Interactions of Fire with Nutrients in the Herbaceous Layer of a Nutrient-Poor Coastal Plain Forest

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ABSTRACT

GILLIAM, F. S. (School of Forestry and Environmental Studies, Duke University, Durham, NC 27706). Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor Coastal Plain forest. Bull. Torrey Bot. Club 115: 265–271. 1988.—Herbaceous layer nutrient relationships and the response to fire were examined in an oligotrophic Coastal Plain flatwoods ecosystem. Herb layer nutrient concentrations for this system were similar to those reported for herb layer plants of other oligotrophic conifer forests, but much lower than those reported for more eutrophic hardwood forests. Nutrient concentrations were similar in herb layer vegetation growing in upland and lowland areas of the study watershed. Nutrients varied in response to burning, with significant increases for K, P, and Mg, decreases for Ca, and no change for N and total ash content. Potassium and P were the only plant nutrients to be correlated significantly (positively) with extractable amounts in the mineral soil. Plant K was positively correlated with plant P, as were Ca:Mg and N:P. Results of this study support the hypothesis that nutrients limit herb layer production under non-fire conditions in these Coastal Plain flatwoods and that post-fire increases in production in these systems are a result of fire-caused increases in nutrient availability.

Key words: plant nutrients, Atlantic Coastal Plain, fire, nutrient limitation.

Nutrient relationships in plants can be influenced by soil factors (e.g., nutrient availability) through an interaction between nutrient requirements of plants and nutrient supply by the soil. For example, Chapin (1980) pointed out that plants adapted to infertile soils exhibit traits, such as slow growth and luxury nutrient consumption, that are quite distinct from plants adapted to soils with high nutrient availability.

Forest vegetation is composed of several strata, such as overstory, understory, and herbaceous layers, which differ with respect to nutrient requirements, life history characteristics, and response to exogenous disturbance. The herb layer, usually defined as vascular plants $\leq 1.0–1.5$ m in height, regulates short-term nutrient flux in many ecosystems (Siccama *et al.* 1970; Peterson and Rolfe 1982). It has been suggested that rapid growth of forest herbs may decrease ecosystem nutrient loss in the early growing season, a time when nutrient availability is high and nutrient uptake by trees is minimal (Muller and Bormann 1976; Blank *et al.* 1980; Peterson and Rolfe 1982).

Ecosystem disturbance usually increases nutrient availability and/or loss, with the amount of increase being proportional to the degree of disturbance and the nutrient status of the system (Vitousek *et al.* 1982; Jordan 1985). Fire in Coastal Plain flatwoods is an example of a periodic disturbance occurring in an oligotrophic (nutrient-poor) ecosystem, and fire-caused increases in nutrient loss are generally slight (Richter *et al.* 1984). Gilliam and Christensen (1986) found that periodic winter fires can significantly increase both cover and species richness of the herb layer in a lower Coastal Plain pine flatwoods in South Carolina. This paper addresses the hypothesis that such post-fire increases are the result of fire-caused nutrient release (Wells *et al.* 1973; Christensen 1977) and examines the nutrient status of herb layer vegetation with respect to soil nutrients and response to fire.

Materials and Methods. STUDY SITE. The study was conducted on Watershed 77 (WS77) of the Santee Experimental Forest, located within the Francis Marion National

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Table 1. pH, organic C, total N and P, and extractable nutrient concentrations for 0–10 cm depth of soils from lowland and upslope sites of WS77. Values in parentheses are one standard error of the mean.

Site	pH_{H_2O}	pH_{KCl}	C (%)	N	P	Ca	Mg	K	N_i[a]	PO_4-P
				μg/cm³						
Lowland	4.49	3.64	3.24	1156	115	230.7	64.6	29.6	5.9	1.9
	(0.04)	(0.03)	(0.27)	(116)	(15)	(38.7)	(8.8)	(1.3)	(0.5)	(0.2)
Upslope	4.42	3.69	2.23	993	90	61.1	16.2	20.5	5.9	2.3
	(0.03)	(0.03)	(0.10)	(125)	(15)	(9.9)	(2.7)	(2.1)	(0.3)	(0.4)

[a] N_i represents the sum of extractable NH_4^+-N and NO_3^--N. N_i was greater than 90% NH_4^+-N in both sites.

Forest in the lower Coastal Plain of South Carolina (33°N, 80°W). WS77 is approximately 160 ha with extremely flat terrain, ranging from about 6.5 m to just over 10 m in elevation. Soils of this region are derived from old, highly-weathered secondary sediments and from montmorillonitic marine deposits. Thus, soils of WS77 tend to be very acidic and low in weatherable minerals (Gilliam 1983). Sample plots for this study were located in two areas differing in topographic position and dominant soil series: 1) Bethera series (clayey, mixed, thermic Typic Paleaquults) in lowland areas along drainages; and 2) Wahee series (clayey, mixed, thermic Aeric Ochraquults) in upslope areas on level ridges (Gilliam and Richter 1985). Soil pH and nutrient concentration data for these series are presented in Table 1. Although these soils occur in areas differing in elevation by only 2–3 m, topographic position strongly influences soil moisture and fertility in low relief watersheds of the region (Gilliam and Richter 1988). The vegetation of WS77 is representative of Coastal Plain pine flatwoods (Christensen 1988). The overstory was dominated by loblolly pine (*Pinus taeda* L., 75% of total overstory basal area), followed by longleaf pine (*P. palustris* Miller, 17%), sweetgum (*Liquidambar styraciflua* L., 4%), and black gum (*Nyssa sylvatica* Marshall, 3%). Dominant shrubs were wax myrtle (*Myrica cerifera* L.), gallberry (*Ilex glabra* (L.) Gray), and lowbush blueberry (*Vaccinium tenellum* Aiton). Broom sedge (*Andropogon virginicus* L.) was the most important herb layer species for WS77 in terms of relative cover (Gilliam and Christensen 1986).

SAMPLING AND ANALYSIS. Five sampling sites were established in each of the two areas—lowland (<7 m elevation) and upslope (>9 m elevation)—following a split-plot design. Each site was comprised of two adjacent 10-m × 10-m sample plots: one burned and one unburned. Approximately 30 ha of the SW corner of WS77 were burned in February 1981, with a backing fire of low to moderate intensity. This fire consumed approximately 1.9 and 2.3 T/ha of forest floor in the lowland and upslope areas, respectively (Gilliam 1983), representing about 10% of the total forest floor in each area, typical of prescribed winter fires for this region (Richter *et al.* 1984). There was little, if any, increase in overstory canopy opening as a result of fire, since it consumed only forest floor materials, herb layer vegetation, and some smaller shrubs and saplings. Unburned plots were effectively protected from the fire by plowed fire lines. Soil sampling and herb layer harvesting were carried out in the summer of 1981.

Mineral soil was taken at two depths (0–5 and 5–10 cm) using a 2-cm sampling tube; organic horizons were discarded (Gilliam and Richter 1985). Five samples were taken in each of the 20 plots and composited into one sample per plot. These were air-dried for about 20 days and then ground in a hammer mill to pass a 2-mm screen. Sub-samples (about 10 g) were extracted with a dilute acid solution (0.05 M HCl plus 0.0125 M H_2SO_4) at a soil/solution ratio of 1:5 (v:v) following Mehlich (1953). Mixtures were shaken 5 min before filtering. Extractable base cations (Ca^{++}, Mg^{++}, K^+) were determined by atomic absorption spectrophotometry (Isaac and Kerber 1971), extractable PO_4^{3-}-P by molybdenum blue colorimetry (Mehlich 1953), extractable NH_4^+-N by isocyanurate colorimetry (Reardon *et al.* 1966), and extractable NO_3^--N by Cd reduction and azo-dye colorimetry (American Public Health Association 1980). Samples were also analyzed for organic C (Graham 1947), Kjeldahl-N (Crooke and

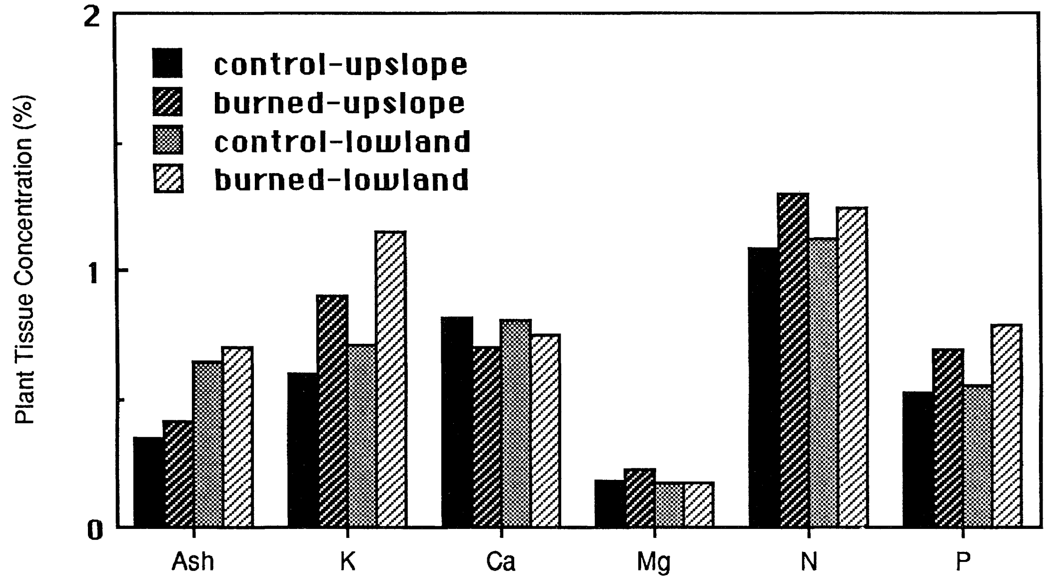

Fig. 1. Ash and nutrient concentrations of burned and unburned herb layer vegetation in upslope and lowland sites. Ash concentrations are 10 times those shown in figure. P concentrations are ¹⁄₁₀ times those shown in figure.

Simpson 1971), and total P (Technicon Industrial Systems 1977).

Herb layer vegetation was sampled by harvesting above-ground parts of all vascular plants ≤1 m in height from two 0.5-m × 10-m transects within each sample plot. Harvested plant material from each plot was composited, oven-dried (70°C), 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, total N, and total P using methods described for soil analysis. Ash content was determined by dry-ashing plant tissue in a muffle furnace at 500°C. Pre- and post-burn herb layer nutrient data were analyzed using paired-sample *t*-tests and differences between upslope and lowland areas were determined with two-tailed, two-sample *t*-tests (Zar 1974).

Results. Nutrient concentrations were similar for unburned herb layer vegetation growing in upslope and lowland areas of WS77 (Fig. 1). Furthermore, except for K, burned herb layer nutrient concentrations were also similar between the two sites. The most conspicuous difference between sites was in tissue ash content, which was significantly higher ($P < 0.05$) for the lowland site.

Nutrients varied in response to burning (Fig. 1). There was a general pattern of increasing concentrations for K, N, and P. However, on the basis of paired *t*-tests (Zar 1974), differences between burned and unburned herb layer concentrations were not significant for N and for P in the upslope site. Neither Ca nor Mg changed significantly in the lowland site, but showed a slight, significant decrease and increase, respectively, in the upslope site. Ash content exhibited little response to fire at either site (Fig. 1). It should be noted that nutrient changes as a result of burning may be confounded as a result of changes in species composition. However, species composition changed only slightly as a result of this fire (Gilliam 1983).

The only plant nutrients that correlated significantly with extractable amounts in mineral soil were K and P. Figure 2 shows the relationship between herb layer K concentrations and extractable K in the top 10 cm of soil for both sites and treatments; similar data for P are presented in Fig. 3. In addition, plant K was highly correlated ($P < 0.01$) with plant P (Table 2). Other highly significant correlations for herb layer nutrients were Ca:Mg and N:P.

Discussion. WS77 is a distinctly oligotrophic ecosystem, typical of the nutrient-

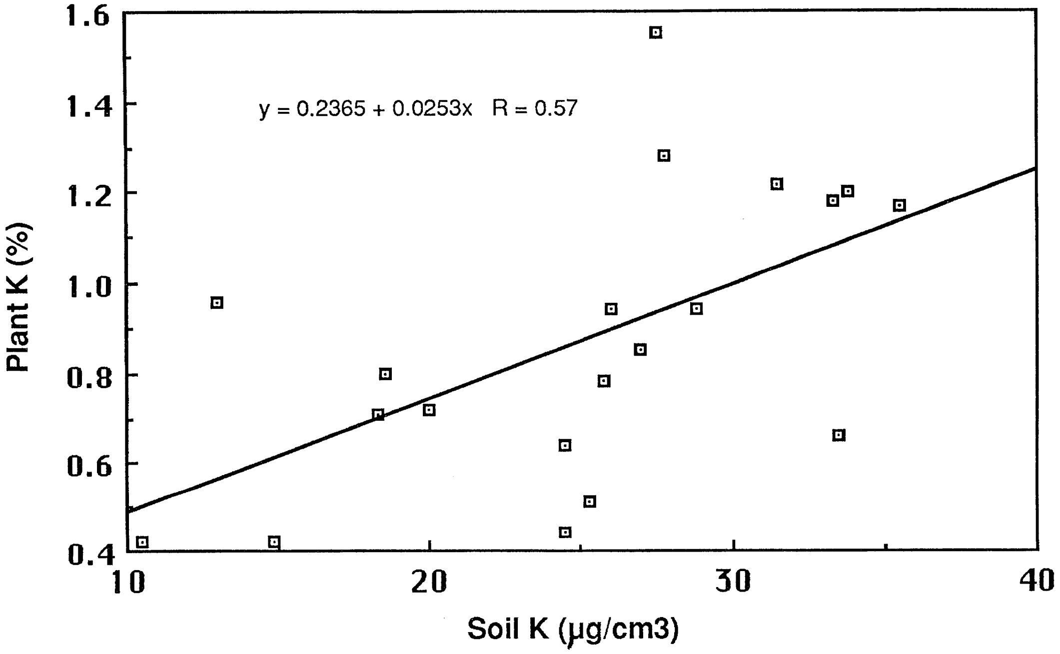

Fig. 2. Relationship of plant K to extractable K in mineral soil.

poor soils of pine flatwoods of the lower Coastal Plain (McKee 1982). Highly weathered secondary parent materials and marine deposits high in montmorillonite clay have resulted in soils which are 1) extremely acidic, 2) low in base saturation, weatherable minerals, and available N and P, and 3) high in clay content (limiting rooting zones) and extractable and exchangeable Al (Tisdale and Nelson 1975; Gilliam 1983; Richter *et*

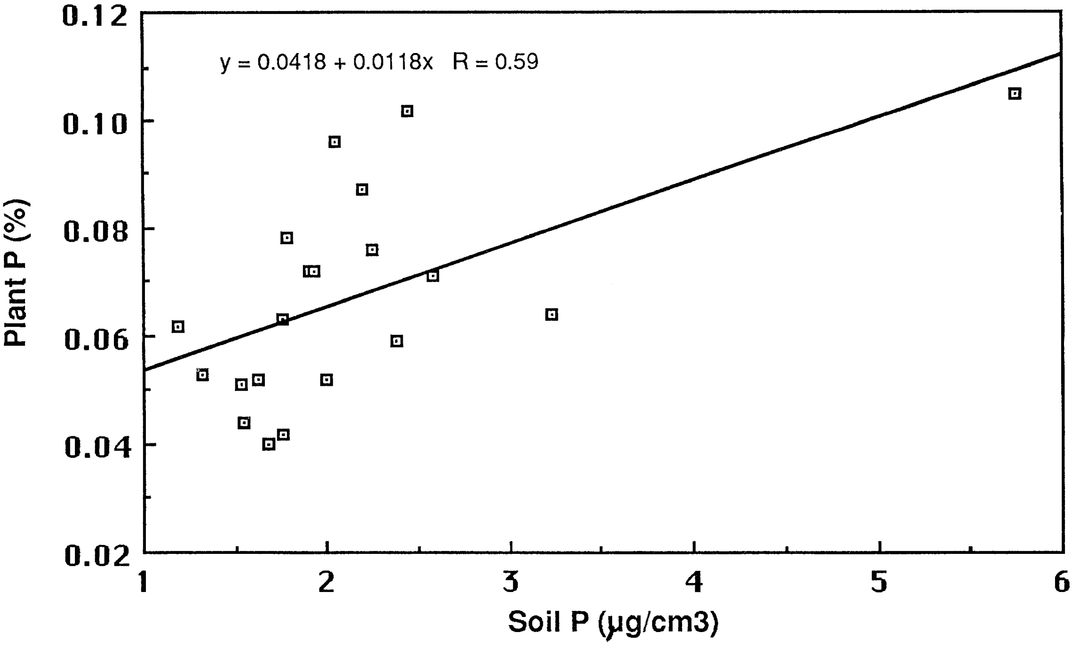

Fig. 3. Relationship of plant P to extractable P in mineral soil.

Table 2. Correlation matrix of herb-layer nutrients for WS77. Values are Pearson product-moment correlation coefficients.

	K	Ca	Mg	N
P	0.77[a]	0.07	0.28	0.61[a]
K	—	−0.08	0.10	0.45
Ca		—	0.73[a]	0.42
Mg			—	0.55

[a] Significant correlation at $P < 0.01$.

Table 3. Correlation matrix for nutrients from 110 plant species (from Garten 1978). Values are correlation coefficients.

	K	Ca	Mg	N
P	0.16	0.09	0.12	0.85[a]
K	—	0.09	0.38[a]	0.02
Ca		—	0.38[a]	−0.07
Mg			—	0.04

[a] Significant correlation at $P < 0.01$.

al. 1984). Consequently, plants growing in these systems are adapted to conditions of extreme nutrient limitations.

One important plant adaptation to nutrient limitation is the maintenance of growth at low tissue nutrient concentrations (Chapin *et al.* 1986). Herb layer nutrient concentrations (in % dry weight) at WS77, combining both burn treatments and sites, were 0.84, 0.77, 0.20, 1.19, and 0.06 for K, Ca, Mg, N, and P, respectively. These values are quite similar to those of other oligotrophic forest systems (Gagnon *et al.* 1958; Garten 1978), presumably the result of several factors, including the predominance of coniferous foliage (acidic, nutrient-poor) in the forest floor. In contrast, K and P concentrations for WS77 were substantially lower than those reported for herb layer vegetation growing in many hardwood forests, e.g., 5.43% K and 0.37% P in an Illinois oak-hickory forest (Peterson and Rolfe 1982).

Shoulders and Tiarks (1980) found significant growth responses to N, P, and K fertilization in a flatwoods pine plantation similar to WS77. Increases in growth and foliage nutrient concentrations were particularly substantial in response to K and P fertilization, indicating that these nutrients may be especially limiting in many Coastal Plain soils. Thus, increases in availability of these nutrients should result initially in their increased uptake (i.e., luxury consumption) by plants (Chapin 1980). Although luxury consumption can occur for all nutrients, this response is most common for K (Thompson and Troeh 1973).

Gilliam and Christensen (1986) estimated species richness and percent cover for the herb layer of 7-ha compartments throughout WS77 which were subjected to a variety of winter and summer fire treatments. They found that only (but not all) winter fire treatments significantly increased herb layer cover (and, hence, production). It was hypothesized that nutrients limit herb layer production under non-fire conditions and that post-fire increases in production in these systems are a result of fire-caused increases in nutrient availability (Wells *et al.* 1973; Christensen 1977). The results shown here indicate that increased uptake of nutrients can occur in response to a winter fire, since, although biomass was not significantly different ($P < 0.05$) between burned and unburned plots (Gilliam 1983), concentrations of K and P were significantly higher in the herb layer of burned plots than in that of unburned plots. Furthermore, these responses are consistent with observed K and P deficiencies in Coastal Plain soils (Wells *et al.* 1973; Shoulders and Tiarks 1980). The correlation of plant nutrient concentrations with extractable amounts in the mineral soil for both K and P further indicates that herb layer nutrient uptake for WS77 should respond positively to fire-caused increases in K and P availability in the soil.

Phosphorus limitation is suggested also in the low P:N ratio (0.05) for the herb layer of WS77. Garten (1976) found a very consistent P:N ratio of 0.1 (1:10) in comparing plant nutrients in 54 terrestrial and aquatic vascular and non-vascular species, with a highly significant correlation for these nutrients in terrestrial vascular plants ($r = 0.90$, $P < 0.001$). Other significant relationships were found for Ca:Mg and Mg:K (Garten 1976). Garten (1978) further calculated a correlation matrix for nutrients from 110 plant species (Table 3) and again found significant correlations for the nutrient pairs of Garten (1976). He concluded that such correlations resulted primarily from similarities in the biochemical functions of nutrients within the plant and he identified the following sets of plant nutrients based on these functions: 1) nucleic acid-protein (P, N, Cu, S, and Fe), 2) structural/photosynthetic (Mg, Ca, and Mn), and 3) enzymatic (Mn, K, and Mg) (Garten 1978).

Correlations for plant nutrients in this study were similar to those of Garten (1978). N:P and Ca:Mg had significant ($P < 0.01$) correlation coefficients of 0.61 and 0.73, respectively. However, there were also conspicuous differences between the two matrices, most notably a highly significant correlation for P:K ($r = 0.77$, $P < 0.01$) for WS77. These results are in agreement with the correlation of P:K ($r = 0.86$, $P < 0.01$) for nine South Carolina Coastal Plain plant species calculated from data in Garten (1978) and indicate the importance of factors other than biochemical interactions (such as low nutrient availability) in affecting plant nutrient relationships.

Given that extractable P and K are low in WS77 soils and are typically deficient at many lower Coastal Plain sites (Tisdale and Nelson 1975; Wells *et al.* 1973), significant correlations between P and K in plants of these sites may result from efficient cycling of P and K within the vegetative biomass of lower Coastal Plain ecosystems. Furthermore, as a result of extreme growth limitations, availability of these nutrients may be influenced by many of the same factors, such as fire.

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