

The Effects of Fire on Nutrient Cycles in Longleaf Pine Ecosystems

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ABSTRACT

Nutrient limitations on soils that support longleaf pine forests and savannas favor the production of litter and debris that is slow to decompose. Such fuel accumulations favor frequent, low intensity fires. Nutrient losses, especially of nitrogen and phosphorus, associated with such fires may be considerable, and may help maintain to low soil fertility. Although availability of some nutrients is enhanced by burning, this enhancement contributes very little to observed patterns of increased plant production following fire. Circumstantial evidence suggests that biochemical changes in soils following fire may contribute to increased postfire fertility. Variability in nutrient changes from location to location within individual fires and between fires may be more important to observed patterns of plant community variation than average effects. The long-term consequences of departures from typical fire regimes on nutrient cycles needs considerable additional study.

INTRODUCTION

The relationship between fire and longleaf pine ecosystems is one of the most celebrated examples of ecosystem dependency on natural disturbance. The importance of this relationship with regard to biodiversity and wildlife management is covered in detail in other papers in this volume. In this paper I shall address four questions. 1. Why are longleaf ecosystems prone to fire? In particular, what roles do soils and nutrients play in regulating fire cycles? 2. What is the impact of fire on ecosystem nutrient inputs and losses? 3. In what ways does fire alter patterns of nutrient cycling and nutrient transformations within ecosystems? 4. What are the consequences of such alterations with respect to plant growth and plant community structure?

The reader is warned in advance that answers to these questions are far from clear. Indeed, we are learning that each question has a diversity of correct answers that depend on a variety of actors including year-to-year changes in climate, specifics of site conditions, and variations in fire regime. Thus, the focus of this paper will not be to provide pat answers to each question, but to discuss the factors underlying the diversity of answers.

LONGLEAF PINE ECOSYSTEM FIRE REGIMES

The "natural" fire regime for longleaf pine ecosystems is not known. However, plant life histories and patterns of fuel accumulation suggest that light to moderate intensity surface fires every two to eight years were typical of pristine landscapes (Wells 1942, Garren 1943, Wahlenberg 1946, Parrott 1967, Christensen 1981). Averaged over centuries, fire consumes approximately 50-100 g m⁻² of organic carbon in savannas (Christensen 1987). This is equivalent to 30-70% of annual carbon fixation in these ecosystems and is equal to the average annual fuel consumption by fire in such heavy fuel, high intensity fire ecosystems as the mixed conifer forests of western North America.

Why are these ecosystems prone to fire? Among the most important determinants of ecosystem fire regimes are regional climate (periodic drought), frequency of ignition (e.g., lightning), site moisture conditions, and fuel quantity and quality. Within a climatic region, fire frequency often is correlated with site fertility; fire are more frequent on nutrient-limited or oligotrophic sites than on eutrophic sites (Christensen 1987). Although the contribution of nutrient limitation *per se* to variations in fire regimes is confounded by correlations

between site nutrient status and moisture, plants growing on oligotrophic soils are more flammable (Rundle 1981) and produce litter that is more slowly decomposed than plants growing on more fertile soils (Vitousek, 1982). Slow rates of decomposition exacerbate nutrient limitations because nutrients accumulate in dead debris and litter.

Soils of longleaf pine ecosystems vary along a moisture gradient from quite xeric entisols to mesic, even wet ultisols that share the property of severe nutrient limitation, especially with respect to nitrogen (see discussion below). Dominants in these ecosystems, such as wiregrass (*Aristida stricta*), produce ligneous fuels of very low nutrient content (Christensen 1977). Decomposition of such fuels is slow, with the consequence that the ratio of dead to live aboveground phytomass rises very rapidly following fire (Parrott, 1967), as does the likelihood of another fire (Christensen 1981). Unlike ecosystems typified by infrequent, high intensity fires, fire-caused nutrient changes in longleaf pine communities occur in frequent, but comparatively small pulses. Once such a fire regime is established, patterns of postfire fuel production will tend to maintain it.

Exclusion of fire from these ecosystems for abnormally long period of time may allow the invasion of longer-lived woody species, with a concomitant decrease in herb biomass (Lewis and Harshbarger 1976, Myers 1985). When fires finally do occur after such fuel changes (as they inevitably will), they are likely to be more intense and accompanied by greater nutrient fluxes. These conditions appear to favor the reestablishment of woody species and perpetuation of a longer fire return interval (Myers 1985).

FIRE AND NUTRIENT BUDGETS

Fire-caused Nutrient Losses

Fire necessarily results in the net loss of nutrients from ecosystems as a consequence of four mechanisms (Binkley and Christensen, 1991): 1. Fire may oxidize or vaporize compounds into the atmosphere. 2. Nutrients may be lost as a consequence of the convection of ash particles into fire generated winds. 3. By increasing mineral nutrient mobility, fires may increase the likelihood of losses due to leaching. 4. fire may accelerate erosion and sediment transport.

The relative importance of these mechanisms varies for each mineral nutrient species. In addi-

tion, variations in fire intensity, site and soil, and topography, climatic patterns and season of burning can influence the relative contribution of each mechanism to overall nutrient loss.

Organic compounds containing nitrogen and sulfur are easily oxidized during fire, resulting in losses of nitrogen and sulfur in approximately direct proportion to the loss of total organic matter (Raison et al., 1985; Binkley and Christensen, 1991). Vaporization losses during fire occur when an element is volatilized but its oxidation state remains unchanged. Metallic cations such as potassium, calcium, and magnesium may be vaporized in small quantities, especially if they are part of organic molecules (Raison et al., 1985). In addition, many nitrogen compounds vaporize at temperatures well below their combustion temperatures (Binkley and Christensen, 1991).

DeBell and Ralston (1970) estimated that nitrogen loss to volatilization and oxidation varied between 30% and 70% of total nitrogen depending on fuel characteristics. Losses were lower in woody and relatively green fuels. Changes in nutrient characteristics associated with burning in dense swards of wiregrass (*Aristida stricta*), a characteristic fuel of longleaf pine stands, are shown in Table 1. These data indicate that nitrogen losses on the order of 3-4 g•kg⁻¹ of fuel consumed may be very typical. The high percentage loss (70%) is very likely a consequence of the high temperature in these fine and very dry fuels (Raison et al., 1985). However, nitrogen loss expressed as g•kg⁻¹ of fuel consumed is relatively low compared to other fuel types. For example, Binkley and Christensen (1991) estimate that such losses are typically on the order of 6 g•kg⁻¹ fuel consumed in woody fuel types. This difference probably reflects the relatively low concentration of nitrogen in longleaf pine ecosystem fuels. Expressed on an area basis, nitrogen losses vary in a predictable fashion in relation to total fuel consumed during fires: 2.2 g•m⁻¹ in wiregrass savannas (Christensen 1977), 5.7 - 9.5 g•m⁻² in galberry flatwoods (Snyder 1986), to 11 g•m⁻² in shrubby flatwoods (Hough 1981).

Losses to oxidation and volatilization are considerably less for mineral nutrients other than nitrogen. For example, Christensen (1977) estimated such losses of P, K, Ca, and Mg to be 47%, 40%, 20%, and 11%, respectively.

Ash redistribution caused by convection can significantly affect nutrient budgets on small spatial scales within fires. In general, ash is enriched in most mineral nutrients (Table 1, Christensen

1977), thus magnifying this potential effect. although specific measurements of this type have not been made, the importance of convectional movement over an entire burn should diminish with increasing fire size.

Because of the variety of mechanisms described below, fire generally increases nutrient mobility, and thus the susceptibility of nutrients to leaching by water flowing through the soil profile. The extent of such leaching depends on the availability of nutrients, patterns of plant uptake and retention, the exchange properties of litter, humus and soils, and postfire patterns of precipitation and evapotranspiration. Because their soils often are coarse textured and have low exchange capacities, it is often assumed that such losses may be significant in longleaf pine ecosystems. Lewis (1974) observed increased concentrations of several nutrient species in superficial groundwater collected beneath recently burned longleaf pine stems, compared to similar collections made beneath unburned areas. Boerner and Forman (1982), using lysimeters, found that leaching losses from New Jersey pine barrens ecosystems (fuels and soils that are similar to those of longleaf pine ecosystems) increased with increasing fire intensity. Losses of Ca, Mg, and K were considerable following an intense wildfire, less following light surface fires, and negligible in unburned areas.

Weiss (1981) hypothesized that leaching losses may vary, depending on season of burning; lower rates occurred in areas burned immediately prior to the growing season when plants can take up released nutrients, and greatest immediately prior to periods of plant dormancy. However, circumstantial evidence indicates that microbial immobilization may minimize nutrient losses during periods when plant nutrient uptake is minimal. Neither Richter (1981) nor Gilliam (1983) found any in-

crease in nutrients in soil water beneath the rooting zone, regardless of season of burning. Season-to-season differences in nutrient loss appear to be related to differences in fire behavior.

Because of the generally subdued topography and well-drained soils characteristic of the coastal plain, fire-caused nutrient losses to erosion are generally negligible. Richter et al. (1982) measure no surface runoff in lower coastal plain pine ecosystems even following heavy rain events relatively on heavy soils. While they observed some increased vertical leaching of nutrients in burned loblolly and longleaf pine soils, there was virtually no increase in lateral transport of these nutrients and no change in water quality of streams draining burned compared to unburned watersheds.

Nutrient Inputs

Nutrient inputs to longleaf pine ecosystems may be from soil weathering, fixation processes and rain and dry fallout. Rates of soil weathering clearly vary among parent materials; they are low on siliceous and comparatively high on calcareous substrates. Very intense fires may accelerate weathering of mineral materials (Swanson 1981), but fires of intensities that are typical of longleaf pine ecosystems probably are unimportant in this regard.

The hypothesis that fire increases nitrogen fixation and thereby accelerates recovery of nitrogen capital lost during fire has received considerable attention (e.g., Wells, 1971; Christensen, 1987). In some, but not all, longleaf pine ecosystems the importance of symbiotic nitrogen-fixing legumes is increased by frequent fire (Christensen 1981). While such an increase in legumes certainly would increase the nitrogen input to the ecosystem, it also

Table 1. Nutrient characteristics of standing crop and ash. Field refers to ash collected from the soil surface immediately after fire, laboratory refers to ash prepared by incineration of standing crop samples in the laboratory. Ash fall was computed on the basis of laboratory incineration data. Ninety-five percent confidence intervals are shown in parentheses.

Element	Nutrient content				
	In standing crop		In Ash		Ash fall
	mg g ⁻¹	g m ⁻²	Field mg g ⁻¹	Laboratory mg g ⁻¹	g m ⁻²
Nitrogen	4.72 (±0.14)	3.38 (±1.8)	8.75 (±2.76)	8.72 (±2.76)	1.15 (±0.49)
Phosphorus	0.42 (±0.02)	0.34 (±0.15)	1.60 (±0.39)	1.42 (±0.90)	0.18 (±0.07)
Potassium	1.30 (±0.04)	1.05 (±0.49)	5.20 (±0.38)	4.78 (±3.41)	0.63 (±0.27)
Calcium	2.50 (±0.19)	2.05 (±0.96)	8.11 (±0.43)	12.15 (±5.1)	1.64 (±0.70)
Magnesium	0.44 (±0.06)	0.35 (±0.16)	2.23 (±0.12)	2.33 (±1.09)	0.31 (±0.13)

would increase nitrogen loss during fire due to higher tissue nitrogen concentrations (Riggan et al. 1988). Jorgensen and Wells (1971) found that fire resulted in increased activity of nonsymbiotic nitrogen-fixing organisms in some coastal plain soils, and they propose that such fixation might compensate for fire-caused nitrogen losses. However, this effect has not been widely documented (Binkley and Christensen, 1991).

For most mineral nutrient species, annual inputs and rain and dry fallout are sufficient to balance the pulsed nutrient losses from fires in longleaf pine forests. For example, using Christensen's (1977) estimates of nitrogen loss in xeric longleaf pine savannas, and assuming a five-year fire return interval, annual nitrogen losses to fire would be approximately $0.4\text{--}0.5\text{ g}\cdot\text{m}^{-2}$. This is considerably less than the annual input of total nitrogen in both precipitation (Boring et al. 1988). Atmospheric inputs of other nutrient species compared to their fire-caused losses are even more favorable (Richter et al., 1983).

Fire and Long-term Nutrient Budgets

There have been no studies of the long-term consequences of varying fire regimes on nutrient budgets in any ecosystem. However, Wells (1971) reported on changes in the total amounts of forest floor and soil nitrogen in pine flatwoods experiencing different burning regimes over a 20-year period. Although the distribution of nitrogen between forest floor and soil varied considerably depending on fire regime, the total nitrogen contained in these two pools was largely unaffected, even by intense annual summer fires. This apparent homeostasis arises in part because nitrogen losses diminish with the decreased fuel consumption characteristic of more frequent, but less severe fires. In addition, compensatory vegetation response, such as more rapid herb growth, may further diminish losses where fire frequency is high. These responses are discussed in more detail below.

FIRE AND NUTRIENT TRANSFORMATIONS

Fire has been observed to cause an increase in mobility and availability of a variety of nutrients, despite overall loss of nutrient capital. These changes arise, in large part, as a consequence of five mechanisms: (2) direct mineral addition in ash; (2) decreased plant uptake; (3) increased microbial activity and decomposition; (4) altered patterns of adsorption and immobilization; (5) changes in ox-

idation-reduction transformations. In general, the specific mechanism determines the patterns and duration of changes in postfire nutrient mobility and transformations.

Patterns of Change

Christensen (1977) studied temporal changes in soil nutrient concentrations in a xeric savanna following fire, and found that concentrations of Ca, Mg, and K increased immediately following the fire event, whereas concentrations of phosphorus were higher in burned areas only after several months. These data suggest that concentrations of the metallic cations are increased by ashfall, but that phosphorus may increase as a consequence of increased decomposition or diminished plant uptake.

Concentrations of soil nutrients along burned and unburned soil profiles two months following fire are shown in Figure 1. Burned area soils were significantly enriched in $\text{PO}_4\text{-P}$, K, Ca, and Mg. Concentrations of $\text{NO}_3\text{-N}$ and $\text{NH}_3\text{-N}$ exhibited very regular seasonal fluctuations in both burned and unburned soils, but did not differ between treatments. After the first growing season, concentrations of most nutrients were equal between burned and unburned areas, with the exception of $\text{PO}_4\text{-P}$ and Mg, which were actually lower in burned than in unburned area soil.

Richter (1980) and Gilliam (1984) found that postfire changes in soil nutrient availability depended on season of burning. For example, winter fire resulted in a significant increase in soil nitrate and ammonium, whereas summer fire resulted in a significant decrease in these nutrients. These changes undoubtedly are linked to variations in production and community response associated with winter and summer burning.

Ashfall

Amounts of total nutrients and amounts of their available forms are indicated in Table 1. The proportion of a particular nutrient's total concentration that is in mineral form (i.e., inorganic) varies with the nature of the fuels, fire behavior, and the particular nutrient in question (Raison, 1979). Considerably less than 1% of total nitrogen in ash from either herbaceous or woody fuel is present as nitrate or ammonium; most is in organic form (Christensen, 1977; Wilbur, 1985). Based on Christensen's estimates of ashfall, direct addition of nitrate, ammonium, or phosphate in ash from a fire in wiregrass fuel is insufficient to detectably alter soil concentrations of these nutrient species.

Nonetheless, ash does represent a reservoir of potentially mineralizable nutrients.

Decomposition and Mineralization

Nutrient pulses following fire often are attributed to increased decomposition and altered microbial activities (Lewis 1974; Christensen, 1977; Binkley and Christensen, 1991). Schoch and Binkley (1986) found that litter decomposition rates were accelerated following a light surface fire in a loblolly pine forest, and that this resulted in increased ammonification. Populations of fungi and bacteria are higher in soils beneath southern pine woods that are periodically burned (every 3-5 years) than beneath similar, but unburned woods (Jorgensen and Hodges (1970, 1971)). However, very intense fires or more frequent burning may have a negative impact on microbial populations (Binkley and Christensen, 1991).

Fire may increase microbial activity through several mechanisms. Increased soil pH resulting from ash addition may create more favorable growth conditions for microbes, especially in the very acidic soils of many longleaf pine sites. However, pH changes due to fire are in most cases modest (Christensen, 1977; McKee, 1982; Gilliam, 1983; Snyder, 1986). Old (1969) and Peet et al. (1975)

found that fire altered the microclimate of prairie soils so as to favor microbial activity. Schneider (1988) observed seasonal differences in plant and nutrient responses that are consistent with the hypothesis that microclimatic changes may be important.

Nitrogen is the soil nutrient most limiting to plant growth in many longleaf pine soils. Although Christensen (1977) found little increase in soil concentrations of available nitrogen, increased tissue nitrogen content coupled with increased production and nitrogen uptake suggested that nitrogen availability had been increased by burning.

Given rapid uptake of available nutrients, if mineralization is increased by fire, increased availability might not be manifest as increased soil concentrations. Christensen and Schneider (1986) studied the effects of burning on soil nutrient mineralization using soil incubation techniques. Soils collected from recently burned and unburned areas were preanalyzed for a variety of nutrients, incubated at 28° C for 30 days, and reanalyzed for these same nutrients. Mineralization rates were higher in the burned area soil for all nutrients except nitrogen. In the case of nitrogen, ammonium and nitrate actually disappeared from the burned soil at a faster rate than from the unburned soil.

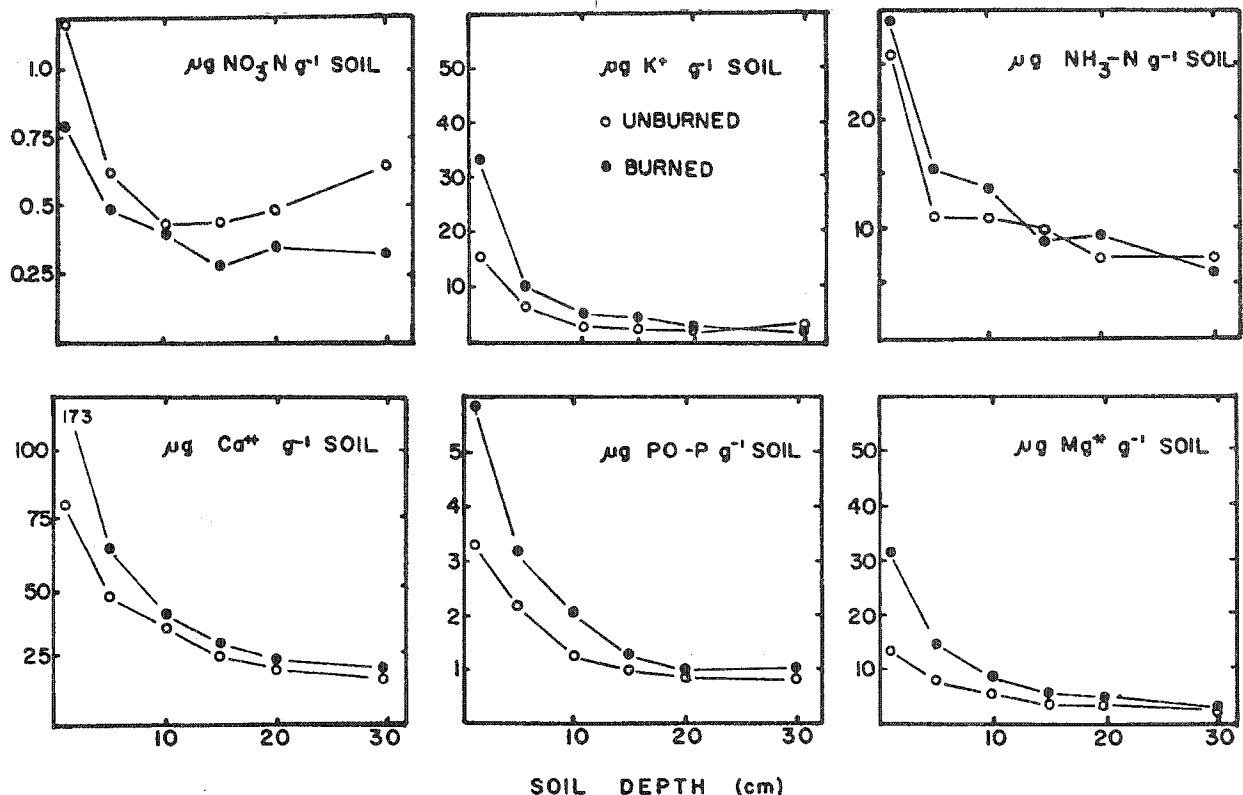


Figure 1 Concentrations of nutrients along the soil profile of unburned (open circles) and burned (closed circles) longleaf pine-wiregrass ecosystems. Each point is the mean of 3 samples taken 60 days after a fire.

This appears to be a consequence of increased microbial activity in recently burned soil. Nonetheless, these data do suggest that, although nutrients may be added in ash in relatively unavailable forms, rapid mineralization may convert them to forms available for plant uptake.

Adsorption and Immobilization

Nutrient availability may be altered by fire-caused changes in soil adsorptive characteristics. Stark (1977) found that soil adsorption of Ca and Mg was increased, while that of Fe was decreased when soils were heated to temperatures above 300°C. Fire has been found to influence the absorptive properties of soils for phosphorus in a variety of ecosystem types (Christensen, 1987).

An often overlooked consequence of burning on nutrient availability is its effect on soil heterogeneity. Rose and Christensen (manuscript) found that variance in nutrient concentrations among soil samples taken within a single areas was greatly increased by burning. This increased variance appears to be a consequence of the uneven distribution of ash. Variance decreases as nutrient concentrations return to their prefire levels. Christensen (1984) proposed that such increased variance might create a variety of establishment opportunities, and may account for the high species richness characteristic of chronically burned sites. This hypothesis has yet to be tested in longleaf pine ecosystems.

FIRE, NUTRIENTS, AND PLANT RESPONSE

Annual aboveground herb-layer production varies between 170 and 400 g•m⁻², with mesic savannas being most productive. Production is stimulated in the first year following burning, however, this increase in production is short-lived (Barnette and Hester 1930; Parrott 1967; Christensen 1977). In western coniferous forests, fires have been found to increase production for somewhat longer periods (Ffolliott et al. 1977; Harris and Covington 1983; Oswald and Covington 1983, 1984).

Saterson and Vitousek (1984) found that below ground production in dry savannas was roughly equivalent to that aboveground. Both appear to be enhanced by burning, but variability among samples made this hypothesis difficult to test.

Christensen (1977) investigated changes in site fertility following fire in wiregrass-dominated savanna using bioassay techniques. He found that soil fertility was considerably higher in the burned area soil immediately following burning, but diminished rapidly during the first growing season. Nutrient enrichment experiments revealed that nitrogen was the most limiting nutrient in both burned and unburned soils, although increased nitrogen uptake in the burned area in the first two months following burning indicated that there was some fire-caused increase in nitrogen availability. Despite the nutrient treatment, plant growth always was greater in burned compared to unburned soil.

Christensen (1977) found that root elongation was greatly inhibited in unburned soil, raising the possibility that low prefire fertility might be a consequence of soil toxins or allelopathy as well as nutrient limitations. Rose and Christensen (unpublished ms) found that addition of agents that bind organic chemicals, including activated charcoal, completely removed the toxicity. They showed that charred ash had the same binding properties as activated charcoal and proposed that the reduced toxicity in burned area soils might be a direct consequence of ash addition.

In addition to soil fertility, production in recently burned areas may be enhanced by changes in microclimate. Such effects have not been investigated in temperate savannas; however, Old (1969) and Peet et al. (1975) found that winter burning increased soil temperatures early in the spring in prairie grasslands, effectively increasing the length of the growing season, and thereby, annual production.

Chronic annual burning appears to depress production. Walker and Peet (1983) found that production in annually burned mesic savanna was 264 g•m⁻²•yr⁻¹ whereas production in an infrequently burned savanna on a similar site was 376 g•m⁻²•yr⁻¹.

Chronic annual fires appear to deplete soil nutrient reserves. Walker and Peet (1983) observed a 2-fold increase in production with fertilization in an annually-burned savanna, but only a 20% increase in an infrequently-burned area.

The effect of fire on production clearly is dependent on the season of burning. Parrott (1967) reported that production was greater in winter versus summer burns in Florida savannas, and Gilliam and Christensen (1986) found that winter burns enhanced production in the first postfire growing

season, whereas summer burns had no effect. The likely cause of these seasonal differences probably is related to differences in nutrient fluxes associated with winter versus summer burns.

SUMMARY

Although many details are uncertain, a general picture of the relationship between fire and longleaf pine ecosystem structure and function is obvious. During interfire years, flammable fuel (primarily standing dead grass culms and, beneath longleaf pines, a nearly equal amount of pine needles) accumulates, and the ratio of dead to live fuel increases. This results in an increase in fire probability. Slow rates of decomposition and nutrient mineralization exacerbate nutrient limitations, reducing production even further. This creates the potential for positive feedback, in that such nutrient limitations may result in the production of litter with low nutrient content; this, in turn, may further slow rates of decomposition (Vitousek 1982). This issue has not been addressed in longleaf ecosystems.

The likelihood of successful establishment from seed during most interfire years is very low, especially for small-seeded herbs. Shading from dominant graminoids and from the thick litter accumulation (Roberts and Oosting 1958) and nutrient limitations (Christensen 1977) undoubtedly combine to create harsh conditions. In addition, accumulation of biochemical residues due to incomplete decomposition of grass culms also may be important (Christensen 1977). This possibility needs further study.

The relative differences between the pre- and postfire environments appear to depend on several factors, including season of burning and past fire history. Winter fires are followed by a brief, but significant, nutrient pulse that stimulates production and flowering. Neither nutrient availability nor production appear to be enhanced by fire during the growing season. There is fragmentary evidence that fire on a too frequent basis may result in considerable nutrient loss, and thereby further accentuate nutrient limitations to production. Such fire-caused nutrient limitations may not be altogether "bad", in that they may favor high diversity (Walker and Peet 1983).

Successful sexual reproduction may be more dependent on microclimate than nutrient changes associated with burning. Due to increased flowering in the first postfire growing season, herb seed rain in savannas is highest in the second postfire year. Microclimatic conditions are more favorable for successful seedling establishment at that time than at any other time during the fire cycle.

Compared to ecosystems burned by infrequent, high intensity fires, nutrient changes associated with burning in longleaf pine forests are modest. Indeed, they may have no immediate detectable effect on plant production. Over long periods of time, however, fires in these ecosystems play a major role in patterns of organic matter decomposition and nutrient cycling. Thus, small variations in fire regimes that are perpetuated over long periods may have dramatic consequences. This issue deserves considerably more study.

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