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Litter decomposition in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics

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To compare litter decomposition and nitrogen (N) dynamics in 16-year-old black locust and pine-hardwood forest stands, weight loss, N concentration, and litter quality of the dominant species in each stand were monitored for 863 days, using litterbags. The species studied were ***Robinia pseudo-acacia*** L. (leaflets and rachises), ***Liriodendron tulipifera*** L., and ***Rubus*** spp. (leaves and stems) in the black locust stand and ***Kalmia latifolia*** L., ***Pinus rigida*** Mill., and ***L. tulipifera*** in the pine-hardwood stand. Between-stand comparison of ***L. tulipifera*** leaf litter indicated a significant stand effect on weight loss during the first 8 months but no significant stand effects on N concentration and net immobilization. Initial lignin content was highly correlated to percent weight remaining and net N immobilization after 33 1 and 863 days. All litter types exhibited an absolute increase in "lignin" that appeared to originate from the more soluble litter fraction. ***Robinia pseudo-acacia*** leaflets, ***P. rigida, K. latifolia,*** and ***Rubus*** stems decomposed slowly, but only the latter two species were in the net N immobilization phase at day 863. ***Rubus*** leaf litter decomposed rapidly, releasing 70% of its original N by day 33 1. The role of ***Rubus*** and other understory species in influencing organic matter and N accretion in these early successional systems is discussed. ***Robinia pseudo-acacia*** leaflets contained 8 1% of their original N at day 863. This retention of N, coupled with its greater potential to form recalcitrant material during decomposition, suggests a mechanism to explain the long-term effects of ***Robinia pseudo-acacia*** on N storage in the forest floor and soil.

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En vue de comparer la décomposition de la litière et la dynamique de l'azote (N) dans des peuplements forestiers âgés de 16 ans de ***Robinia pseudo-acacia*** et de pin-feuillus, les auteurs ont exercé un suivi de la perte de poids, de la concentration en N et de la qualité de la litière de l'espèce dominante dans chaque peuplement, sur une période de 863 jours, en utilisant des sacs à litière. Les espèces étudiées sont ***Robiniapseudo-acacia*** L. (folioles et rachis), ***Liriodendron tulipifera*** L. et ***Rubus*** spp. (feuilles et tiges) dans le peuplement de ***Robinia,*** et ***Kalmia latifolia*** L., ***Pinus rigida*** Mill., et ***L. tulipifera*** dans le peuplement mixte de pin et feuillus. La comparaison inter-peuplement de la litière de ***L. tulipifera*** a indiqué un effet significatif des peuplements sur la perte de poids durant les 8 premiers mois, mais aucun effet de peuplement relatif à la concentration de N et à son immobilisation nette. Le contenu initial en lignine était fortement corrélé avec le pourcentage de poids résiduel et l'immobilisation nette de N aprb 331 et 863 jours. Tous les types de lititre ont montré une augmentation absolue en lignine qui semblait originer de la fraction plus soluble de litière. Les folioles de ***R. pseudo-acacia,*** de ***P. rigida*** et de ***K. latifolia*** et les tiges de ***Rubus se*** sont décomposées lentement mais seulement les deux dernières esptces étaient dans la phase d'immobilisation nette de N au jour 863. La litière de feuilles de ***Rubus*** s'est décomposée rapidement, ayant libéré 70% de son N original après 331 jours. Les auteurs discutent du rôle de ***Rubus*** et autres espèces de la sous-végétation sur l'accrttion de la matitre organique et de N dans ces systèmes de début de succession. Les folioles de ***R. pseudo-acacia*** contenaient 81% de leur N d'origine au jour 863. Cette retention de N, couplée avec son plus grand potentiel à former ***un matériel récalcitrant*** durant la décomposition, suggère un mécanisme pour expliquer les effets à long terme de ***R. pseudo-acacia*** sur le storage de N dans la couverture morte et le sol.

[Traduit par la revue]

Introduction

The chemical quality of litter, through its interaction with macroclimate and the litter biota, largely regulates the rate of organic matter (OM) and nitrogen (N) turnover in the forest floor (Cromack 1973; Fogel and Cromack 1977; Meentemeyer 1978; Aber and Melillo 1982; Melillo et al. 1982). Litter quality is thought to be related to the N requirement and successional status of a species (Aber and Melillo 1982). Species occurring early in succession generally have higher N contents and lower lignin contents than those occurring later in succession. Exceptions to this generality are the two early successional tree species pin cherry (***Prunus pensylvanica*** L.) (Melillo et al. 1982) and the symbiotic N-fixer black locust (***Robinia pseudo-acacia*** L.) (Bartuska and Lang 1981; White 1986), which have both high lignin and high N contents. Aber and Melillo (1982) found that pin cherry had a higher N immobilization rate than species with either lower lignin or lower N contents. Whether this same relationship is seen with black locust or other early successional species is not known.

Black locust frequently becomes established on mesic sites in the southern Appalachians after clear-cutting or pasture

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abandonment (Boring and Swank 1984). The prolific growth of black locust, blackberry (*Rubus* spp.), vine species, and other early successional species after clear-cutting results in the rapid recovery of important ecosystem properties such as leaf area and net primary production (Boring et al. 1987). Large accumulations of OM and N in the forest floor of black locust dominated stands (Auten 1945; Boring and Swank 1984) have been attributed to high rates of litter production (White 1986) and a relatively slow leaf decomposition rate, which in turn has been attributed to the high lignin content of black locust leaves (Bartuska and Lang 1981). The large amount of leaf fall in black locust stands represents one of the major pathways for recycling symbiotically fixed N. Is the N in black locust litter mineralized rapidly or does the high leaf lignin content cause litter to be a temporary sink in the N cycle during early succession? Understanding the factors controlling the rate of N transfer from black locust litter is of prime importance to the further elucidation of this species' role in forest succession and, when considering this species international importance (Keresztesi 1980), its role in site restoration and site productivity.

The objectives of this study were (i) to compare the OM and N dynamics in decomposing litter of the dominant species in black locust and pine-hardwood stands in the southern Appalachians; (ii) to determine the initial litter quality variables of these early successional species that best correlate with litter decay and N immobilization; *(iii)* to evaluate the changes in lignin, cellulose, acid detergent soluble material (ADS), and N in decomposing litter to better understand the factors that regulate N and OM turnover in these systems; and (iv) to determine whether there are site differences between the two stands that could significantly affect the decomposition and N dynamics of tulip poplar *(Liriodendron tulipifera)* litter, which was abundant in both stands.

Study site

The study was conducted on an 8.86-ha, north-facing watershed (WS 6) at the Coweeta Hydrologic Laboratory located in the southern Appalachian Mountains of western North Carolina (35" N latitude, 83" W longitude). The mean annual temperature is 13°C, the mean annual precipitation is 181 cm, and the mean elevation is 1000 m.

In 1958, WS 6 was clear-cut, converted to fescue grass (*Festuca*), limed, and fertilized. Two more fertilizer and lime applications were made, in 1960 and 1965 (Johnson and Swank 1973). In 1966 and 1967 the grass cover was killed by herbicide applications (Douglass et al. 1969) and, thereafter, the watershed was allowed to revegetate naturally. In 1980 the watershed was dominated by black locust, blackberry and raspberry species (*Rubus* spp.), and numerous vine species *(Vitis aestivalis* Michaux, *Clematis virginiana* L., and *Smilax* spp.). Other important woody species were mountain laurel (*Kalmia latifolia* L.), tulip poplar *(Liriodendron tulipifera* L.), pitch pine (*Pinus rigida* Mill.), sassafras *(Sassafras albidum* (Nuttall) Nees.), and red maple (*Acer rubrum* L.) (nomenclature follows that of Radford et al. 1968). In 1982, 21% of the black locust trees were standing dead, and 18% had greater than 50% crown damage, primarily resulting from damage by the locust stem borer (*Megacyllene robiniae* Forster) (Montagnini et al. 1986).

Methods

Sample collection, processing, and experimental design

Freshly senescent leaves of tulip poplar, black locust (leaflets and rachises were separated), mountain laurel, and pitch pine were collected on screens placed beneath each species during October and November 1983. Only leaves falling on screens during dry periods were collected to avoid the effects of leaching after abscission. The senescent leaves of the woody biennial blackberry *(R. allegheniensis* Porter and *R. argutus* Link) were picked directly from 1st-year stems. These leaves were judged senescent when autumn colors were apparent and when the rachis was easily detached from the main stem. Blackberry canes (stems) were taken from 2nd-year stems. Tulip poplar leaves collected under trees in both stands were mixed thoroughly to reduce sample heterogeneity. This was important since litterbags of this species were placed in both stands for the purpose of detecting major differences between stands.

Litter was returned to the laboratory and air dried on screens. After at least 1 week of air drying, approximately 3 g of leaf litter was placed in 10 x 10 cm litterbags made of polypropylene shade cloth, which had a mesh size of approximately 2 mm. Dry weight determinations (65°C) were made on subsamples of each litter type and dry weight correction factors were determined. Blackberry canes were cut into approximately 6- to 8-cm sections before being placed in litterbags.

Eight 2 x 2 m plots were randomly located in each stand. Thirteen litterbags of each species or litter type were randomly placed in each of eight plots within a stand on November 28, 1983. The litter types studied in the PHW stand were the leaves of mountain laurel, pitch pine, and tulip poplar. Litterbags containing blackberry leaves, blackberry canes, tulip poplar leaves, black locust leaflets, and black locust rachises were placed in the BL stand. The three species studied in each stand accounted for approximately 60% of the total litterfall in their respective stands (White 1986). One set of litterbags was collected immediately to determine weight loss due to handling. This same set of litterbags was analyzed for nutrients and litter quality and served as the day 0 measurement. Eight litterbags per litter type were collected approximately monthly through October 26, 1984. Thereafter, four litterbags per litter type were collected July 11, 1985, and six per litter type were collected April 7, 1986, which represents the final collection date reported here (fewer litterbags were collected on these two dates so that the study could be continued into the next year). On each collection date, litterbags were returned to the laboratory, where foreign material (insects, green vegetation, rock fragments) was removed. The litter was then dried at 65°C to constant weight, ground through a l-mm mesh, and stored for further analysis.

Sample analysis

Ash-free dry weight determinations were made on subsamples of each sample by ashing in a muffle furnace at 500°C for 4 h. All values in this study are reported on an ash-free dry weight basis. Additional subsamples were analyzed for total Kjeldahl N by colorimetric analysis for ammonium, using a Technicon autoanalyzer (Technicon Industrial Systems 1970), following a micro-Kjeldahl digestion. Percent C was determined for day 0 samples by using a Leco carbon determinator CR-12 (Leco Corp., St. Joseph, Ml). Samples from each stand and collection date were pooled by species for analysis of percent lignin, cellulose, and ADS (acid detergent soluble material), using the method of Goering and Van Soest (1970), which consists of acid detergent fiber determination followed by hydrolysis with 72% sulfuric acid. The lignin fraction consists not only of "true" lignin but also may contain a variety of other constituents such as cutin, maillard products, and tannin–protein complexes (Van Soest and Robertson 1980). ADS is essentially all plant material that is not cellulose or lignin. Lignin, cellulose, and ADS content of samples corresponding to days 0, 37, 123,214, 331, 588, and 863 were determined using the method of Goering and Van Soest (1970).

The litter quality of samples from days 68, 95, 151, 185, and 241 was determined using near-infrared reflectance spectroscopy

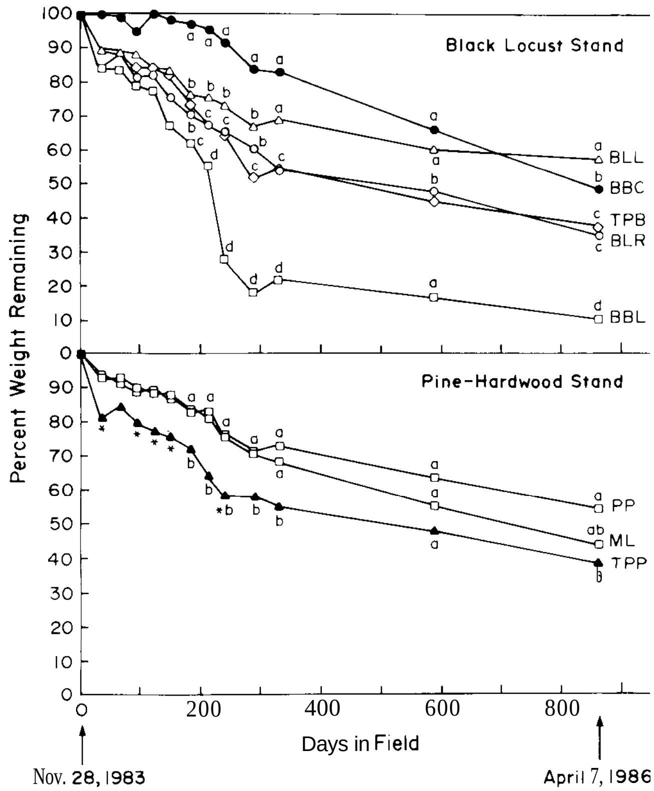

FIG. 1. Change in percent weight remaining over time for the five litter types in the black locust stand and the three litter types in the pine-hardwood stand. Litter type codes are BBL, blackberry leaves; BBC, blackberry canes; BLL, black locust leaflets; BLR, black locust rachises; TPP, tulip poplar (PHW stand); TPB, tulip poplar (BL stand); ML, mountain laurel; and PP, pitch pine. For days 185 through 863, points with different letters indicate significant differences (P < 0.05) between litter types within a stand. *(in the lower graph), significant difference between the BL and PHW stand for tulip poplar leaves.

(NIRS), a recently developed method of forage quality analysis. The advantage of this method over traditional techniques is that once calibration data are generated, litter quality can be determined rapidly (samples analyzed in less than 1 min) without alteration of the sample material. The specific operational principles, methods of analysis, and data treatment are discussed in detail by Marten et al. (1985). Briefly, in this method, samples are ground in a cyclone mill fitted with a l-mm screen, placed in a plastic sample cup consisting of a 3.8-cm (diameter) quartz window, and scanned using a monochromator. This method is based on the fact that each of the major organic constituents of plant material has near-infrared absorption characteristics that allow differentiation between components. In this study, the values determined from standard wet chemistry techniques (Goering and Van Soest 1970) were used to develop calibration data, from which equations were generated. These equations were used to predict the lignin and cellulose content in material of unknown composition. Four different calibration data sets were used to generate equations. The primary factors distinguishing these calibration data sets were the ranges of litter ages and litter types represented by the samples used. Most of the equations used in this study were derived from calibration data containing samples representing all litter types and all sampling dates throughout the 1st year of decomposition. The species-specific equations for predicting percent lignin had standard error of prediction values (standard deviation of residuals) ranging from 0.42 to 2.14. The standard error of prediction for the cellulose equations ranged from 0.96 to 1.78.

Data analysis

An analysis of variance (GLM procedure, SAS 1982) was performed on data of percent weight remaining and N concentration to determine if there were significant species, time, and species x time interaction effects within each stand. A one-way ANOVA was performed on the individual effects followed by the Duncan's multiple-stage test to determine whether significant differences existed (P < 0.05) among litter types on a given collection date as well as among collection dates for a given litter type. However, the experimental error rate is not controlled in the Duncan test and results in a greater probability of type 1 errors. An ANOVA procedure was also performed on data from tulip poplar leaves, which were placed in both stands to determine if there were significant site, time, and site x time interaction effects. When applicable, a t-test was used to compare means between sites for this species.

Results

Weight-loss patterns and initial litter quality

All litter types in the BL stand except for blackberry canes exhibited an initially rapid loss during the 1st month, corresponding to the loss of readily soluble components, followed by a more gradual loss during the winter months through March or April (Fig. 1). A relatively rapid loss was observed through the summer and autumn months. From November 1984 through April 1986 (331-863 days), all litter types except blackberry canes showed a small amount of weight loss (from 11 to 19%), whereas blackberry canes lost 34% of their original weight. By the end of the study period (day 863), black locust leaflets had significantly more weight remaining than any other litter type. Black locust rachises and tulip poplar showed similar amounts of weight loss throughout the study period, while blackberry leaves lost significantly more weight than all other litter types from days 151 through 863. Blackberry leaves lost over 75% of their weight by day 33 1.

The patterns of weight loss described for BL stand litter were also observed in the PHW stand, but the initial phase of weight loss was less rapid for leaves of pitch pine and mountain laurel leaves than for the other litter types (Fig. 1). These two species exhibited almost identical patterns of weight loss for the first 289 days of the study, with moutain laurel leaves appearing to show greater mass loss after day 331, but the difference was not significant. The major difference between tulip poplar and the other two PHW litter types can be explained by the large initial mass loss of the former. After day 68 the rate of weight loss appeared similar.

An ANOVA was used to assess whether or not there were significant site (or stand) effects on the decomposition of tulip poplar leaves. Both main effects, site and time, were significant (P < 0.0004 and O.OOOl), but the interaction of these two variables was also significant ($P < 0.0260$), indicating that the effect of site on weight loss was not consistent through time (Wieder and Lang 1982). Although some statistically significant differences existed between stands during the early stages of decomposition (Fig. 1), it is questionable whether these differences are biologically significant. The N concentration in the remaining tissue was not significantly affected by the stand in which the leaves were placed.

Initial litter quality for the eight litter types is given in Table 1. A correlation analysis of the relationship between initial litter quality of the eight litter types and the percent weight remaining at day 863 is given in Table 2. The cor-

TABLE 1. Concentration of lignin, cellulose, acid detergent soluble material (ADS), and N in various types of senescent litter. The ratios of C:N, lignin:N, and cellulose:lignin are also given

	Initial litter quality						
Litter type	Lignin (%)	Cellulose (%)	ADS (%)	N (%)	C:N	Lignin:N	Cellulose: lignin
Black locust leaflets	18.1	16.4	65.5	2.20	23	8.2	0.91
Blackberry leaves	5.3	19.2	75.5	2.14	26	2.5	3.62
Black locust rachises	15.2	36.8	47.9	1.25	44	12.2	2.42
Tulip poplar (BL)	15.1	26.9	58.0	1.01	40	15.0	1.79
Tulip poplar (PHW)	15.1	26.9	58.0	1.01	40	15.0	1.79
Pitch pine	22.4	23.9	53.8	0.48	95	46.3	1.07
Blackberry canes	19.4	52.1	28.5	0.44	114	44.4	2.69
Mountain laurel	19.1	18.9	62.1	0.42	127	45.1	0.99

TABLE 2. Pearson correlation coefficients of initial litter quality versus the percent weight remaining in all litter types after 863 days

	Initial litter-quality parameter				
Dependent variable	Lignin (%)	N (%)	Lignin:N	C:N	Cellulose: lignin
% weight remaining (863 days)	0.94 (0.001)	– 0.39 (0.34)	0.54 (0.17)	0.39 (0.33)	– 0.80 (0.017)

NOTE: Significance levels are given in parentheses

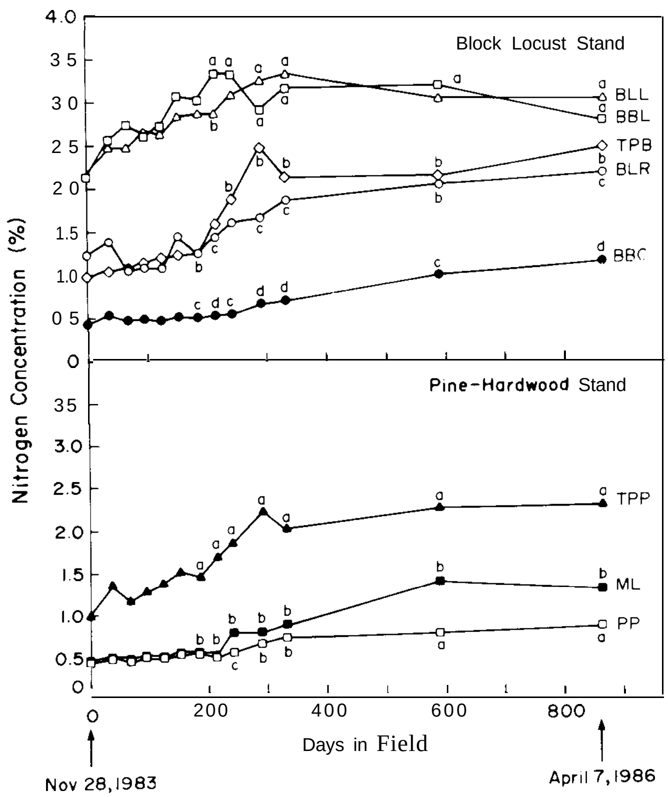

FIG. 2. Change in nitrogen concentration over time for the five litter types in the black locust stand and the three litter types in the pine-hardwood stand. Litter type codes are as for Fig. 1. For days 185 through 863, points with different letters indicate significant differences ($P < 0.05$) between litter types within a stand.

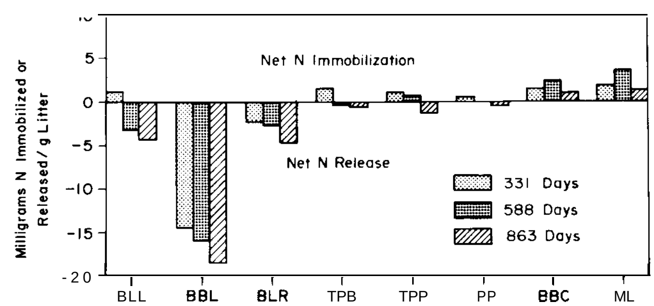

FIG. 3. Net N immobilization or release after 331, 588, and 863 days for each of the eight litter types. Litter type codes are as for Fig. 1. Litter types are given from left to right in decreasing order of initial N concentration.

relation of initial lignin content and percent weight remaining was highly significant. The only other litter-quality parameter that was significantly correlated ($P < 0.05$) with the percent weight remaining was the ratio of cellulose to lignin. When black locust leaflets were excluded from the correlation analysis (data not shown), initial N concentration, in addition to lignin content, was highly correlated with litter decay, as were the other litter quality variables that included N (lignin:N and C:N). Black locust leaflets have the somewhat unusual combination of high lignin and high N content (Table 1), which might explain this difference.

Litter nitrogen dynamics

Nitrogen concentration increased steadily in all litter types during the first 214 days of the study (Fig. 2). Thereafter, different patterns of N concentration change emerged. Only blackberry leaves showed a significant decrease in N con-

TABLE 3. Initial N concentration and the maximum net N immobilized (N_{max}) are given for the eight litter types in the two stands

Litter type	Initial N concentration (mg N/g)	Maximum N immobilization	
		Day	N_{max} (mg N/g)
Black locust leaflets	22.0 (0.4)	151	1.92 (0.25)
Blackberry leaves	21.4 (0.4)	61	1.67 (1.27)
Black locust rachises	12.5 (0.3)	–*	— (-)
Tulip poplar (BL stand)	10.1 (0.4)	289	2.68 (0.76)
Tulip poplar (PHW stand)	10.1 (0.4)	289	2.82 (0.72)
Pitch pine	4.8 (0.2)	331	0.52 (0.24)
Blackberry canes	4.4 (0.3)	588	2.40 (0.49)
Mountain laurel	4.2 (0.2)	588	3.63 (0.99)

NOTE: N_{max} is explained in the text. "Day" represents the collection day on which N_{max} was observed. Standard errors are given in parentheses.
*Net N immobilization was not observed.

TABLE 4. Pearson correlation coefficients of initial litter quality versus the net N immobilized by all litter types after 331 and 863 days

Dependent variable	Initial litter-quality parameter				
	Lignin (%)	N (%)	Lignin:N	C:N	Cellulose: lignin
N immobilized, mg					
331 days	0.87	-0.60	0.52	0.43	-0.77
	(0.005)	(0.11)	(0.19)	(0.29)	(0.03)
863 days	0.88	−0.78	0.68	0.60	−0.68
	(0.004)	(0.02)	(0.07)	(0.12)	(0.07)

NOTE: Significance levels are given in parentheses.

centration (from day 588 to day 863). The most significant N concentration increases from day 331 to day 863 were observed for blackberry canes, mountain laurel, and pitch pine, which generally decomposed slower and had the lowest initial N concentrations of all litter types.

In general, N concentration increased as OM was lost, at least during the 1st year of decomposition (Figs. 1 and 2). Significant ($P < 0.05$) inverse linear relationships between the percent OM remaining through the course of decomposition and N concentration in the remaining material were observed for all litter types (data not shown). This inverse linear relationship has been reported for a variety of litter species over a broad range of environments (Aber and Melillo 1980).

The actual net amount of N immobilized or released by each type of litter is shown in Fig. 3. The litter types are arranged from left to right in order of decreasing initial N concentration at days 331, 588, and 863. Blackberry leaves and black locust rachises were the only litter types in the net release phase at day 331. Black locust leaflets, tulip poplar, and pitch pine were all in the net release phase at least by day 863. Mountain laurel and blackberry canes, the litter types with the lowest initial N concentration, were still in the net immobilization phase at day 863.

The maximum amount of N immobilized, N_{max}, along with the day in which N_{max} was observed, is given in Table 3. Those species with higher initial N concentrations reached N_{max} sooner, but the value of N_{max} was lower than for litter types with low initial N concentrations. With the exception of pitch pine, the longer the time period preceding N_{max}, the higher the N_{max} value.

Results from a correlation analysis (Table 4) of initial litter quality and N immobilization indicated the strong positive effect of initial lignin content on the net N immobilized or released at days 33 1 and 863. The ratio of cellulose to lignin was significantly correlated to N immobilization after 33 1 days but not after 863 days. A significant negative relationship was observed between initial N concentration and N immobilization after 863 days. The fact that both lignin and the ratio of cellulose to lignin were also significantly correlated with the percent weight remaining (863 days) suggests a strong relationship between the rate of OM loss and N immobilization, at least during the 1st year of decomposition.

Litter-quality changes through time

The changes in the absolute amounts of OM, lignin, cellulose, ADS, and N for the eight litter types are illustrated in Fig. 4. For any litter component, an increase above the amount present at day 0 represents an absolute increase in that component and for N, net immobilization. The ADS fraction consists primarily of a soluble portion (sugars, polyphenols, protein), and a relatively insoluble portion (the hemicelluloses), as well as any other compound that is not analyzed as lignin or cellulose. For most litter types, the loss of ADS during the first 37 days of the study exceeded the amount of OM loss during this period, indicating the chemical conversion of some portion of the ADS fraction

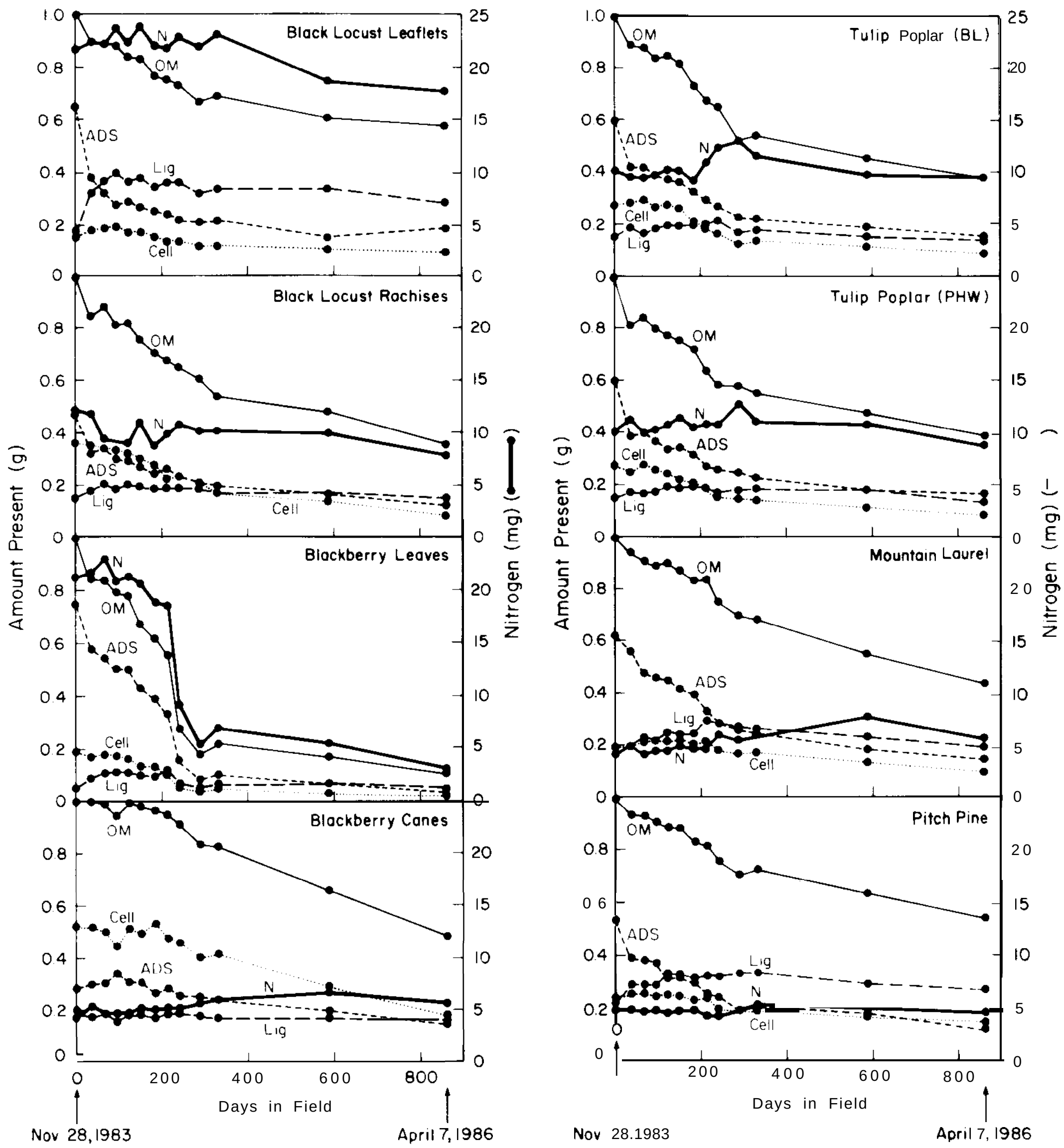

FIG. 4. The changes in absolute amounts of lignin (Lig), cellulose (Cell), acid detergent soluble material (ADS), nitrogen (N), and total organic matter (OM) through time plotted for each litter type in the two stands. These components are standardized to 1 g and are given as the absolute amount present on each collection date. Nitrogen (mg) is given on the right axis.

to either cellulose or the acid-insoluble fraction, lignin. An absolute increase in lignin content was observed during this 1st month for all litter except blackberry canes, which had the lowest initial ADS content. The apparently negative relationship between ADS and lignin can be seen most clearly for black locust leaflets, pitch pine, mountain laurel, and to a lesser degree, tulip poplar (Fig. 4). This relationship persisted through the initial 3 to 5 months of the study, depending on the litter type. Black locust leaflets and pitch pine had the highest lignin content of all species throughout the study period, but the absolute increase in lignin occurred earlier in black locust leaflets. No litter type showed a decrease in absolute lignin content.

After the initial loss of ADS, cellulose and ADS content became more similar for most species, and at some point in time, depending on the litter type, the patterns of loss from these fractions became more similar as well (Fig. 4). An absolute decrease in cellulose content was observed for most litter types during the summer when loss of total OM was greater. It was also during this period when absolute increases of N were most evident for tulip poplar, blackberry canes, mountain laurel, and pitch pine. After an initial N loss, the absolute amount of N in black locust rachises increased through day 588, but not above the initial amount at day 0.

Discussion

Organic matter dynamics

The annual pattern of OM loss in the southeastern United States has been described by a three-component curve, characterized by an initial rapid loss of soluble compounds, very little loss during the colder winter months, and accelerated weight loss during the summer, when macroclimatic conditions are more favorable for decomposer activity (Olson and Crossley 1963; Seastedt et al. 1983). This pattern was observed during the 1st year of this study (Fig. 1). Seastedt et al. (1983) characterized the weight-loss pattern of chestnut oak (*Quercus prinus* L.) during the 2nd year of decomposition as a two-component curve, similar to the 1st-year pattern but without the initial leaching phase. In the present study, detailed weight-loss patterns during the 2nd year cannot be described since samples were only collected on days 588 and 863. All litter types showed a significant weight loss during this period (days 331–863), but the rate of weight loss appeared to be much less than during the 1st year of decomposition with the exception of blackberry canes (Fig. 1). Weight loss reported for the species in this study may be less than what one might expect during a period of normal precipitation. For the period October 26, 1984, through April 7, 1987 (days 331–863), precipitation amounts were substantially below normal.

Organic matter dynamics can be further examined by comparing the changes of the major organic constituents through time. The soluble portion of ADS was lost primarily during the 1st month of decomposition, but additional amounts were released through the first few months (Fig. 4) until ADS probably consisted primarily of hemicellulose, which has a decay rate more similar to that of cellulose (see Swift et al. 1979; Berg et al. 1982). After the initial loss, the ADS fraction should not be viewed simply as hemicellulose since some of the degradation products of both hemicellulose and cellulose are soluble and would be measured in the ADS fraction. The degradation of cellulose and the remaining ADS dominated total OM loss through day 863 with little or no loss of the lignin fraction.

An absolute increase in lignin content was observed for all litter types. Results in Fig. 4 suggest that the increase in lignin is due mainly to the complexing of materials contained in the ADS fraction. Absolute increases in lignin have been attributed to the complexing of soluble polyphenols with protein (Schlesinger 1985; Berg and Theander 1984) as well as to the microbial synthesis of lignin-like materials (Clark and Paul 1970). Berg and Theander (1984) also discuss the formation of phenolics and other aromatic compounds (which might be analyzed as lignin) from the degradation of carbohydrates alone, or in the presence of amino groups, via the Maillard reaction by heat treatment under mild pH conditions.

Although the initial lignin content of black locust leaflets was somewhat less than that of pitch pine and mountain laurel, its relative and absolute lignin content equalled or surpassed these litter types early in the course of the study (Fig. 4), indicating its greater potential to form recalcitrant compounds during decomposition. In general, as decomposition proceeds, litter becomes increasingly dominated by the lignin fraction until the fraction of holocellulose (hemicellulose + cellulose) in the total lignocellulose fraction reaches an asymptotic value (Berg et al. 1984). The rates of loss for lignin and holocellulose subsequently become approximately equal. The quality and the amount of material remaining at this point may be a relative indicator of that litter type's contribution to humus formation (Berg et al. 1984). Based on this general relationship, the higher acid-insoluble or lignin fraction in black locust leaflets during the latter stages of decay suggests that this species may contribute relatively more to humus formation than the other litter types in this study.

Site differences

Results indicated no major site effects on OM and N dynamics in tulip poplar leaves. Since more exogenous N was potentially available for immobilization in the BL stand, in the form of insect frass (White 1986), throughfall (organic and inorganic forms) (L. R. Boring, unpublished data), and soil NO_3 and NH_4 (Montagnini et al. 1986), N immobilization was expected to be greater in this stand. Bocock (1963) found that frass, green litter, and precipitation contributed to the N immobilized in *Quercus petraea* (Mattuschka) Liebl. litter. Evidence in the literature also suggests that N immobilization is greater in forests where legumes are prominent (Hirschfield et al. 1984; O'Connel 1986). If differences existed between the BL and PHW stands, in terms of their influence on N dynamics, the effects would more likely be detected in litter of poor substrate quality or lower initial N content (McClaugherty et al. 1985).

Initial litter quality and weight loss

Initial lignin content correlated best with the final percent weight remaining (day 863). In other studies, lignin content (Cromack 1973; Fogel and Cromack 1977), lignin:N ratio (Melillo et al. 1982), and C:N ratio (Edmonds 1980) have been shown to correlate best with weight loss. The importance of a given litter quality variable appears to be related to both the geographical location of the study and the range of species or litter types evaluated. For the species used in this study neither initial N content, C:N, or lignin:N was highly correlated with the percent weight remaining. When black locust leaflets were excluded from the correlation analysis, however, initial N content was highly correlated to weight loss (r = 0.96). This species, having a high N and high lignin content, decomposed relatively slowly, suggesting the overriding influence of lignin on decay. It has also been shown that excess N can inhibit lignin degradation by the white-rot fungus *Phanerochaete chrysosporium* Burds, through the inhibition of lignolytic enzyme production (Reid 1979; Kirk 1980). Whether this relationship exists in forest litter is not known. Thus, while initial N content may influence the decomposition rate, initial lignin content exerts a greater control over decomposition.

The cellulose:lignin ratio was the only other variable that was significantly correlated to weight loss. The cellulose:lignin ratio did not vary directly with lignin content among litter types (Table 1), indicating that this variable is not simply a function of lignin content. Since lignin is known to interfere with cellulose degradation by preventing access of degradative enzymes to cellulose (as well as hemicellulose) (Fogel and Cromack 1977), this ratio may be a general indicator of the availability of cellulose to microbes.

The combination of high initial N and lignin content observed for black locust (Table 1) (Bartuska and Lang 1981) has also been observed for other early successional woody species such as pin cherry (Melillo et al. 1982) and the N-fixing tree red alder (*Alnus rubra* Bong.) (Edmonds 1980). Aber and Melillo (1982) have drawn similarities between successional patterns in the southeastern United States, where black locust is important, and the northern hardwoods, where pin cherry is important. They also suggest that successional patterns in the northern hardwoods are very different from patterns in the Pacific Northwest, with red alder being a high N and low lignin species. Edmonds (1980), however, reported a relatively high lignin content for red alder leaves and, although it decomposed fairly rapidly during the 1st year of decomposition, it decomposed much slower during the 2nd year, when after 2 years,

TABLE 5. Initial N concentration and the percent original N remaining after 863 days in the field. The relative lignin content (863 days) in also given

Litter type	Initial N concn. (mg N/g)	% original N (at 863 days)	% lignin (at 863 days)
Black locust leaflets	22.0	81	49.1
Blackberry leaves	21.4	14	41.8
Black locust rachises	12.5	63	41.4
Tulip poplar (BL stand)	10.1	95	36.7
Tulip poplar (PHW stand)	10.1	87	35.4
Pitch pine	4.8	92	50.5
Blackberry canes	4.4	124	32.1
Mountain laurel	4.2	132	44.4

the annual decay rate of this species was not significantly different from that of Douglas-fir (*Pseudotsuga menziessii* Mirb. Franco) and other conifer species. Furthermore, high rates of litter production (Gessel and Turner 1974; Radwan et al. 1984) and forest floor accumulation (Zavitkovski and Newton 1971; Luken and Fonda 1983) have been reported for red alder. We suggest that these three species, black locust, pin cherry, and red alder, function similarly during forest development in terms of(i) high rates of OM production and (ii) accumulation of OM and nutrients in the forest floor.

Litter nitrogen dynamics

Net N immobilization after 863 days was positively correlated to initial lignin content and negatively correlated to initial N concentration and appeared to be influenced by the rate of OM loss. By the end of the study period only mountain laurel and blackberry canes were still in the net immobilization phase. This supports the suggestion by Staaf (1980) that litter with the lowest initial N concentration should have a longer immobilization phase. The litter types with the highest initial N concentrations, blackberry leaves and black locust leaflets, reached N_{max} earlier (days 61 and 151) than all other species, but their N_{max} values were less than those observed for tulip poplar, blackberry canes, and mountain laurel (Table 3). The range of N_{max} values reported in this study (0.0 to 3.6 mg N/g) is similar to the range reported by McClaugherty et al. (1985) for hardwood and conifer species in Wisconsin (0.8 to 3.2).

Aber and Melillo (1982) found that the rate of N immobilization (net N immobilized per year) was higher for the species (pin cherry) that had both a high N and a high lignin content. Their explanation was that total immobilization increases with increasing lignin content and decay rate increases with increasing N content. Species with higher rates of decay exhibit higher rates of N concentration increase. This does not appear to be supported in this study since net N immobilization (after 331 days) for black locust leaflets, also high in N and lignin, was not significantly different from that of tulip poplar, mountain laurel, pitch pine, and blackberry canes. This suggests that the relationship observed by Aber and Melillo (1982) may only be applicable within a range of N concentrations. The N concentration of black locust leaflets is substantially higher than that of pin cherry (2.2 vs. 1.2%). Bosatta and Staaf (1982) have suggested that there is a critical C:N ratio for a given litter type, where no further immobilization can occur. Because of the high initial N concentration in black locust leaflets, this litter type may be relatively more limited in terms of the net amount of N that it can immobilize.

In this study, emphasis has been placed on the net amount of exogenous N immobilized or the net N mineralized or released from the various litter types. Although black locust immobilized significantly less N than most other litter types after 588 and 863 days (Fig. 3), it is important to realize that the initial N concentration for most of these species is much lower than that of black locust leaflets. This becomes more significant when considering the proportion of initial N that remains after 863 days (Table 5). At day 863, an amount equivalent to 81% of the original N in black locust leaflets remained, and of the OM remaining at this time, 50% was lignin. Since the lignin fraction in some species has been shown to contain significant quantities of N (Berg and Staaf 1981; Berg and Theander 1984) and since the absolute increase in lignin is brought about largely by the complexing of phenolic compounds and carbohydrates with N containing compounds, it is reasonable to expect that a sizable portion of the total N in black locust leaflets is bound in this recalcitrant fraction. The retention time of this lignin-bound N in the forest floor soil system would be determined by the rate of lignin degradation and the proportion of the lignin fraction that is converted to stable soil OM or humus.

Implications for nutrient cycling in succession

We suggest that a large fraction of the symbiotically fixed N by black locust is in a form that functions as a temporary N sink during succession because of (*i*) the high rates of litter production and forest floor accumulation in black locust stands (Auten 1945; Boring and Swank 1984; White 1986), (*ii*) the large potential to form recalcitrant material during decomposition, and (*iii*) the potential to retain N. The N that accumulates in the sizeable forest floor and soil OM pools may eventually be utilized by the species that replace the relatively short-lived black locust.

While black locust may contribute to relatively long-term OM and N storage in the ecosystem, the shorter term effects of its presence appear to be increased N availability (Montagnini et al. 1986) and the enhanced growth of associated tree, shrub, and herb species (Chapman 1935; Auten 1945; Friederich and Dawson 1984). The greater N availability is at least partially attributable to the relatively large inputs of insect frass and fine organic particulates which originate not only from the dominant canopy species, black locust, but also from the prominent understory herbaceous and vine component (White 1986; L. R. Boring, unpublished data).

The shrub and vine component (including blackberry species) also contributed significantly, both in terms of leaves and stems, to total litter production (White 1986). These species influence N dynamics through the potentially high uptake of the mobile inorganic N fraction during the growing season and through the contrasting decomposition dynamics of their leaves and stems. The leaves of blackberry species decompose quickly, resulting in rapid turnover of a portion of the seasonally sequestered N, while the canes of this species decompose slowly and immobilize significant quantities of exogenous N. These processes are important in regulating seasonal patterns of N availability as well as influencing long term OM and N accretion in these early sucsessional southern Appalachian forests. Understory species, whose positive roles in forest development have received little attention (O'Connel 1986), are generally viewed as undesirable competitors by many forest managers. In light of the findings presented here and elsewhere, these species appear to play an important role in ecosystem development and long-term productivity.

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