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THE SIGNIFICANCE OF FIRE IN AN OLIGOTROPHIC FOREST ECOSYSTEM

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Abstract—Past and present climate conditions have interacted with soil development to result in distinctly oligotrophic (nutrient-poor) conditions in many southeastern U. S. Coastal Plain ecosystems. Fire historically has been an important abiotic component in these systems favoring the dominance of plant species which require fire for successful regeneration and growth. This study examined the role of periodic fire in several components of an oligotrophic lower Coastal Plain pine flatwoods ecosystem. Except for some loss of nitrogen (N) from the forest floor, experimental burns had slight effects on nutrient loss from the system. Fires volatilized an average of 24 kilograms N per hectare. Much of this loss is balanced by annual net (precipitation input minus stream flow output) ecosystem increases in N. Fire increased nutrient availability in the soil, an increase which coincided with increases in the biomass and species diversity of the herbaceous layer. Thus, fire is important in maintaining nutrient availability in these nutrient-poor soils. Evidence presented in this study support the idea that pine flatwoods are especially limited by phosphorus (P) and potassium (K) availability and that fire significantly increases available levels of P and K in the soil. Fire is considered here a characteristic property of the ecosystem, one which integrates all hierarchical levels of organization of the system.

INTRODUCTION

General hypotheses concerning the importance or role of fire in ecosystems appear difficult to make, given the great variety of ecosystem types wherein fire occurs at a sufficient frequency to be considered a component of the system. It is a reasonable hypothesis, however, that a predominant role of fire, regardless of ecosystem type, is to increase or maintain the availability of an essential (usually growth-limiting) resource, either energy (sunlight), nutrients, or water. The specific role of fire would be determined by which resource, or combination of resources, is limiting in a particular ecosystem. For example, in tallgrass prairie, which has nutrient-rich soils, but experiences substantial build-up of plant detritus which intercepts both light and water, fire appears to be important in maintaining availability of energy and water, but not nutrients.

The Coastal Plain of the southeastern United States has long been a region of great interest to fire ecologists, as evidenced by earlier reviews by Wells (1942) and Garren (1943), and more recently by Christensen (1981). This is a region wherein past and present climatic factors have influenced soil development in a way that resulted in oligotrophic (nutrient-poor) conditions (Gilliam 1990). Such conditions have, in turn, favored the dominance of plant species, such as pines, which require fire for successful reproduction and growth. These species, adapted to low soil fertility, produce acidic, low-nutrient detritus, thus maintaining oligotrophic conditions, a scheme that represents co-development of biotic and abiotic components of the ecosystem (Jenny 1980).

The main objective of this study was to examine the effects of fire on several components of a pine flatwoods ecosystem of the lower Coastal Plain of South Carolina. These results were used to address the hypothesis that fire, as an integral part of the system, serves a significant function in increasing nutrient availability. A second objective of this study is to look at the specific role of fire at each hierarchical level of organization of the system (ecosystem, community, and population) to address the contention that fire is "incorporated" (sensu O'Neill and others 1986) at the level of the ecosystem.

In addition to the presentation of previously unpublished data, this paper provides a brief synthesis of several aspects of the Santee Watershed Study. These include studies on the effects of fire on water quality (Richter and others 1982, 1984), precipitation chemistry (Richter and others 1983), soil nutrients (Gilliam and Richter 1985, 1988; Gilliam 1990), and effects of fire on herbaceous layer vegetation (Gilliam and Christensen 1986; Gilliam 1988).

MATERIALS AND METHODS

Study Site

The study was carried out on Watershed 77 (WS77) of the Santee Experimental Forest. This forest is within the Francis Marion National Forest in South Carolina, approximately 50 kilometers north-northwest of Charleston (33°N, 80°W). WS77 is 165 hectares in area and is typical of lower Coastal Plain pine flatwoods ecosystems. Topographic relief of this and other first-order watersheds of the region varies by 5.5 meters. Prior to the start of the study, WS77 had not been burned for 40 years.

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WS77 soils are clayey, mixed, thermic, vertic Aquults of the Bayboro, Bethera, Carolina, and Wahee series. Although these soils are of mixed minerologies they are generally derived from old and highly-weathered secondary sediments of an alluvial origin and from montmorillonitic deposits of a marine origin. The soils tend to be extremely acidic, infertile, and low in weatherable minerals (Gilliam 1990). Each of the four series are described as very strongly acidic in reaction to at least 130 centimeters (Hatchell and Henderson 1976).

Vegetation of WS77 is characteristic of Coastal Plain pine flatwoods. The dominant overstory species were pines, loblolly pine (Pinus taeda L.--75 percent of the overstory basal area) and longleaf pine (P. palustris Miller--17 percent). Other canopy species were sweetgum (Liquidambar styraciflua L.--4 percent), black gum (Nyssa sylvatica Marshall--3 percent), and shortleaf pine (P. echinata Miller--2 percent). Dominant shrub species included nearly equal mixtures of wax myrtle (Myrica cerifera L.), gallberry (Ilex glabra (L.) Gray), and lowbush blueberry (Vaccinum tenellum Aiton.). The herb layer was dominated by broom sedge (Andropogon virginicus L.), with switch cane (Arundinaria gigantea (Walter) Muhl.) abundant along seeps and stream channels.

The climate for this region is classified as humid mesothermal (Trewartha 1954), with mild winters and warm, moist summers. Mean monthly minimum temperatures for January and July (extreme months) are 4 and 20°C, respectively, whereas mean monthly maximum temperatures are 12 and 32°C. Seasonal patterns of precipitation, stream flow, and evapotranspiration for WS77 are shown in fig. 1. Precipitation averaged 135 centimeters annually, while stream flow averaged 35 centimeters annually. Precipitation typically exceeded evapotranspiration throughout the year (fig. 1).

Sampling

Precipitation and Stream Flow

Nutrient inputs were estimated from weekly precipitation sampling and chemical analysis. Precipitation was sampled with a network of nine bulk collectors and volume was determined directly using a method described in Thiessen (1911).

Similarly, nutrient outputs were estimated from chemical analysis of weekly stream flow grab samples taken behind the calibrated weir at WS77. Weekly flow volume was calculated from continuous stream height monitoring. Daily flow volume was calculated from these readings by U. S. D. A. Forest Service Computations. All sampling (precipitation and stream flow) was carried out for 6 years.

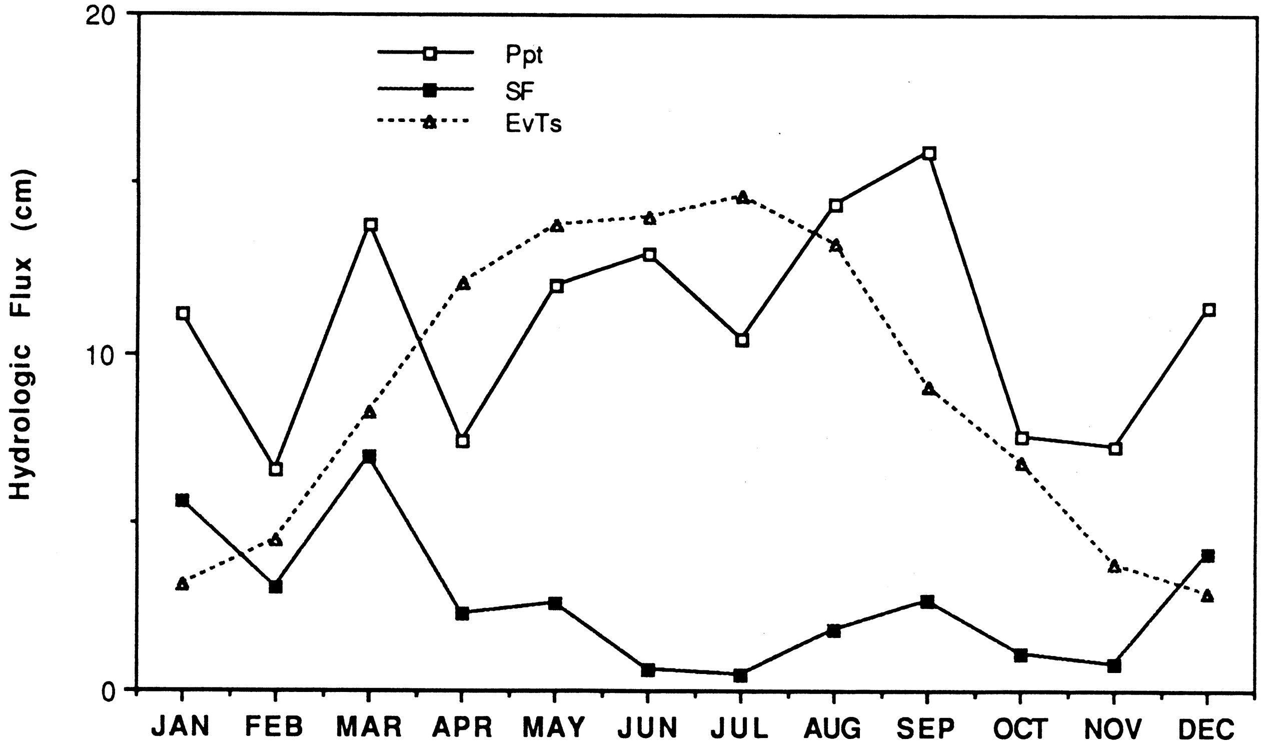

Figure 1.-Mean monthly fluxes of precipitation (Ppt), stream flow (SF), and evapotranspiration (EvTs) for WS77.

Fire Effects

WS77 was divided into 20 compartments of approximately 8 hectares. Fires were administered as summer or winter prescribed fires, largely as backing fires. A total of nine fires administered during this study. See Gilliam and Christensen (1986) for a complete description of compartments and fire treatments. Briefly, nine compartments receiving either winter-only fires, winter and summer fires, or no fire (control) were chosen randomly from the 20 compartments of the watershed.

Effects of fire were estimated from sampling (usually both before and after the fire) within 10 10-meter x 10-meter plots in each compartment. Forest floor and mineral soil were sampled both before and after the burn. Forest floor was sampled with a 14.7-centimeter diameter litter cutter; mineral soil was sampled with a 2.0-centimeter diameter soil corer to a depth of 20 centimeters and cores were divided into 0-5 centimeters, 5-10 centimeters, and 10-20 centimeters depths. Five subsamples taken randomly within each plot were composited for each sample type.

Overstory and shrub layer vegetation were sampled once prior to burning. All stems >0.6 centimeters diameter (at 1.5 meter in height) within each plot were identified and measured, either for diameter (trees) or canopy cover (shrubs).

The herbaceous layer, defined as all vascular plants ≤ 1 meter in height, was sampled in five of the 10 plots in each compartment to determine 1) herb layer cover and biomass, 2) species richness and diversity, and 3) nutrient content. Herb layer cover was estimated non-destructively in two 0.5-meter x 10-meter transects in each of the five sample plots. The transects were subdivided to yield 10 1-square meter subplots. Per cent cover was estimated visually for each species in all subplots. Biomass was estimated by harvesting three separate 50-meter x 0.5-meter transects. These transects were subdivided into 75 0.5-meter x 2-meter subplots.

A separate design was used to determine nutrient concentrations of herb layer vegetation in burned and unburned areas. Ten pairs of sample plots were established in the topographic extremes of WS77, five in upslope areas and five in lowland areas. One plot of each pair was burned and the other was left unburned. Herb layer vegetation was sampled by harvesting all above-ground parts within the two transects as described previously. All herb sampling (cover estimates, biomass harvests, and nutrient analysis harvests) was carried out in the summer.

Analyses

Precipitation and Stream Flow

Precipitation and stream flow were analyzed for pH with a glass electrode. Metal cations (Na^+, K^+, Ca^{++}, Mg^{++}) were determined with atomic absorption spectrophotometry (Isaac and Kerber 1971). Ammonium ($NH4^+$) was determined by isocyanurate colorimetry (Reardon and others 1966), NO_3^- by Cd reduction and azo-dye colorimetry (APHA 1976), PO_4^{3-} by molybdenum blue colorimetry (Mehlich 1953), and $SO_4^=$ by turbidimetry (Schlesinger and others 1982).

Mineral Soil

Samples of mineral soil were air-dried and ground in a hammer mill to pass a 2-millimeter screen. Measured samples of about 10 grams each were extracted with a dilute double-acid solution at a 1:5 soil/solution ratio according to Mehlich (1953), a method established for acid, clay soils. Extractable elements were determined as described above.

Herb Layer Vegetation

Harvested herb layer material was oven-dried and ground in a Wiley mill. Plant tissue was digested using a H_2SO_4-H_2O_2 method (Lowther 1980) and analyzed for Ca, Mg, K, N, and P as described above.

Data Analysis

Fire effects on soil were tested using t-tests to compare pre-burn soil pH and nutrient cation concentrations and those of post-burn soils. T-tests were also used to test the effects of fire on plant tissue nutrient concentrations by comparing burned and unburned means. In each case the level of significance was $p<0.05$. Linear regression analysis was used to generate a model relating herb layer cover to biomass. The level of significance was $p<0.01$ (Zar 1974).

RESULTS AND DISCUSSION

Ecosystem-Level Effects of Fire

Although nutrient budgets are somewhat incomplete in this study, the components studied provide reasonable estimates of total nutrient flux. For example, soil surveys suggest minimal deep seepage loss because of poorly drained throughout WS77 (U.S.D.A. 1980). Denitrification should also be minimal, due to low NO_3^- production in these extremely acidic soils. Finally, N fixation is probably low because of the low frequency of legumes in the forest (Gilliam and Christensen 1986) and because non-symbiotic N fixers are generally rare in acidic forest soils (Alexander 1977). Thus, input/output data may be strongly indicative of the nutrient status of the

Table 1. Input-output budgets for cations in precipitation and stream flow for WS77. Data represent averages from 1976-1982.

Input-Output	H^+	Na^+	K^+	Ca^{++}	Mg^{++}	NH_4^+	NO_3^-	$SO_4^=$	Cl^-	PO_4^{3-}
	keq/ha/yr									
Precipitation	0.54	0.27	0.03	0.26	0.13	0.06	0.12	0.50	0.45	0.01
Stream Flow	0.05	0.49	0.03	0.37	0.22	0.01	0.00	0.51	0.61	0.01
Net (I-O)	+.49	-.22	0	-.11	-.09	+.05	+.12	-.01	-.16	0

ecosystem. Table 1 shows precipitation and stream flow nutrient budgets for the entire 6-year period of the study. Hydrogen ion was greatly conserved by the system, with precipitation H^+ inputs exceeding stream flow outputs by an order of magnitude. Also conserved were $NH4^+$ and NO_3^-. Although such patterns are not conclusive, these data suggest that N, commonly limiting in forest ecosystems, may be a limiting nutrient in this forest.

There were net annual outputs of Na^+, Ca^{++}, Mg^{++}, $SO4^=$, and Cl^- over the study period (table 1). Although many of the soils of this region were derived from highly-weathered sediments of an alluvial origin, net outputs of these ions indicates that, for WS77, further weathering is taking place and that these parent material sediments were largely of a marine origin.

None of the nine fires in the six years of the study had any significant effect on stream flow nutrient output (Richter and others 1982). The main loss of nutrients due to fire was an average volatilization of 24 kilograms N per hectare from the forest floor (Richter, and others 1984). Assuming a fire cycle of 5 to 7 years (Christensen 1981), however, this loss is balanced by annual accumulations of inorganic N (2.4 kilograms per hectare per year--calculated from table 1) and organic N (approximately 2 kilograms per hectare per year--Richter 1980) from precipitation.

Nutrient budgets were balanced for K and P (table 1), suggesting strongly that K and P (in addition to N) may be growth-limiting in these soils. As discussed in Gilliam (1988), this contention is supported further by comparisons of nutrient concentrations in herb layer vegetation from similar and contrasting ecosystems (table 2). Among these sites, including hardwood forests and other conifer forests, K, N, and P concentrations were typically lowest for herb layer vegetation from WS77 (table 2).

Table 2. Herbaceous layer nutrient concentrations for various sites.

Site/Study	K	Ca	Mg	N	P
	%				
Eastern Illinois hardwoods/ Peterson and Rolfe (1982)	3.79	1.17	0.42	2.32	0.36
Northern hardwood forest/ Siccama, and others (1970)	3.18	0.74	0.33	2.38	0.18
Northeast Minnesota/ Grigal and Ohmann (1980)	3.25	2.28	0.50	1.38	0.34
Central New York State/ Bard (1949)	3.01	2.00	----	1.93	0.21
Boreal forest/ Gagnon, and others (1958)	0.51	0.81	0.24	----	0.19
Lower Coastal Plain/ Garten (1978)	0.60	0.85	0.16	----	0.18
Coastal Plain flatwoods/ Gilliam (1988)	0.84	0.77	0.20	1.19	0.06

Nutrient Availability and Uptake

The effect of fire on extractable soil nutrients was minimal and varied with season of burn (table 3). Summer burns seemed to have little influence on soil nutrients, except for a significant decrease in extractable $NH4^+$. For winter burns, however, there were significant increases in pH and extractable K^+, Ca^{++}, and NH_4^+. Although data for extractable P are not shown here, increases in extractable P in these soils in response to fire has been demonstrated (Gilliam 1983). Therefore, there is an indication that fire may increase availability of limiting nutrients.

Gilliam and Christensen (1986) summarized the response of herb layer cover and species richness of WS77 to fire. They sampled nine randomly chosen compartments representing six fire treatments, including winter- and summer-burned compartments and unburned control compartments. They found that only (but not all) winter fires had appreciable effects on the herb layer. Thus, it should be stressed that, depending on the ecosystem component being studied, fire effects may be seasonal and highly variable. Furthermore, such variability itself can have great significance on the level of the ecosystem (Christensen 1981). For the purpose of comparison, specific results for a particular winter fire will be presented in this paper.

Tissue nutrient concentrations for herb layer vegetation were significantly ($p < 0.05$) higher in burned plots than unburned plots for K, N, and P (fig. 2). There were no significant differences for Ca and Mg. This pattern suggests that fire may increase the availability of K, N, and P.

The relationship of herb layer cover and harvested biomass for each species in the three harvest transects is shown in fig. 3. This relationship yielded the equation

$$y = -0.03 + 1.81x \tag{1}$$

where y is herb biomass in grams per square meter and x is herb cover in per cent. The correlation coefficient was 0.94 and was significant at $p < 0.01$. The relationship is based on mean values for individual species. Thus, given the highly significant correlation, equation (1) can be used to estimate biomass for individual species in plots of the burned and unburned compartments. Biomass was summed for all species in each plot to yield total herb layer biomass per plot.

Average cover was significantly ($p < 0.05$) higher in the winter burn plots compared to the control plots (37 percent vs. 16 percent, respectively; table 4). Using equation (1) for each individual species in these plots, this difference translated to a greater than two-fold increase in herb layer above-ground biomass (65 grams per square meter versus 28 grams per square meter).

Table 3. T-test comparisons of pre- vs. post-burn soils at different depths and seasons of burning.

Summer burn

Depth/Treatment	pH	K^+	Ca^{++}	Mg^{++}	NH_4^+
	µeq/g				
0-5 cm/Pre-burn	4.38	0.7	12.2	5.5	1.1
0-5 cm/Post-burn	4.35	0.7	11.0	5.4	0.6*
5-10 cm/Pre-burn	4.48	0.3	6.6	4.1	0.7
5-10 cm/Post-burn	4.48	0.3	6.4	4.0	0.2*
10-20 cm/Pre-burn	4.58	0.2	6.1	4.7	0.4
10-20 cm/Post-burn	4.65	0.2	5.8	4.4	0.1*

* indicates significant difference (p<0.05) between pre- and post-burn means

Winter burn

Depth/Treatment	pH	K^+	Ca^{++}	Mg^{++}	NH_4^+
	µeq/g				
0-5 cm/Pre-burn	4.16	0.9	4.8	2.5	0.7
0-5 cm/Post-burn	4.26*	1.1*	7.3*	3.0	0.9*
5-10 cm/Pre-burn	4.35	0.5	3.4	2.2	0.3
5-10 cm/Post-burn	4.45*	0.5	3.2	1.9	0.4*
10-20 cm/Pre-burn	4.48	0.4	3.6	2.8	0.3
10-20 cm/Post-burn	4.58	0.3	2.6	2.3	0.4*

* indicates significant difference (p<0.05) between pre- and post-burn means

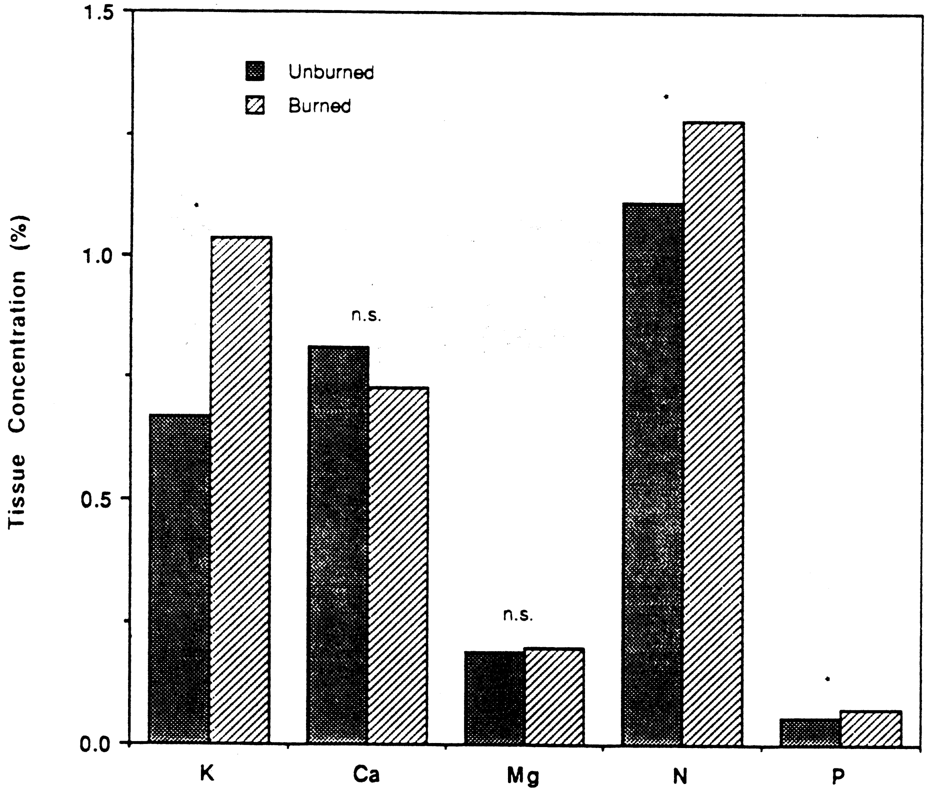

Figure 2.-Nutrient concentrations of burned and unburned plot herb layer vegetation. *Indicates significant difference between burned and unburned treatments at $p<0.05$.

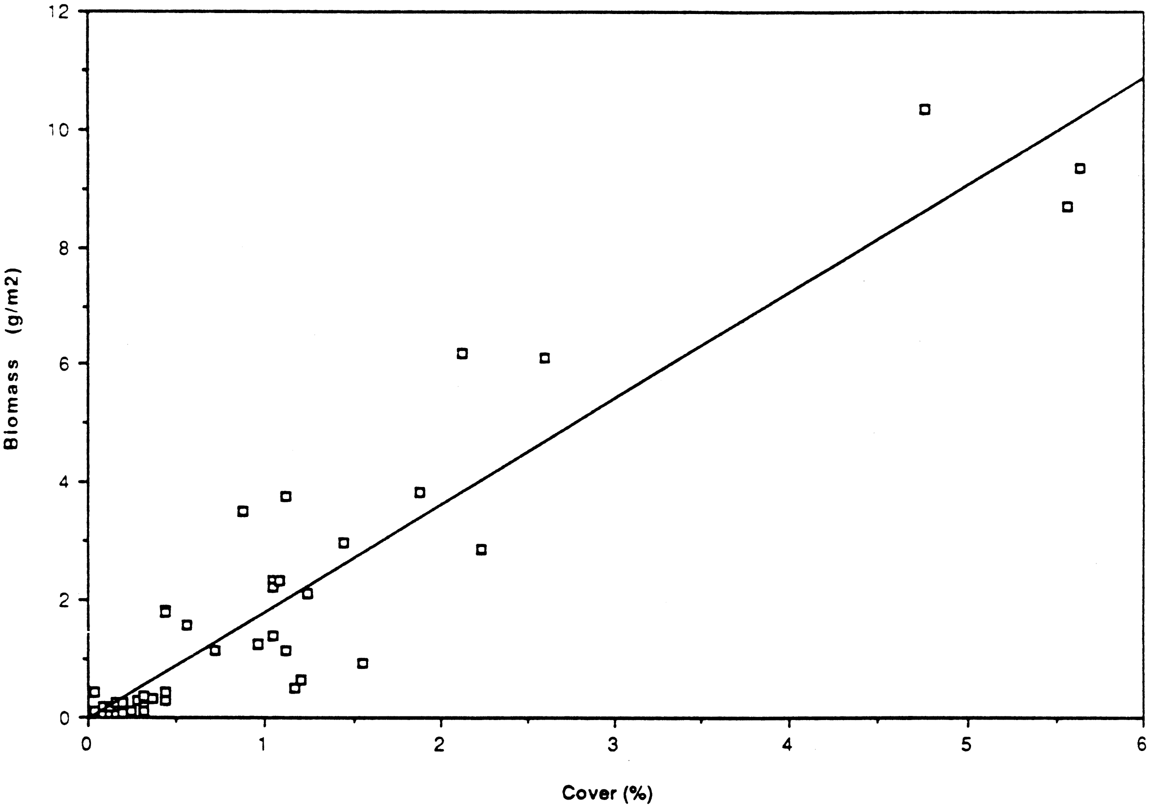

Figure 3.-Relationship of herb cover and harvested herb biomass for WS77. Each point represents average biomass and cover values for individual species. See text for equation.

Table 4. Herbaceous layer cover, biomass, species richness, Shannon-Weiner diversity, and nutrient content for burned and unburned plots of WS77. Error values are one standard error of the mean.

Treatment	Cover (%)	Biomass (g/m^2)	K	Ca	Mg	N	P	Diversity	Richness (spp./plot)
			kg/ha						
Control	16.2±2.7	28.3±4.7	1.9	2.2	0.5	3.1	0.2	1.95±0.15	16.5±2.3
Winter burn	36.7±3.7	65.1±6.3	6.8	5.0	1.3	8.3	0.5	2.50±0.10	29.5±1.9

Herb layer nutrient content was approximated by applying the appropriate nutrient concentration data from fig. 2 to unburned and burned herb layer biomass means in table 4; i.e., "burned" K, N, and P values from fig. 2 were used with "winter burn" biomass from table 4 and "unburned" values in fig. 2 were used with "control" biomass. Since fire did not significantly influence Ca and Mg concentrations, overall mean values from fig. 2 for these nutrients were used with mean biomass values from table 4.

Not surprisingly, using this method, increases in herb layer nutrient content were especially pronounced for K, N, and P. These increases were >3.5-fold, 2.7-fold, and >2.5-fold for K, N, and P, respectively (table 4).

It merits repeating that these degrees of differences, whether for herb cover, biomass, or nutrient content, are not indicative of all fires in this ecosystem, since some fires (especially summer fires) had no appreciable influence on the herb layer. These data, therefor, provide a meaningful comparison representative of the potential effects of fire in this system.

Community-Level Effects of Fire

Although the major emphasis of much of this work has been on ecosystem-level effects of fire, the herbaceous layer is also useful in assessing the effects of fire on the level of the plant community, especially with respect to effects on species diversity and composition. Herb layer species diversity was measured for each plot in winter burn and control compartments as the Shannon-Weiner Diversity Index (H), using the equation

$$H = -\sum_{i=1}^{n} [p_i \cdot \ln(p_i)] \tag{2}$$

where p_i is the decimal fraction of individuals of the ith species and n is the total number of species.

Fire significantly increased species diversity of the herb layer for this particular winter burn (table 4), a response typical for other winter fires of WS77 (Gilliam and Christensen 1986). The value of H reflects both numbers of species present as well as their relative importance, measured here as relative cover. Thus, much of the increase in the diversity index was from a significant increase in species richness, from 17 species per plot in control compartments to 30 species per plot in winter burn compartments (table 4).

In addition to increasing the numbers of species in burned plots, fire altered species composition as well (table 5). Grass species in particular increased in importance in burned areas. Indeed, for the species listed in table 5, fire did not so much alter which species were important as it altered species cover, on both an absolute and a relative basis.

Table 5. Important species for the herbaceous layer in burned and unburned plots of WS77. Nomenclature follows Radford, and others (1968).

Control		Winter burn	
Species	Relative Cover (%)	Species	Relative Cover (%)
Lonicera japonica	16.3	Andropogon virginicus	21.4
Andropogon virginicus	15.2	Liquidambar styraciflua	8.5
Ilex glabra	12.1	Vaccinum tenellum	5.9
Vaccinum tenellum	8.8	Vitis rotundifolia	5.8
Myrica cerifera	7.6	Vaccinium elliottii	5.4
Liquidambar styraciflua	6.5	Rubus betulifolius	5.1
Rubus betulifolius	4.3	Ilex glabra	4.0
Pinus taeda	2.7	Myrica cerifera	3.2
Mitchella repens	2.3	Festuca elatior	2.7
Vitis rotundifolia	2.1	Lonicera japonica	2.7

Population-Level Effects of Fire

Fire will affect populations of plant species differentially, depending on the species' life history characteristics and resource requirements. Many species in southeastern Coastal Plain ecosystem not only respond positively to relatively high fire frequencies, but actually are dependent on fire for successful reproduction and growth. A well-documented example of such a fire-dependent species is longleaf pine. There are excellent accounts of the relationship between fire and longleaf pine, the most recent of which focuses on the importance of fire in several aspects of its population dynamics (Platt and others 1988).

Woody species data for WS77 provides an example of the effects of long-term fire exclusion on longleaf pine, since WS77 had not been burned for approximately 40 year prior to the initiation of the study. Figure 4 is a size class frequency distribution comparing longleaf pine to loblolly pine, which is a much less fire-dependent species. The distribution pattern for loblolly pine is typical of a successfully regenerating species, with high frequencies of small stems and attenuating numbers toward larger size classes. In contrast, the pattern for longleaf pine (e.g., extremely low frequencies of small stems) is indicative of greatly suppressed regeneration. Thus, long-term fire-exclusion and greatly reduced fire frequencies cause sharp declines in longleaf pine populations.

Conclusions

This Coastal Plain pine flatwoods ecosystem is distinctly oligotrophic and fire, as an integral part of the system, serves a significant role in increasing nutrient availability. It is thus notable that P and K typically increase in availability after fire.

The importance of fire on the plant community level was evident in its effects on the herbaceous layer. Although these effects were variable (especially varying with season of burn), fire can cause substantial increases in species diversity, apparently by altering microenvironments and ultimately increasing resource availability.

Fire also plays a vital role in the life history and population dynamics of several plant species in pine flatwoods systems. Data presented here demonstrate the importance of fire in maintaining successful regeneration of the canopy co-dominant species, longleaf pine.

Thus, fire effects appear to be integrated across all hierarchical levels of organization, from the population to the community to the ecosystem. Fire serves significant functions that are both required and unique at each level.

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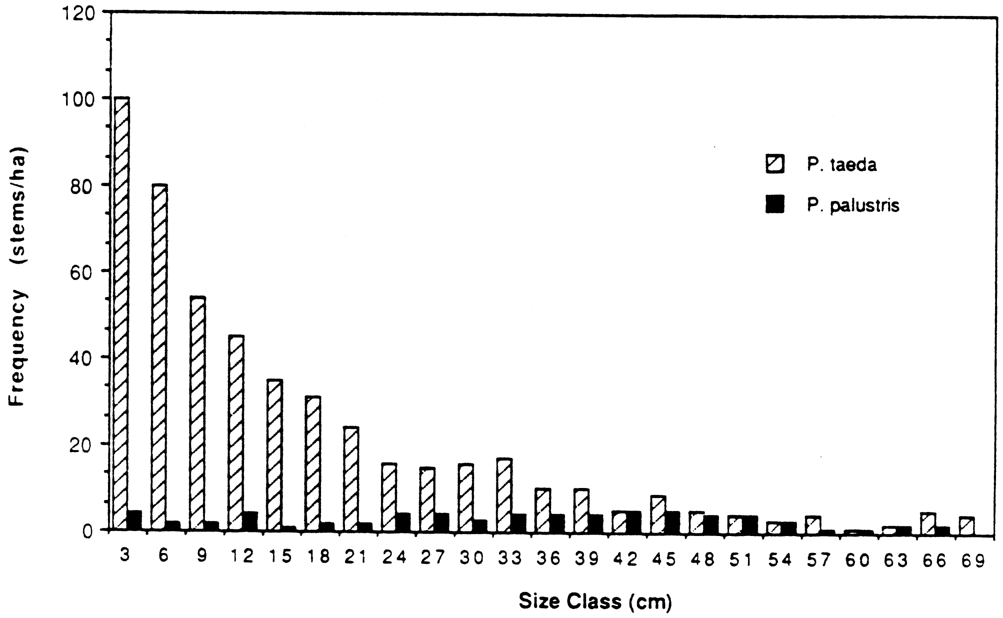

Figure 4.-Size-class distributions for loblolly pine (P. taeda) and longleaf pine (P. palustris) for WS77.

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