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Influences of Community Composition on Biogeochemistry of Loblolly Pine (Pinus taeda) Systems

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ABSTRACT.—Litterfall and decomposition processes were compared among four forest plantations that were dominated by loblolly pine (*Pinus taeda* L) but that differed in terms of presence or absence of deciduous and herbaceous components. Based on aboveground litterfall, the pine-only community was the most productive but had the slowest turnover of organic matter in the forest floor. The presence of deciduous and/or herbaccous vegetation caused more rapid turnover of forest litter and altered the nature of immobilization/mineralization patterns for N and P in the same material. Temporal patterns of N and P changes in the forest floor were much more dynamic in mixed pine-deciduous communities and suggest more intense competition between microbes and vegetation for those elements. Mineralization pulses are more frequent and occur on a different temporal scale in the pine plus deciduous communities also. Results are discussed in terms of their potential importance during ecosystem restoration/manipulation efforts that increase or decrease the presence of particular vegetation components within forest communities.

INTRODUCTION

The importance of nutrient cycling to the sustainability of forest systems is well recognized (Kimmins, 1987) and has been incorporated in studies which focus on long-term productivity in a number of ecosystem types including loblolly pine (*Pinus taeda*) (Powers et *al.*, 1990). Although numerous investigations have described macroelement circulation within loblolly pine ecosystems (Switzer and Nelson, 1972; Wells and Jorgensen, 1975; Jorgensen *et al.*, 1980; Lockaby and Taylor-Boyd, 1986; Polgase et *al.*, 1992; and many others), those studies have represented the integrated effect of multiple plant species and vegetation strata growing together within a single system. There is little understanding of the contribution of major vegetation components to system biogeochemistry (*i.e.*, the. manner in which that integrated effect is developed).

The nature of nutrient circulation between evergreen vs. deciduous systems and the effects of those disparate systems on soils are uncertain (Binkley, 1994). Although some authors (Rodin and Basilevich, 1967 and Vogt *et* al., 1986) report that, in general, deciduous systems exhibit higher N Iitterfall contents than evergreen, Gower and Son (1992) noted that this may not be the case when both species types are grown on the same soil. Although Cower and Son did observe different N mineralization rates among the five species compared, there were no consistent trends between deciduous vs. evergreen plantations.

Increasing levels of subdominant oak within ponderosa pine stands have been shown to exert a major influence on forest floor nutrient contents of those systems (Klemmedson, 1987). In general, N, P, Ca, and K concentrations were increased by the presence of oak and the vertical distribution of elements was shifted downward (*i.e.*, more heavily toward the H layers). Lefevre and Wemmedson (1980) suggested that the presence of oak contributed to a more favorable decomposition environment in pine stands and observed that F layer thickness was inversely related to oak basal areas.

Comparisons of decomposition processes associated with four forest types in Africa indicated that, although the form of the mass loss curves were similar, there were differences in decay rates among types (Lisanework and Michelsen, 1994). Rate differences did not seem to be strongly related to nutritional status of litter. All litters initially had wide N:P ratios (indicating P limitation in the decomposition process) but accumulated N and P differently as decomposition progressed. However, in contrast to the work of Cower and Son (1992). the four forest types were on different sites so that soil variability probably influenced their results to a greater degree.

It is evident that vegetation communities which reflect disparate species composition may cycle nutrients differently. However, our knowledge is not sufficiently developed to enable us to anticipate the nature of shifts in biogeochemistry that could result from species changes. Similarly, we do not understand the manner in which major and minor vegetative components of ecosystems contribute to an integrated biogeochemical cycle. Thus, the objective of this study was to determine the degree to which nutrient transfer in litterfall and decomposition vary as a function of vegetation composition within young loblolly pine systems. Specifically, we hypothesized that the elimination of deciduous woody and/or herbaceous vegetation would reduce the rate of mass, nitrogen and phosphorus turnover in the forest floor.

METHODS

Study area.—This study was superimposed onto an existing experimental design which had been installed to compare loblolly pine productivity in stands with different community composition. The site was located in the Upper Coastal Plain of central Alabama (near the town of Tallassee, 32°30'N, 86°00'W) on land that had been heavily farmed for cotton during the early and mid-twentieth century. A stand of mixed pine-deciduous species occupied the site in the interim between agricultural activity and installation of the present plots. Soils on the site belong to the Cowarts series (Typic kanhapludults) and precipitation averages 1360 mm annually almost entirely as rain. Forest vegetation on Cowarts soils typically exhibits strong growth responses to N applications indicating that forest communities growing on kanhapludults are normally nitrogen deficient (Lee Allen-NC State University, pers. comm.).

Study installation.—In 1984 a randomized block design with four replications and four treatments in each was established (Miller *et* al., 1991). The treatments included (1) no suppression except for vines, (2) suppression of deciduous-woody vegetation, (3) suppression of herbaceous vegetation and (4) suppression of both deciduous-woody and herbaceous vegetation. The duration of herbaceous vegetation suppression was four years while that of deciduous-woody vegetation will continue until harvest at approximately age 30. Suppression of vegetation categories was achieved with the use of directed sprays and wick (*i.e.,* contact) applications of several herbicides. Each of the four square treatment plots within each block was 0.1 ha.

At the beginning of the present investigation (1991), the four treatments had produced distinctly different communities in terms of composition and structure (Table 1). In the eighth year following treatment, little deciduous woody vegetation was present in treatments 2 and 4. Approximately one third of the total basal area in the remaining two treatments (*i.e.,* 1 and 3) was predominantly sweetgum (*Liquidambar styraciflua* L.) and water oak (*Quercus nigra* L.). As expected, herbaceous cover was prominent in treatments 1 and 2. There was very little herbaceous cover in treatments 3 and 4. The fourth replication was not used in the present study, because its deciduous species composition differed excessively from that of the other three replications.

TABLE I.-Composition 8 years after establishment of four vegetation treatments

Treatment (component suppressed)	Woody basal area		Pine (%)	% herbaceous cover		
	Total (m^2/ha)	Dec[1] (%)		Grasses	Forbs	Vines
1. None	12	36	64	20	5	4
2. Deciduous woody	12	—	100	26	10	11
3. Herbaceous	15	41	59	2'	2	0
4. Dec + Herb	21	—	100	1	1	0

[1] Dec = deciduous woody

Litterfall was sampled during the fall (*i.e.,* September to December) of 1991 with six 0.5 m^2 traps located on each treatment plot with the restriction that half of the traps were placed adjacent to individual pines while the remaining half were positioned in inter-row areas. The purpose of litterfall sampling at that time was to provide foliar litter for insertion into litterbags. This litter was separated into pine, sweetgum, and red oak categories (the latter consisting of water oak and southern red oak (*Quercus falcata* Michx.), air-dried, and placed into nylon mesh litterbags (6-mm mesh on the upper side and l-mm mesh on the lower). Dry weights (70 C for 48 h) were determined separately for pine and hardwood components of iitterfall.

Bags were filled with 10 g (air-dry) of litter of a species mix associated with their treatment of origin: treatment 1—60% pine, 24% sweetgum, 5% red oak, and 11% miscellaneous; treatment 2-98% pine and 2% miscellaneous; treatment 3—34% pine, 29% sweetgum, 22% red oak, and 15% miscellaneous; treatment 4—100% pine. All bags were constructed with 0.64 cm and 0.32 cm openings on the upper and lower sides, respectively. Initial N:P ratios within litterbags were quite low and ranged from 3 to 4, values which have been reported to imply that P is not limiting to the decomposition process (Vogt *et al.,* 1986).

Ten litterbags were placed within the Oa layer of each plot on three replications in March 1992 and were collected according to the following schedule: 0 (to estimate handling loss), 0.5, 1, 2, 5, 7, 9, 12, 18 and 20 months. However, after the two month collection, a wildfire destroyed one of the replications being used in the present study as well as the fourth that was not being used. Thereafter, the study proceeded with two replications.

Upon retrieval from the field, litter was dried at 70 C for 48 h, weighed and ground to pass a 20-mesh sieve. Total N and P were analyzed using a LECO thermal combustion apparatus and color-metric determinations after dry-ashing and suspension of ash in HCI respectively. N and P contents within bags were calculated by multiplying concentrations by litter mass and then expressing content changes with time as a percentage of the original content.

To estimate the annual inputs of N and P to the forest floor, additional litterfall sampling was conducted on a monthly basis from mid-1993 to mid-1994. The second, continuous annual sampling period was performed since the fall, 1991 sampling was significantly sep arated temporally from any subsequent sampling. The 1993-1994 sampling followed the same protocol as the 1991 sampling in terms of trap numbers, collection frequency and sample handling.

Statistical analyses consisted of analysis of variance at 20 months to compare the following response variables among treatments: percent mass, N, P remaining as well as total, deciduous and pine litterfall mass and N, P content. In addition, a single-exponential, nonlinear model was used to calculate rates of mass loss (k) for each treatment and these were then

TABLE 2.-Percent of original mass, carbon, nitrogen, and phosphorus remaining and decomposition rate coefficients compared among four treatments at 20 months

Treatment (component suppressed)	Mass*	C	N	P**	Rate* (k)
1. None	37.3 ab	41.68 b	128.3 a	75.9 ab	0.06 a
2. Deciduous woody	39.7 ab	43.37 ab	104.4 a	67.2 ab	0.05 b
3. Herbaceous	33.6 b	38.91 b	109.6 a	65.8 b	0.07 a
4. Dec + Herb	51.7 a	58.05 a	124.3 a	83.4 a	0.04 c

* Means within columns followed by the same letter are not significantly different ($P = 0.05$) except for $P = 0.10$ in the case of phosphorus (**)

compared via ANOVA. Means were separated using Duncan's New Multiple Range Test. and probabilities of a greater F of less than 10% are reported.

RESULTS

Decomposition dynamics.-At the termination of the litterbag sampling period (day 580), percent mass remaining differed between treatments 3 and 4 (Table 2). Mass loss was most rapid in treatment plots where herbaceous vegetation had been eliminated for four years (treatment 3) and slowest in pine-only communities (treatment 4). The largest numerical difference occurred between pine-only and the other three treatment types. Percent of carbon remaining followed the same trends as mass (Table 2).

Litter in all treatments exhibited net immobilization at day 580. Although N immobilization was greatest in the pine-only and no suppression treatments, no statistical differences were apparent among treatments in terms of percent N remaining even at the 10% probability level (Table 2). Litter P in all treatments was less than 100% of the original amount reflecting net mineralization at day 580. Conversely, the treatments differed ($P < 0.10$) in the percent of original P remaining with the pine only treatment retaining a greater proportion than treatment plots where the herbaceous component had been suppressed (Table 2).

Ratios of litter N:P at day 580 remained narrow (*i.e.,* less than 10) indicating that P was not limiting to decomposition (Vogt *et al.,* 1986). The treatments diverged in terms of this ratio with the treatments where a deciduous component was maintained (treatments 1 and 3) having significantly higher values than the pine-only treatment.

Decomposition rate coefficients indicated significantly slower rates of mass loss in treatments without deciduous vegetation (treatments 2 and 4) (Table 2). Litter turnover times (*i.e.,* 1/k) in treatments with a deciduous component averaged 15 years whereas those without were approximately 20 years. Eradication of both deciduous and herbaceous vegetation (treatment 4) was associated with the slowest litter turnover exhibited by any treatment (i.e., 22 years).

Comparisons of immobilization/mineralization patterns indicated different temporal behavior of N vs. P (Figs. 1-2). Regardless of the treatment, N displayed two immobilization phases during the 580 day period whereas P exhibited an early immobilization phase and mineralization thereafter. In the case of N, the slower litter turnover. of treatment 4 was manifested in the longer time between immobilization phases within that treatment vs. those of treatments 1-3 (Fig. 1a-d). There were no obvious differences in the P patterns among the four treatments (Fig. 2a-d).

Litterfall.—Annual foliar litter production was significantly greater for the pine-only treatment than in the remaining three treatments (Table 3). As expected, annual production

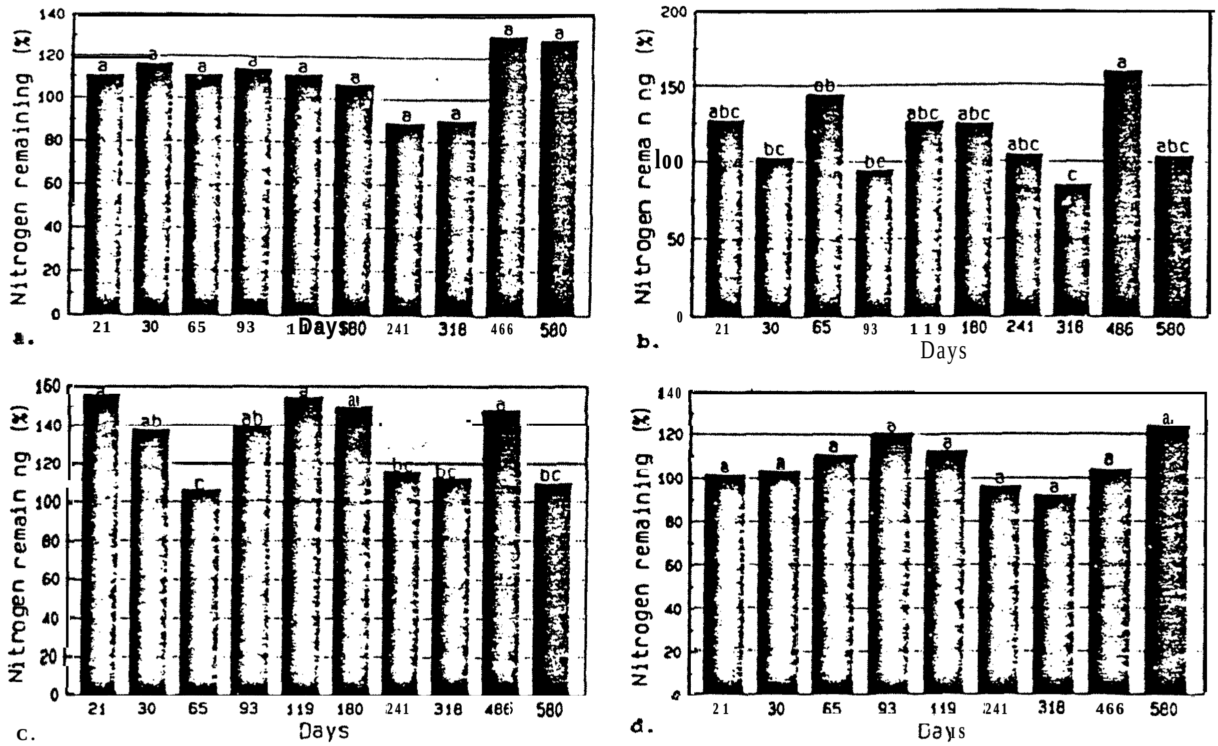

FIG. I.-N immobilization/mineralization patterns associated with a. no vegetation suppression (Trt I), b. deciduous vegetation suppression (Trt 2), c. herbaceous vegetation suppression (Trt 3), d. deciduous and herbaceous vegetation suppression (Trt 4)

of deciduous litter was greatest in the two treatments where deciduous vegetation had not been suppressed. Deciduous litter production was essentially absent in treatments 2 and 4. However, treatments 1 and 2 also produced 62 and 167 g/m* of herbaceous biomass respectively in 1991 (J. Miller, pers. comm.) so that treatment 2 may be the most productive aboveground. If litterfall is used as a surrogate for aboveground NPP (regardless of whether herbaceous production is included), no clear relationship between decomposition indices and treatment productivity is apparent.

Annual N and P litterfall content did not differ significantly among treatments (Tables 4 and 5). However, when the N and P contents of deciduous and pine litterfall were scrutinized separately, differences were apparent in relation to the apportioning of those elements. While the majority of N and P in litterfall was transferred in association with senesced pine foliage (regardless of the treatment type), those treatments with a significant deciduous component transferred 25 to 48% of their total litterfall P in deciduous litter (i.e., communities 1 and 3, respectively). In the case of N, 35 to 45% of total litterfall transfer was associated with those treatments, respectively.

DISCUSSION

In general, mass loss in the present study was more rapid than that reported for older loblolly pine systems by Jorgensen et al. (1980) for the same time period regardless of the treatment involved. However, in addition to differences in stand age, the inconsistencies may be attributable to methodological differences in measuring deco&position. Also, Jorgensen *et al.* (1980) reported net losses of both N and P during the first 21 months of litter exposure in contrast to the increases reported here for N.

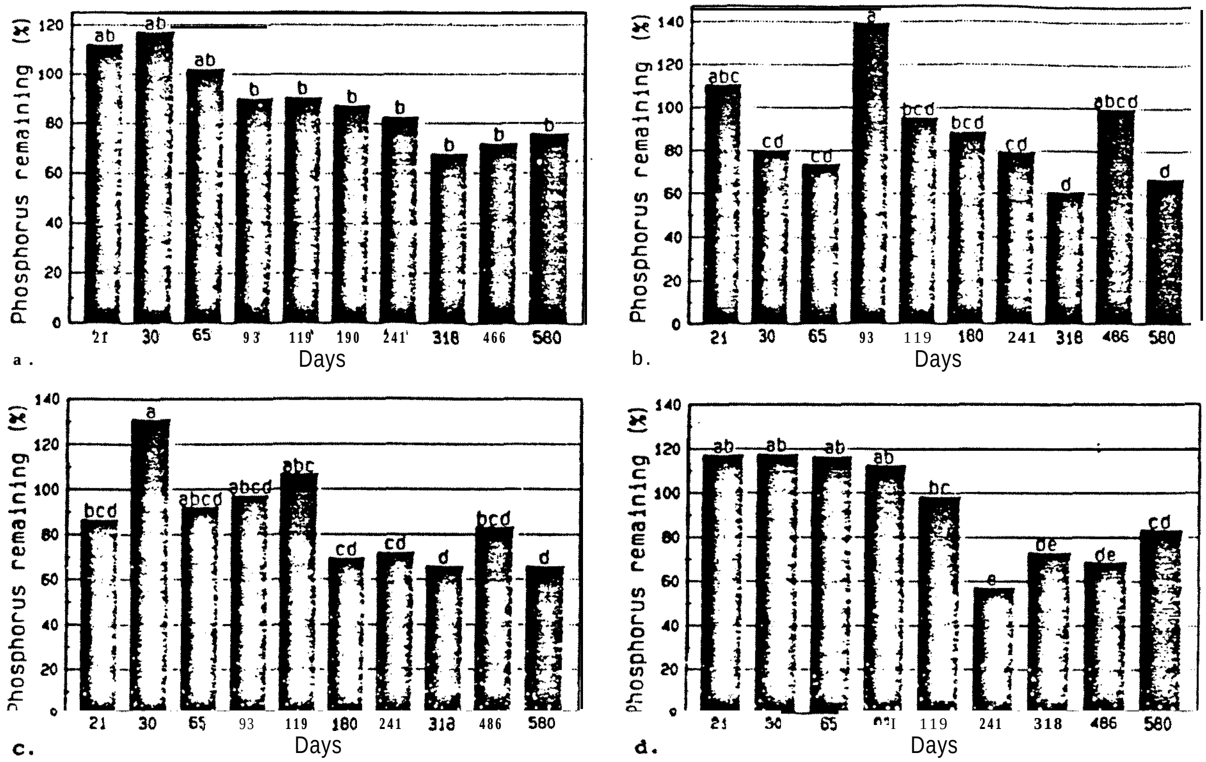

FIG. 2.-P immobilization/mineralization patterns associated with a. no vegetation suppression (Trt 1), b. deciduous vegetation suppression (Trt 2), c. herbaceous vegetation suppression (Trt 3), d. deciduous and herbaceous vegetation suppression (Trt 4)

Our results agree with those of Gower and Son (1992) in terms of the lack of differences between pine-only treatments vs. those with a significant deciduous component in relation to total annual transfer of N and P in litterfall. Forest floor mass turns over more quickly in treatments where either the deciduous, herbaceous, or both components were not sup pressed. The most rapid mass turnover was associated with treatments where the herbaceous stratum was maintained. However, there is less evidence that forest floor N and P follow those trends. Although the proportions of original P remaining in litterbags are numerically less in treatments which include components other than pine, there is less distinction (statistically or numerically) among treatments in terms of N remaining.

These data suggest that, in conjunction with more rapid floor turnover in some communities, microbial activity may be higher and, thus, competition between microbes and

TABLE 3.—Annual litterfall ($g/m^2/yr$)* in four treatments associated with loblolly pine plantations in central Alabama

Component suppressed	Deciduous	Pine	Total
1. None	115.6 a	325.1 bc	440.7 b
2. Deciduous woody	2.8 b	449.5 ab	452.3 b
3. Herbaceous	161.3 a	268.0 c	429.3 b
4. Dec + Herb	0.8 b	597.8 a	598.6 a

* Means in columns followed by the same letter were not different at the $P < 0.05$ level

TABLE 4.—Annual P transfer ($g/m^2/yr$) associated with litterfall in four vegetation treatments

Component suppressed	Deciduous	Pine	Total
1. None	1.15 a	3.28 b	4.43 a
2. Deciduous woody	0.02 b	4.48 ab	4.50 a
3. Herbaceous	1.83 a	3.00 b	4.83 a
4. Dec + Herb	0.00 b	5.33 a	5.33 a

vegetation for N and P may be greater there also. This conjecture is based on the greater vertical distances between immobilization peaks vs. mineralization troughs displayed in Figures la-c and 2b-d vs. those of Figures Id and 2a.

The influence of the herbaceous component on mass turnover is pronounced. Since herbaceous material was not included within litterbags, this influence must reflect modification of the decomposition environment. However, the nature of that modification was not assessed in this study.

There is also little evidence of a direct relationship between our aboveground NPP surrogate (i.e., annual litterfall) and forest floor turnover rates. This conclusion is in agreement with similar observations made by Binkley (1994). It is thus possible that relationships between the two which have been suggested to occur (Gholz and Fisher, 1954; Shepard, 1985; Lockaby and Taylor-Boyd, 1986) may become much more complex when systems with different species composition are compared. Our data support the hypothesized relationship between nutrient restitution via litterfall and aboveground NPP (Vitousek, 1982; Birk and Vitousek, 1986). Although not statistically significant, annual litterfall N and P transfer was highest in the treatment with the highest litterfall value (*i.e.,* treatment 4).

These results accentuate the idea that species composition causes major biogeochemical differences between vegetation communities supported by similar substrate. However, it is also clear that, while evergreen vs. deciduous communities use and circulate nutrients quite differently, the relationship(s) between biogeochemistry and community productivity are complex and are confounded with the availability of other growth factors.

Our data support the assertion that evergreens are more efficient in terms of nutrient use (Monk, 1966; Chapin et *al.,* 1980). While most of those reports have dealt with reabsorption or internal translocation efficiency, our results may indicate that nutrient circulation at the community level is more efficient also. The latter assertion is true if communities with heavy proportions of evergreen can exhibit high productivity while displaying no evidence of increased mineralization rates in aboveground litter. This ability is partially due to the well documented, lower, annual nutrient requirement of pines vs. that of many deciduous species (Kramer and Kozlowski, 19'19). However, it has also been suggested that

TABLE 5.—Annual N transfer ($g/m^2/yr$) associated with litterfall in four vegetation treatments

Component suppressed	Deciduous	Pine	Total
1. None	4.57 a	8.50 b	13.07 a
2. Deciduous woody	0.04 b	13.31 ab	13.35 a
3. Herbaceous	6.03 a	7.42 b	13.45 a
4. Dec + Herb	0.00 b	17.07 a	17.07 a

evergreen systems tend to cycle larger quantities of nutrients in fine root turnover than in litterfall compared to deciduous systems (Vogt *et* al., 1986). Consequently, evergreen systems may not be more efficient than deciduous but may rely on a different prioritization of nutrient circulation mechanisms.

The results presented here may be important in helping to understand the manner in which ecosystem restoration/manipulation efforts may inadvertently alter biogeochemical and productivity functions as particular vegetation components are promoted or discouraged within some forest communities. There presently is significant interest in increasing the deciduous component of upland pine communities of the southern United States (Pearson *et al.,* 1987) while efforts are aimed at decreasing that component in longleaf pine (*Pinus palustris*) systems within the same region. As those changes are implemented, land managers will need as much information as possible regarding the manner in which their attempts at manipulation may, in turn, alter interrelated functions.

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