stately pines, flowery plains, and extensive green savannas, (p. 43)

First, from the sea coast, fifty miles back, is a level plain, generally of a loose sandy soil, producing spacious high forests, of *Pinus taeda, P. lutea, P. squarrosa, P. echinata,* (p. 50—from Savannah to Augusta, Ga.)

This plain is mostly a forest of the great long-leaved pine (*P. palustris* Linn.) the earth covered with grass, interspersed with an infinite variety of herbaceous plants, and embellished with extensive savannas, (p. 52—from Savannah to Augusta, Ga.)

I was led into a high pine forest; the trees were tall, and generally of the species called Broom-pine (*P. palustris* Linn.) the surface of the ground covered with grass, herbage, and some shrubbery: (p. 71—St. Simon Island, Ga.)

I came to the open forest, consisting of exceedingly tall straight Pines (*Pinus palustris*) that stood at a considerable distance from each other, through which appeared at N.W. an almost unlimited plain of grassy savannas, (p. 146—Six Mile Springs—near Lake George, Fla.)

For the first four or five miles we traveled westward, over a perfectly level plain, which appeared before and on each side of us, as a charming green meadow, thinly planted with low spreading Pine trees (*P. palustris*). The upper stratum of the earth is a fine white crystalline sand, the very surface of which being mixed or incorporated with the ashes of burnt vegetables, renders it of sufficient strength or fertility to clothe itself perfectly with a very great variety of grasses, herbage, and remarkably low shrubs, together with very dwarf species of Palmetto . . . . (p. 153—west of Six Mile Springs, Fla.)

Crossing another large deep creek of St. Juan's, the country is a vast level plain, and the soil good for the distance of four or five miles, though light and sandy, producing a forest of stately pines and laurels, with some other; and a vast profusion of herbage, such as *Rudbeckia, Helianthus, Silphium, Polymnia, Ruellia, Verbena, Rhexia, Convolvulus, Sophora, Glycine, Vitia, Clitoria, Ipomea, Urtica, Salvia graveolens, Viola,* and many more. (p. 160—Fla.)

The extensive Alachua savanna is a level green plain, above fifteen miles over, fifty miles in circumference, and scarcely a tree or bush of any kind to be seen on it. It is encircled with high,

> sloping hills, covered with waving forests . . . . (p. 165—south of Gainesville, Fla.)
>
> Following a hunting path eight or nine miles, through a vast pine forest and grassy savanna, well timbered, the ground covered with a charming carpet of various flowering plants, (p. 180—from St. Augustine to St. Mark's, Fla.)
>
> We next entered a vast forest of the most stately pine trees that can be imagined, planted by nature, at a moderate distance, on a level, grassy plain, enamelled with a variety of flowering shrubs, (p. 191—Capola, Fla.)

Other explorers, travelers, or botanists such as Lawson in 1714, Catesby in 1722, Michaux in 1802, Elliott (1821–24), Lyell in 1849, Long in 1889 (Lotti 1971, Perkins 1971), Nash (1895), Gano (1917), and Harper (1911, 1914, 1962) recorded similar descriptions of the upland vegetation. All of these descriptions are evidence that the original uplands usually supported pine savannas (Fig. 1), and were seldom occupied by closed forests devoid of grassland understories that are presently commonplace over widespread portions of the Southeast.

GRASSLAND COMPOSITION

Although Bartram (VanDoren 1940; Harper 1942) and a few other early botanists were impressed with the richness and diversity of the flora of the pine understories, detailed studies of the floristic composition are lacking for numerous counties, regions, and entire portions of states in the Southeast (R. K. Godfrey, personal communication). In north Florida and south Georgia, for example, only one comprehensive floristic analysis was found (Thorne 1954). Thorne's study covered approximately 5000 mi^2 in extreme southwestern Georgia, encompassing 14 counties and parts of four others, and documents the richness and extensiveness of grassland-prairie species even though much of the area was disturbed by modern man. The families with the largest number of species are those characteristic of grasslands (Curtis 1959), the most important being the Compositae (255 species), Gramineae (194 species), Cyperaceae (164 species), and Leguminosae (106 species). Other families with

more than 20 species that are typical of most North American grasslands include the Scrophulariaceae, Rosaceae, Euphorbiaceae, Labiatae, Umbelliferae, Orchidaceae, Onagraceae, Cruciferae, Ranunculaceae, and Convolvulaceae.

Almost all the genera represented by large numbers of species (Thorne 1954) are also common to grasslands and marshes or wet prairies throughout most of the United States. They include the genera: *Carex* (54 species), *Panicum* (49 species), *Rhynchospora* (34 species), *Cyperus* (22 species), *Eupatorium* (21 species), *Solidago* (21 species), *Aster* (20 species), *Desmodium* (18 species), *Hypericum* (18 species), *Paspalum* (16 species), *Asclepias* (15 species), *Polygala* (14 species), *Xyris* (13 species), *Eragrostis* (12 species), *Euphorbia* (12 species), *Viola* (12 species), *Lespedeza* (11 species), *Verbena* (11 species), *Aristida* (10 species), and *Coreopsis* (10 species).

The ratio of monocotyledons to dicotyledons also reflects the graminoid component of the understory since Thorne's flora contained nearly 500 species of monocots, as compared to approximately 1000 species of dicots.

Obviously, not all the species included in these selected families occur in the understories of pine savannas. As a result, some of Thorne's families were examined by individual species to determine their habitat preferences. Appendix I lists those species that usually occupy open pine forests, pine savannas, forest openings, or marshy areas, species that could have contributed to the original grassland understories, whether they be xeric, mesic, or hydric. Even this limited number of native species still reflects the diversity of these southeastern pine understories (see Appendix I). The Gramineae are represented by 53 species, Cyperaceae by 34, Leguminosae by 43, Labiatae by 11, Scrophulariaceae by 13, and Compositae by 65 species. A large number of these selected species are also characteristic of grasslands in the Middlewest, Great Plains, and elsewhere.

Grassland understories are still present on some southeastern uplands, particularly where management practices have maintained open stands of pines. For example, a 22-acre upland site on Tall Timbers Research Station, located in extreme north Florida, which had been maintained by annual burning supported 161 herbaceous

species, including 32 grasses, 28 legumes, and 33 composites (see Appendix II). There were an additional 18 tree species and 24 woody plants. Of the 203 species present, only one-fourth were woody, with most of the species diversity being contributed by the herbaceous component. This diversity is typical of other areas that have been maintained as savannas, and some sites that have received less disturbance by man in the past contain even richer understories. Ecologists generally believe that species diversity in a plant community tends to provide stability. Therefore, if land managers in the Southeast are trying to insure natural stability in upland vegetation types thereby providing a measure of protection from catastrophes, they might analyse current management practices as they relate to these understories. Such things as fire exclusion, hardwood invasion, underplanting of savannas, high-density tree plantations, site preparations that destroy or disturb the native rootstocks and sod, and monoculture forestry are certainly destructive to these otherwise rich grassland understories and usually result in losses in diversity.

GRASSLAND COMPARISONS

The understory composition is similar throughout the southeast pineywoods, probably differing within the formation more from south to north, or from Coastal Plain to Piedmont sections, than it does from east to west. The north-south differences are augmented, among other things, by a number of sub-tropical floristic elements that are confined to the southern edge of this formation. The vegetation types with the greatest similarities to southeastern savannas are the Big Thicket of east Texas and the Gulf Coast prairies and marshes (Penfound and Hathaway 1938), to the extent that they might even be considered as peripheral parts of the southeastern savannas. The Big Thicket contains most of the species found in the Southeast, along with grassland species usually found farther west. Comparing Gould's (1969) checklist of the Texas Big Thicket with Thorne's (1954) southwestern Georgia floral list, 49 percent or 130 of the 267 grasses found in east Texas also occurred in Georgia. Similarily, 66 of the 122 Big Thicket legumes (54 percent) were also found in Georgia. The Big Thicket vegetation is a transition zone between

the southeastern pineywoods and the tall-grass prairie. Farther north the ecotones between the tall-grass prairie and the eastern deciduous forest also contain a number of southeastern grassland species although the overstory components of these savannas differ completely. The greatest similarities probably occurred over the longest distances along these prairie-forest transitions or savannas, oak openings, and brush prairies in Arkansas, Missouri, Illinois, and Ohio. A number of the understory species found in the deep South occur as far north as Iowa, Wisconsin, Minnesota, and even North Dakota along prairie-forest borders. For example, Crex Meadows Wildlife Area in extreme northwestern Wisconsin (Vogl 1961), an area of brush prairie savanna and marshland, had 54 percent of its genera and 46 percent of its species in common with Thorne's (1954) study in Georgia.

The species richness of the southeastern pine savannas can be ascertained by comparing them to other grasslands. The adjacent Texas Big Thicket, for example, contains as many or more species than comparable areas in the Southeast. A total of 267 species of Gramineae and 122 species of Leguminosae (Gould 1969) were recorded in the east Texas vegetation type, while southwest Georgia contained 194 grasses and 106 legumes (Thorne 1954). But when the grassland flora of the west Texas High Plains, with its lower number of species, is compared with southwestern Georgia, the number of species in common is reduced. The High Plains, by contrast, are represented by only 141 grass and 38 legume species (Gould 1969) despite the presence of short, mid, and tall-grass prairie elements.

The Wisconsin Crex Meadows area supported 220 species in 52 families over roughly 36 mi^2 (Vogl 1961) as compared to 1539 species in 150 families over approximately 5000 mi^2 in southwest Georgia (Thorne 1954). Although these two areas are not directly comparable because of differences in areas, the greater variety found in the Southeast can be demonstrated by comparing Crex Meadows' 24 grasses, 13 legumes, and 50 composites with the 22 acre site at Tall Timbers, Florida (Appendix II) with 32 grasses, 28 legumes, and 33 composites. A final comparison of the prairie flora of Nelson Co., North Dakota, covering about 1000 mi^2 (Dix and Smeins 1967), again illustrates the greater diversity of grassland species in the South-

east, with the North Dakota area supporting 266 species of which approximately 40 were grasses and 15 were legumes as compared to 194 grasses and 106 legumes in southwest Georgia (Thorne 1954).

Although valid and accurate comparisons are difficult to make because of differences in study area sizes, nomenclature, study objectives, and investigators, the above comparisons and the species listed in Appendix I and Appendix II demonstrate that the understory vegetation of the open pinelands or savannas of the Southeast contain floristic elements comparable to that of tall-grass prairies elsewhere. These southern understories are as rich in prairie species, and as diverse in total numbers, if not more diverse, than the prairies of the Great Plains. Proper management of the vegetation of the Southeast will not be accomplished until managers and ecologists recognize that the natural vegetation is a grassland with trees superimposed on it and needs to be managed and utilized accordingly.

SAVANNA MAINTENANCE

Numerous investigators (Nash 1895, Harper 1906, 1911, 1943, 1962, Garren 1943, Ahlgren and Ahlgren 1960, Komarek 1964, 1971, Lotti 1971, Perkins 1971) claimed that most southeastern uplands were once subject to frequent, if not annual, burning as a result of the high incidence of lightning, since fires could spread over large areas without being impeded, and because of the aborigines' widespread use of fire. The effects of this frequent burning on the vegetation have been usually considered in negative ways such as retarding the encroachment of hardwoods on the pinelands and the possible harmful effects on the soils and soil organisms (Garren 1943, Ahlgren and Ahlgren 1960). Only when range and wildlife managers began to verify that frequent and annual burning could increase forage and game were the positive effects considered.

Fire affects the grassland component of southeastern pinelands in a number of ways. Most investigators (Garren 1943, Ahlgren and Ahlgren 1960) agree that fire checks the encroachment or retards the growth of the fire-sensitive hardwoods and other woody species in areas occupied by the more fire-resistant pines (Fig. 2) (Davis 1959). Fire also controls conifer reproductive success and stand

FIG. 2. Repeated fires are needed to maintain southeastern pine savannas. The grassland understory benefits from fire, and the fire-resistant pines are favored over the fire-sensitive hardwoods. The pine savanna in the foreground has been burned annually while the dense thicket of young hardwoods, pines, shrubs, and vines in the background has been without fire for 12 years.

densities. If fire is eliminated, hardwood invasion and replacement usually result in the conversion of open savannas to closed forests as tree sizes and densities increase and shrubs and vines spread. The closing of the canopies results in a reduction in the quantity and quality of sunlight reaching the ground layer, light necessary for the productive existence of the herbaceous plants. As these sunloving grassland species reduce photosynthesis and drop to compensation point and below, the rain of hardwood litter on the forest floor physically blankets and perhaps allelopathically retards the growth and continued existence of the grassland understory (Fig. 3).

Frequent burning in these tall-grass prairie savannas is also necessary to remove the prodigious annual amounts of grassland litter produced with the more than 50 inches (127 cm) of annual precipitation and the long growing seasons. These accumulations physically

FIG. 3. In the absence of surface fire, the grassland understory soon fades and is shaded out, and the ground becomes blanketed with hardwood litter as in the interior of this plot unburned for 12 years.

impair the sustained healthy production and growth of the grassland species. Fires not only remove the choking litter accumulations, but also reduce them to ash whereby it is more readily available for growth (Wolters 1972). Fire increases productivity by stimulating both the above and below-ground growth (Harper 1940, Lemon 1949, Lay 1956, Cushwa et al. 1969), increases seedstalk production of grasses (Biswell and Lemon 1943, Burton 1944, Czuhai and Cushwa 1968), sometimes even initiating it (Parrott 1967), increases flowering in forbs (Lemon 1967), increases certain species like legumes (Hodgkins 1958, Hilmon and Hughes 1965a, Cushwa et al. 1966, Martin and Cushwa 1966, Cushwa et al. 1968, 1970, Cooper 1971), and improves the nutrient content of the grassland species (Halls et al. 1952, 1956, Woods 1959, Duvall 1962, Hilmon and Lewis 1962, Duvall and Whitaker 1964, Hilmon and Hughes 1965b). All

these things are necessary for the maintenance of the grassland understory, for without repeated disturbance by fire the grassland species become decadent, deteriorating until they can no longer compete with the advancing woody plants and trees. In fact, grassland cover in a weakened and shaded condition is conducive to invasion and replacement by woody plants.

To illustrate some of the effects of fire on the understory vegetation, data obtained in 1971 from 24 unburned and 24 burned Tall Timbers fire study plots (Anonymous 1962) are presented. The unburned plots (W16 A,B,C; W20 A,B,C; W25 A,B,C; W35 A,B,C; W50 A,B,C; W50 X,Y; W75 Y; W75 A,B,X; U A,B,C) had not been burned for 12 years, but prior to that had been treated with annual winter fires. The burned stands (W1 A,B,C; W2 A,B,C; W3 A,B,C; W4 A,B,C; W5 A,B,C; W7 A,B,C; W9 A,B,C; W12 A,B,C) had been subjected to controlled winter burns of various frequencies. Each of the 0.5 acre square plots was sampled with two 30 m line-intercepts that were used to measure the ground layer cover to the closest cm. The first line-intercept was placed parallel to the front side of the plot containing the identifying marker or corner post tag. The second line-intercept was placed parallel to the first, along the back side of the plot, and each 30 m line-intercept started 7.62 m (25 ft) inside the plot from each of two of the adjoining plot boundaries or sides.

The burned plots were treated with either annual fires (W1 = 12 fires), or burning every second winter (W2 = 6 fires), every third winter (W3 = 4 fires), every fourth winter (W4 = 3 fires), every fifth winter (W5 = 2 fires), or burning every seventh, ninth, and twelfth winters (W7, W9, W12 = 1 fire each) starting in 1960. Each treatment type was replicated in three plots, and the percent covers obtained from each pair of line-intercepts were averaged for all three plots.

The average percent cover of all grasses for each of three burned or unburned plots are graphically presented in Fig. 4. The average percent cover of the burned grasses ranged from 41.7 percent in the plots burned every other year, for a total of 6 fires, to 1.5 percent cover in plots burned once in 1966. The unburned average percent cover ranged from 3.7 to 12.1 percent, a variation that was related

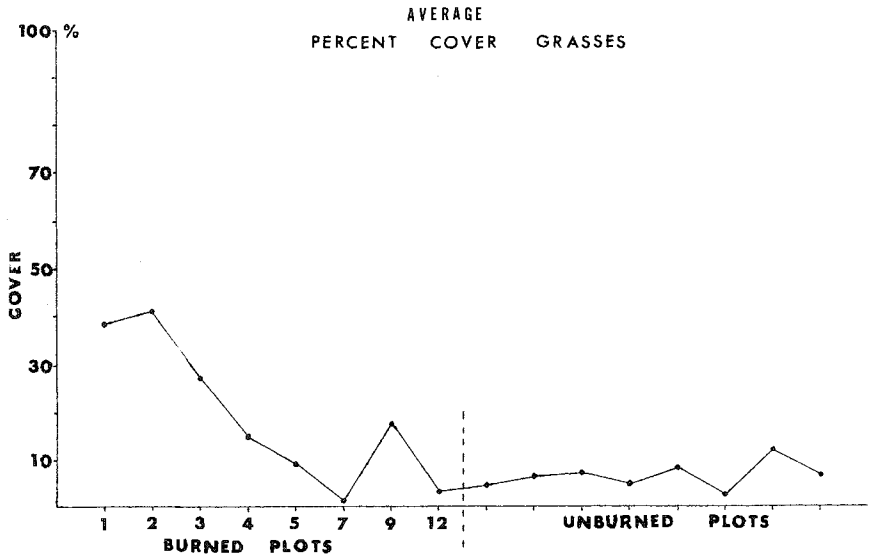

FIG. 4. The average percent cover of grasses (each average obtained from three replicate plots) of eight different burning treatments are compared with the averages of eight sets of plots unburned for 12 years. Each plot was sampled with two 30m line-intercepts. The numbers of the burned plots correspond to their burning frequencies during the past 12 years, thus plots 1 have been burned annually for 12 years, plots 6 have been burned twice, and plots 12 have been burned once during the 12th year.

to the variations in vegetation and topography present in the plots. Annual and biennial burning maintained the highest grass covers, which declined sharply starting with a fire every third year. Plots burned only once in the 12-year study period supported essentially the same low amounts of grass cover as the unburned plots.

Differences in the average percent covers of forbs (herbaceous or non-woody plants excluding the grasses) between the burned and unburned plots were less dramatic (Fig. 5). The burned average percent forb cover ranged from 26.3 percent with annual burning to 2.4 percent with one burn during 7 years. The unburned average forb cover ranged from 1.8 to 13.0 percent. But frequent burning, including once every third winter, maintained denser forb covers than were obtained in any of the unburned plots, again reflecting the favorable response of the understory to repeated burning.

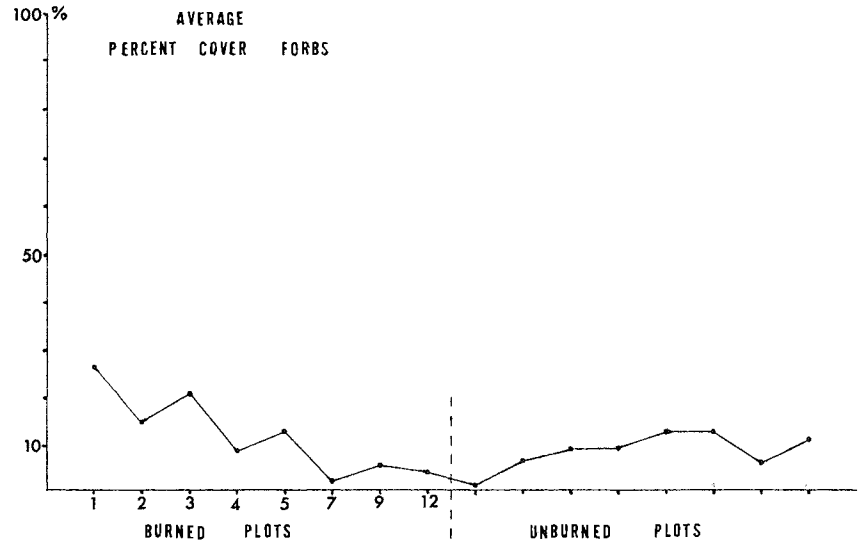

FIG. 5. Average percent cover of forbs in eight sets of burned plots compared with eight sets of plots unburned for 12 years. The forbs included all non-woody herbaceous plants other than grasses.

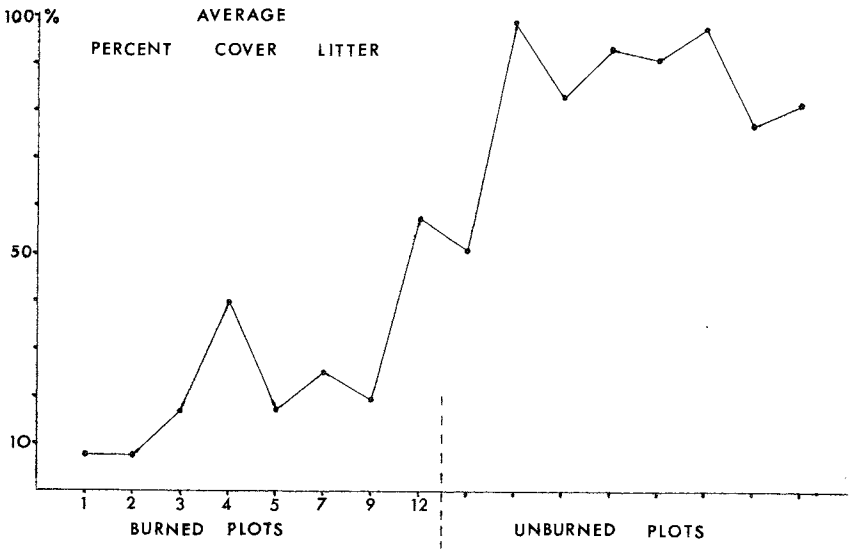

FIG. 6. Average percent cover of litter in eight sets of burned plots compared with eight sets of unburned plots. The litter consisted of all dead but undecomposed plant material on the ground.

Although the forb species' compositions were not recorded, the burned plots were dominated by typical prairie herbs while the unburned plots largely contained shade-tolerant herbs characteristic of hardwood forest.

The average percent cover of litter or dead but undecomposed plant material was much more abundant in the 24 unburned plots than in the 24 burned plots (Fig. 6). In addition, the litter composition differed considerably between the burned and unburned plots, consisting almost entirely of dried grasses, pine needles, and dead forbs in the burned plots as compared with a predominance of oak leaves with lesser amounts of pine needles in the unburned plots. Litter cover averages were the lowest on annually (7.8 percent) and biennially (9.6 percent) burned plots. The litter covered from 50.0 to 98.3 percent of the unburned plots, exclusively dominating large portions of most of these plots.

The responses of the understory grasses, forbs, and litter are interrelated and are, in turn, related to the overstory. Frequent burning maintains a vigorous and healthy grassland understory, and keeps the litter at low levels, decomposing plant accumulations for immediate use by living plants. The fire-stimulated increases in growth, flowers, and seedstalks, which are related to increases in soil nutrients, including nitrogen, provide abundant, continuous, contiguous, and highly flammable fuels necessary for freely spreading and recurring fires. At the same time, repeated fires maintain open overstory canopies, which allow adequate sunlight to reach the understory. Fire also selectively favors the pines over the hardwoods, so that the highly flammable pine needles are the most common form of litter contributed by the overstory (Fig. 7). In the unburned stands the less flammable to nearly non-flammable oak (*Quercus* spp.) leaves soon begin to build up, creating discontinuities in the surface fuels as they form moist mats and smother understory plants. The high densities of hardwood trees that invade the unburned plots or spring up from fire-induced sucker sprouts, which are normally checked by recurring fires, quickly produce a dense shade that not only hampers the continued growth of the sun-loving understory, but also changes moisture and burning conditions of the surface fuels. In addition, the young crowded hardwoods begin to intercept the

FIG. 7. The loosely-arranged, finely-divided, and dried grassland understory, along with fallen pine needles provides continuous fuels readily conducive to the free spread of surface fires.

pine needles falling from the overstory pines that previously fell to the forest floor. This results in part of the fuel load being transferred from the grassland understory to the overstory where it can contribute to crown fires.

When all factors are considered, frequent fire must be included as an intricate part of southeastern pine savannas, for without the continued presence of fire, dramatic changes in the vegetation occur to a point where frequent fires are virtually excluded and the grassland understory ceases to exist. In addition, the pines thrive with repeated surface fires. Harper (1943) stated that ". . . . . coddling the pines by protecting them from fire would be about as shortsighted a policy as moving the Eskimos to a warmer climate to make them more comfortable. Neither would thrive very long in the unaccustomed climate especially if subjected to unrestricted competition."

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APPENDIX I

Selected list of grassland families and species taken from Thorne's (1954) vascular plant list of southwestern Georgia.

Gramineae—Grass Family

Agrostis hyemalis Ticklegrass
Andropogon elliottii
A. gerardi Blue stem
A. hirtiflorus
A. scoparius Little Blue Stem
A. tener
A. ternarius
A. virginicus
Anthaenantia villosa
Aristida lanosa
A. purpurascens
A. stricta
Arundinaria gigantea Giant cane
A. tecta Small cane
Axonopus compressus Carpet grass
Cenchrus echinatus Sandbur
Ctenium aromaticum Toothache grass
Danthonia sericea Oat grass
Elymus virginicus Wild-rye

Eragrostis hirsuta
E. refracta
Erianthus giganteus Giant plume grass
Festuca octoflora Sixweeks Fescue
Glyceria striata Manna grass
Gymnopogon ambiguus
Heteropogon melanocarpus
Hydrochloa caroliniensis Floating-leaf grass
Leersia hexandra
Muhlenbergia expansa
M. torreyana
Panicum aciculare
P. agrostoides
P. anceps
P. commutatum
P. hemitomon Maidencane
P. hians
P. laxiflorum
P. scoparium
P. virgatum Switch grass
Paspalum ciliatifolium
P. floridanum
P. laeve
P. plicatulum
Setaria geniculata
Sorghastrum elliottii
S. nutans Indian grass
S. secundum
Sphenopholis filiformis Wedge grass
Sporobolus junceus
Stipa avenacea Needlegrass
Tridens ambiguus
T. flavus Tall red-top
Uniola sessiliflora

Cyperaceae—Sedge Family

Carex digitalis
C. glaucescens
C. longii
C. striatula
C. styloflexa
C. verrucosa
Cyperus compressus
C. densicaespitosus
C. globulosus
C. haspan
C. pseudovegetus
C. retrofractus
C. retrorsus
C. strigosus
Eleocharis microcarpa
E. obtusa
E. tricostata
E. tuberculosa
Fimbristylis autumnalis
F. drummondii
Fuirena breviseta Umbrella-grass
Lipocarpha maculata
Rhynchospora cephalantha
R. fasicularis
R. fiilifolia
R. globularis
R. glomerata
R. grayii
R. harveyi
R. perplexa
R. plumosa
Scirpus rubricosus
Scleria baldwinii
S. ciliata

Xyridaceae—Yellow-eyed-grass Family

Xyris ambigua
X. caroliniana
X. fimbriata
X. flexuosa
X. jupicae

Commelinaceae—Spiderwort Family

Tradescantia ohiensis

Juncaceae—Rush Family

Juncus biflorus
J. dichotomus
J. effusus
J. elliottii
J. marginatus
J. polycephalus
J. scirpoides

Liliaceae—Lily Family

Aletris aurea
Allium microscordion
Lilium michauxii Turk's-cap-lily
Nothoscordum bivalve False-garlic
Polygonatum biflorum Solomon's-seal
Smilacina racemosa False Solomon's seal
Yucca smalliana Bear-grass

Amaryllidaceae—Amaryllis Family

Agave virginica Rattlesnake-master

Iridaceae—Iris Family

Iris virginica Southern blue flag
Sisyrinchium arenicola

Rosaceae—Rose Family

Agrimonia microcarpa
Amelanchier arborea Shadbush, Juneberry
Crataegus uniflora Dwarf thorn
Fragaria virginiana Wild strawberry
Prunus serotina Wild black cherry
P. umbellata Hog plum, Sloe
Pyrus angustifolius Crab apple
P. arbutifolia Red chokeberry
Rosa carolina Pasture rose
R. palustris Swamp rose
Rubus argutus
R. cuneifolius Sand blackberry
R. trivialis Dewberry

Leguminosae—Legume Family

Amorpha fruticosa Indigobush
Amphicarpa bracteata Hog-peanut
Astragalus intonsus Milk-vetch
Baptisia alba False-indigo
B. lanceolata
B. leucantha
Cassia fasciculata Partridge-pea
C. nictitans Sensitive plant
Centrosema virginianum Butterfly pea
Clitoria mariana Butterfly pea
Crotalaria ovalis
C. purshii
Desmodium canescens Tick trefoil
D. ciliare
D. laevigatum
D. lineatum
D. nudiflorum
D. paniculatum
D. viridiflorum
Erythrina herbacea Cherokee bean, Cardinal spear
Galactia mollis
G. volubilis
Indigofera caroliniana Indigo
Kuhnistera pinnata Summer farewell
Lespedeza capitata
L. repens
L. stuevei
L. virginica
Lupinus villosus
Petalostemum albidus
Phaseolus polystachios Wild bean
Psoralea canescens
Rhynchosia difformis
R. simplicifolia
R. tomentosa
Schrankia microphylla
Sesbania vesicaria Bladder pod
Strophostyles umbellata
Tephrosia ambigua Hoary pea
T. spicata
T. virginiana Goat's-rue, devil's shoestring
Trifolium carolinianum Clover
Zornia bracteata

Geraniaceae—Geranium Family

Geranium carolinianum

Polygalaceae—Milkwort Family

Polygala grandiflora
P. incarnata
P. lutea Bachelor's button
P. nana Bachelor's button
P. polygama
P. ramosa

Euphorbiaceae—Spurge Family

Acalypha gracilens
Cnidoscolus stimulosus Tread softly, spurge-nettle
Croton argyranthemus
C. glandulosa var. *septentrionalis*
Euphorbia corollata
E. maculata Milk-purslane
E. nutans
Stillingia sylvatica Queen's root
Tragia urens

Anacardiaceae—Sumac Family

Rhus copallina Dwarf Sumac
R. glabra Smooth sumac
R. radicans Poison-ivy
R. toxicodendron Poison-oak

Rhamnaceae—Buckthorn Family

Ceanothus americanus Red root, New Jersey-tea
C. microphyllus

Guttiferae—St. John's-wort Family

Ascyrum hypericoides St. Andrew's cross
A. pumilum
Hypericum denticulatum var. *acutifolium*
H. gentianoides Poverty weed
H. mutilum Dwarf St. John's-wort
H. punctatum

Cistaceae—Rockrose Family

Helianthemum carolinianum Rockrose, Frostweed
Lechea patula
L. villosa

Violaceae—Violet Family

Viola lanceolata
V. pedata
V. septemloba

Cactaceae—Cactus Family

Opuntia pollardi Common prickly-pear

Onagraceae—Evening-primrose Family

Gaura filipes
Ludwigia hirtella
L. linearis
L. microcarpa
L. pilosa
L. virgata
Oenothera biennis Evening-primose
O. fruticosa Sundrop
O. laciniata

Asclepiadaceae—Milkweed Family

Asclepias amplexicaulis Milkweed
A. humistrata
A. tuberosa Butterfly weed
A. verticillata

Polemoniaceae—Phlox Family

Phlox floridana
P. glaberrima Smooth phlox
P. pilosa

Labiatae—Mint Family

Dicerandra linearifolia
Hyptis radiata
Lycopus rubellus Bugle weed, Water-hoarhound
Monarda punctata spp. *punctata*
Pycnanthemum flexuosum Mountain mint
P. incanum
Salvia azurea Sage
S. lyrata Lyre-leaved sage
Scutellaria elliptica
S. integrifolia
Trichostema dichotomum

Scrophulariaceae—Figwort Family

Aureolaria virginica
Buchnera floridana Blueheart
Gerardia fasciculata spp. *fasciculata* False-foxglove
G. tenuifolia
Gratiola pilosa
G. ramosa
Linaria canadensis Blue toadflax
L. texana
Lindernia anagallidea False-pimpernel
Mecardonia acuminata
Pedicularis canadensis Woody betony
Penstemon australis Beard tongue
Veronica peregrina Neckweed

Compositae—Composite Family

Ambrosia artemisiifolia Common ragweed
Antennaria plantaginifolia Pussy's-toes
Aster adnatus Aster
A. concolor
A. dumosus
A. lateriflorus
A. pilosus
A. sagittifolius
Balduina uniflora
Berlandiera pumila Greeneyes
Bidens bipinnata Spanish needles
Boltonia diffusa
Chrysopsis gossypina Golden-aster
C. graminifolia
C. mariana
C. nervosa
Cirsium horridulum Yellow thistle
Conyza canadensis
Coreopsis lanceolata
C. major
C. nudata
Elephantopus tomentosus
Erechtites hieracifolia Fireweed
Erigeron strigosus Daisy fleabane
E. vernus
Eupatorium album
E. aromaticum Wild-hoarhound
E. capillifolium Dog-fennel
E. compositifolium Dog-fennel
E. hyssopifolium
E. recurvans
E. rotundifolium False-hoarhound
E. tortifolium
Gaillardia lanceolata Blanket flower, bandana-daisy
Gnaphalium falcatum
G. obtusifolium Rabbit-tobacco

Haplopappus divaricatus
H. tenuifolium Bitterweed
Helianthus angustifolius Sunflower
H. radula
Heterotheca subaxillaris
Hieracium gronovii
Iva microcephala
Krigia virginica
Lactuca canadensis Wild lettuce
Liatris elegans
L. graminifolia var. *elegantula*
L. spicata
L. tenuifolia
Lygodesmia aphylla
Prenanthes serpentaria
Pterocaulon undulatum Black root
Pyrrhopappus carolinianus False-dandelion
Rudbeckia hirta Black-eyed susan
Silphium asteriscus Rosin weed
S. compositum
Solidago altissima
S. bootii
S. microcephala
S. odora
Tetragonotheca helianthoides Pineland-ginseng
Trilisa odoratissima Vanilla plant
Verbesina virginica Frost weed
V. angustifolia
Xanthium strumarium Cocklebur

APPENDIX II

Partial list of species present on a 22-acre upland site on Tall Timbers Research Station, Leon Co., Florida. (List courtesy of R. Komarek and A.F. Clewell)

Gramineae—Grass Family

Andropogon tener
A. ternarius
A. virginicus
Aristida virgata
Digitaria sanguinalis
Eragrostis hirsuta
E. spectabilis
Erianthus coarctatus
E. contortus
E. giganteus
Gymnopogon ambiguus
Heteropogon melanocarpus
Panicum aciculare
P. anceps
P. angustifolium
P. arenicoloides
P. boscii
P. chrysopidifolium
P. lanuginosum
P. oligosanthes
P. ravenelii
P. sphaerocarpon
Paspalum boscianum
P. floridanum
Setaria geniculata
Sorghastrum elliotii
S. nutans
Sphenopholis filiformis
S. obtusata
Sporobolus junceus
Tridens flavus
Tripsacum dactyloides

Leguminosae—Legume Family

Baptisia leucantha
Cassia fasciculata
C. tora
Centrosema virginianum
Crotalaria ovalis
C. spectabilis
Desmodium ciliare
D. laevigatum
D. lineatum
D. paniculatum
D. tortuosum
D. viridiflorum
Erythrina herbacea
Galactia volubilis
Lespedeza angustifolia
L. cuneata
L. hirta
L. procumbens
L. repens
L. striata
L. stuevei
L. virginica
Petalostemum albidus
P. caroliniense
Rhynchosia mollissima

Strophostyles umbellata
Stylosanthes biflora
Tephrosia spicata

Compositae—Composite Family

Ambrosia artemisiifolia
Aster dumosus
A. sagittifolius
Bidens bipinnata
Chrysopsis graminifolia
C. mariana
Conyza canadensis
Elephantopus elatus
Erigeron strigosus
Eupatorium aromaticum
E. capillifolium
E. coelestinum
E. compositifolium
E. hyssopifolium
E. incarnatum
Gnaphalium falcatum
G. obtusifolium
G. peregrinum
Haplopappus divaricatus
Helianthus angustifolius
H. hirsutus
Hieracium gronovii
Lactuca canadensis
Liatris graminifolia
Polymnia uvedalia
Prenanthes autumnalis
Pyrrhopappus carolinianus
Sericocarpus tortifolius
Silphium asteriscus
Solidago altissima
S. nemoralis
S. odora
Vernonia angustifolia

Additional Species

Acalypha gracilens
Agalinis fasciculata
Agave virginica
Arenaria lanuginosa
Asclepias tuberosa
A. variegata
A. verticillata
Aureolaria flava
Buchnera floridana
Bulbostylis ciliatifolia
Carex albolutescens
Chenopodium ambrosioides
Commelina angustifolia
Cnidoscolus stimulosus
Cuscuta campestris
Cyperus plukenettii
C. filiculmis
C. rotundus
Diodia teres
Dyschoriste oblongifolia
Eryngium yuccifolium
Euphorbia corollata
E. maculata
E. nutans
Galium circaezans
G. pilosum
Gentiana villosa
Habenaria quinqueseta
Hedyotis procumbens
Helianthemum carolinianum
Hypericum punctatum
Ipomoea pandurata
Juncus dichotomus
Lechia minor
L. villosa
Lepidium virginicum
Linaria canadensis
Lobelia puberula
Monarda punctata
Monotropa uniflora
Oenothera biennis
O. fruticosa
O. laciniata
Oxalis dillenii
Passiflora incarnata
Penstemon australis
Physalis arenicola
P. virginiana
Piriqueta caroliniana
Plantago virginica
Polygala grandiflora
P. polygama
Polypodium polypodioides
Pteridium aquilinum
Richardia scabra
Ruellia caroliniensis
Rumex hastatulus
Rhynchospora globularis
R. harveyi
Scleria pauciflora
Silene antirrhina
Sisyrinchium arenicola
Specularia biflora
Stillingia sylvatica
Tillandsia usneoides
Tragia urens
Trichostema dichotomum
Verbena canadensis