THE DISTRIBUTION OF NITROGEN AND PHOSPHORUS IN FOREST FLOOR LAYERS OF OAK-HICKORY FORESTS OF VARYING PRODUCTIVITY

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Abstract: The forest floor plays a major role in the storage and recycling of nutrients which, in turn, are important in maintaining the growth and productivity of forest ecosystems. The development of forest floor organic layers as influenced by litter quality and site quality is unclear. Previous studies in this lab have shown that the size and distribution of available nutrient pools in the forest floor fractions are related to site productivity.

The objectives of this project are to: (1) determine the biomass distributions of forest floor organic fractions across oak-hickory forest sites along a productivity gradient, (2) determine the distribution of nitrogen and phosphorus in these fractions, and (3) determine the relative contribution of nutrients from each forest floor fraction to the available nutrient pool as site productivity changes. Each forest floor-soil core was grossly separated into O_i, O_e, O_a, and mineral soil (A) layers in the field. In the laboratory, the O_a and A layers were further separated into size fractions via wet sieving and flotation. Biomass, total N, and total P were determined for each fraction.

INTRODUCTION

The sustained growth and long-term productivity of forest ecosystems are dependent, in large part, on nutrient availability and uptake. Nutrient inputs from the atmosphere and rock weathering are important to the long-term development of soils and ecosystems, but on an annual basis nutrient recycling within ecosystems forms the major source of nutrients for plant use. Although the forest floor contribution to the total nutrient pool within a site may be relatively small, it is the location where, by weathering and microbial action, nutrients are eventually released from decomposing organic matter and made available for plant uptake and utilization.

Often nutrient dynamics in the forest floor have been studied by following the decomposition dynamics via litterbag studies. Most of these studies are short term (1-3yrs.), and do not take organic matter beyond the "recognizable" stage (Berendse and others 1987, McClaugherty and others 1985, Melillo and others 1982). On the other hand, there are numerous studies that fractionate soil to particle size to determine the presence of soil organic matter (SOM) and its nutrient contents. With most studies, fractionation techniques combine sieving (dry and wet) with sedimentation by gravity and centrifugation in water (Cameron and Posner 1979, Satoh 1976, Suzuki and others 1975, Suzuki and Kumada 1976), or sieving in combination with density separation with liquids of varying specific gravities (Ladd and Amato 1980, Ladd and others 1977a & b, Sollins and others 1984, Sollins and others 1983, Spycher and others 1983, Spycher and Young 1977, Turchenek and Oades 1979, Young and Spycher 1979). These techniques have all been applied to organic material that is smaller than the sand sized fraction, hence "unrecognizable". Few studies have taken undisturbed core samples and analyzed the organic matter that is found in the larger than sand fraction (Ohta and Kumada 1978), or followed nutrients throughout the profile from freshly fallen litter to soil organic matter (Rustad 1994).

This paper is part of a comprehensive, long-term study examining nutrient cycling processes in oak-hickory dominated forest stands throughout the state of Indiana. The study reported in this paper will examine the forest floor physical and chemical characteristics of a range of forest systems, and will quantify the biomass and nutrients

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contained in forest floor organic fractions in oak-hickory sites found along a productivity gradient. The organic material was purified into fractions of differing size from freshly fallen litter to the upper few centimeters of mineral soil. The objectives were to: (1) determine the biomass distributions of forest floor organic fractions across oak-hickory forest sites along a productivity gradient , (2) determine the distribution of nitrogen and phosphorus in these fractions, and (3) determine the relative contribution of nutrients from each forest floor fraction to the available nutrient pool as site productivity changes.

METHODS

Study Site Descriptions

In the preliminary stages of this study, a large number of sites throughout the state of Indiana were surveyed. To be considered, all sites had to be dominated by oak-hickory species with these species comprising at least 50% of the total stand basal area. The initial list of stands was comprised of a gradient of potential site productivities; i.e. site indices ranging from approximately 55 to 95 feet (base-age of 50 for oak species). The relative productivity of these sites was subjectively judged using a combination of data for soil moisture supplying capacity, soil nitrogen supplying capacity, and indicator plant communities (Van Kley and others 1994). The parent material of the soils ranged from thick loess deposits over glacial till with a high moisture holding capacity and high plant available water to outwash sand deposits with very low plant available water holding capacity. Nitrogen supplying capacity in the upper 30 cm of the mineral soil was determined in all stands in the initial pool of sites using 14-day anaerobic incubations (Powers 1980).

From this initial list of stands, five stands best representing a site productivity gradient were chosen throughout the state of Indiana. The selected stands were second-growth, oak-hickory forests with dominant overstory trees in each stand ranging in age from 80-120 years with no signs of disturbance for at least 20 years. The site of highest productivity, identified as Nelson-Stokes (NS), is located in Putnam County in the Entrenched Valley Section of the Central Till Plain Natural Region (Homoya and others 1985). The Russell silt-loam soil (Fine-silty, mixed, mesic Typic Hapludalf) on this site developed from moderately thick loess deposits overlying glacial till. The overstory vegetation is dominated by white oak (*Quercus alba,* L.), northern red oak (*Quercus rubra,* L.), and assorted hickory species (*Carya* spp., Nutt), with a subcanopy dominated by sugar maple (*Acer saccharum,* Marsh.). The site index for oak on this site is approximately 85-90 ft. at a base age of 50 years.

The second site, Feldun Purdue Agricultural Center (Feldun), is located in Lawrence County in the Mitchell Karst Plain Section of the Highland Rim Natural Region (Homoya and others 1985). The soil is a Caneyville silt-loam (Fine, mixed, mesic Typic Hapludalf) developed from a thin layer of loess covering an older paleosol. The site is underlain by limestone bedrock within 60 cm of the surface of the soil. The vegetation is dominated by black oak (*Quercus velutina*, Lam.) , northern red oak, tulip poplar (*Liriodendron tulipifera*, L.), and beech (*Fagus grandifolia*, Ehrh.). The site index for oak is approximately 75-80, and for tulip poplar approximately 95.

The third site is located at the Southern Indiana Purdue Agricultural Center (SIPAC) in DuBois County. This site is located in the Crawford Upland Section of the Shawnee Hills Natural Region (Homoya and others 1985). The soil is a Wellston silt-loam (Fine-silty, mixed, mesic Ultic Hapludalf) derived from moderately thick loess deposits over paleosols derived from weathered sandstone and siltstone. The overstory vegetation is dominated by white oak, hickory, and northern red oak with a subcanopy dominated by sugar maple. The site index for oak is approximately 65-70.

The fourth site is located in Clark State Forest in Clark County in the Knobstone Escarpment Section of the Highland Rim Natural Region (Homoya and others 1985). The soil is Rarden silty-clay loam (Fine, mixed, mesic Aquultic Hapludalf) derived from a very thin layer of loess over soil derived from weathered shale. The overstory vegetation is comprised primarily of white and black oak. The site index for oak is approximately 55-60.

The fifth site is located at the Jasper-Pulaski Fish and Wildlife Area (JP) in Jasper County. This area is in the Kankakee Sand Section of the Grand Prairie Natural Region (Homoya and others 1985). The soil is a Plainfield fine sand (Mixed, mesic Typic Udipsamment). The site is located in an area of outwash sand reworked into dunes. The vegetation is composed almost entirely of white oak and black oak. The site index for oak is approximately 55-60.

In each of the five stands, three plots each measuring approximately 0.75 ha in size were established at random locations. Table 1 describes the basal area and relative dominance of the major species in each of the five sites. Data summarizing indices of potential site productivity: standing above-ground biomass, annual leaf-fall inputs, N-mineralization potential of the soil to 30 cm, soil moisture-holding capacity, and annual precipitation are presented in Table 2.

Table 1: Species composition of the five study stands. The first row under each species gives its basal area (m^2/ha), and the second row under each species gives its relative dominance in each respective stand (%). SI= site index for oak at a base age of 50 yrs.

Species	Nelson-Stokes (NS) (SI= 85-90)	Feldun (Feld) (SI= 75-80)	SIPAC (SI) (SI= 65-70)	Clark (Cl) (SI= 55-60)	Jasper-Pulaski (JP) (SI= 55-60)
White oak	20.6	1.7	22.0	16.0	15.2
	56.7	4.8	68.0	77.5	67.1
Black oak	0.0	11.9	0.2	2.7	6.4
	0.0	33.9	0.6	12.9	28.4
Northern red oak	3.5	3.1	2.4	0.0	0.0
	9.6	8.9	7.4	0.0	0.0
Hickory spp.	4.3	3.5	3.4	1.1	0.0
	11.9	10.1	10.6	5.2	0.0
Sugar maple	4.6	2.3	4.0	0.1	0.0
	12.7	6.6	12.3	0.4	0.0
Beech	0.3	3.7	0.0	0.0	0.0
	0.9	10.4	0.1	0.0	0.0
Tulip poplar	0.5	7.5	0.0	0.0	0.0
	1.3	21.4	0.0	0.0	0.0
Misc.	2.5	1.3	0.3	0.7	1.0
	6.9	3.9	1.0	4.0	4.5
Total Basal Area	36.3	35.0	32.3	20.6	22.6

Table 2. Study site characteristics that represent indices for potential site productivity.

Site	Above-ground Biomass (kg/ha)	Annual leaf-fall (kg/ha)	Annual N via leaf-fall (kg/ha)	N Min. Potential (ug/g)	Avail. Water Capacity (cm/cm)	Annual ppt. (cm)
Nelson-Stokes	246,358	4890	43	58.6	0.23	107
Feldun	221,830	4836	47	52.3	0.18	114
SIPAC	210,319	5145	50	37.2	0.19	107
Clark	124,260	4317	35	36.0	0.19	102
Jasper-Pulaski	124,765	3947	37	13.0	0.05	94

Forest Floor Fractionation

Immediately following leaf fall, twelve 1/10 m^2 forest floor/soil cores from each site (4 per plot) were separated into four principle layers corresponding to the natural horizons: O_i, O_e, O_a, and A mineral soil. The procedure involved placing the sampler on the forest floor, cutting along the edges down through the profile, and hand collecting each horizon. The O_i was all freshly fallen material, the O_e was decomposing but still recognizable material, and the O_a was highly organic but unrecognizable material. The A was sampled to 5 cm below the bottom of the forest floor or O_a horizon. The forest floor in these stands could be best described as mulls to moders. As such, clear delineations are lacking between forest floor organic layers. There is a great deal of mixing of the various forest floor organic layers. In addition, in some of the more mesic stands, litter decomposition proceeds very rapidly. In these stands, much of the litter mass from the previous year decomposes before the current year's leaves senesce, and mixing of various forest floor components can be extensive. In concept, a forest floor horizon is a zone of certain generic characteristics. The nature of the forest floor of the temperate deciduous forests represented in this study is characterized by extensive mixing of the various organic layers. The mixing of horizon components require further separation under laboratory conditions to isolate relatively homogenous components.

Following in-the-field separation, the individual forest floor horizons were hand sorted on a 2 mm sieve to remove any contaminating material from adjacent horizons (Figure 1). Any material falling through the sieve from the O_i, O_e, and O_a layers was included in the O_a horizon. Once contaminating material (i.e. roots, coarse organic material, gravel) was removed from the O_a and the A, these layers were sieved on the 2 mm sieve and the 2 mm fraction was further fractionated by flotation in water (Cameron and Posner 1979) and wet sieving. The entire horizon was placed in 2.5 L of deionized/distilled H_2O, stirred, and allowed to settle for 10 minutes. The floating fraction was removed, placed on a nest of two sieves (250 and 75 um), rinsed until the water cleared, and air dried. This procedure was repeated for the sinking fraction. The floating fractions from the O_a and the A were combined because this (< 2 mm sized organic material) was considered a separate component from the mineral A horizon. Sieve sizes were selected to correspond with studies that fractionated soils into particle sizes (i.e. Sollins and others 1983, Spycher and others 1983, Suzuki and others 1975). In most studies, the 250 um sieve was the largest used, and was used to break up aggregations to obtain the smaller particles. This study is not intended to reach specific particle size, the intent is to capture representative stages of decomposition based on size (aggregations included) as they are found "in nature". Therefore, the 250 um sieve captures all components of "coarse sand" sized (2 mm-250 um), and the 75 um sieve captures all components of "medium sand" sized (250-75 um). In review, for each sample point, four horizons were collected in the field, and eight size fractions were obtained after the final wet sieving step. From this point, the fractions will be

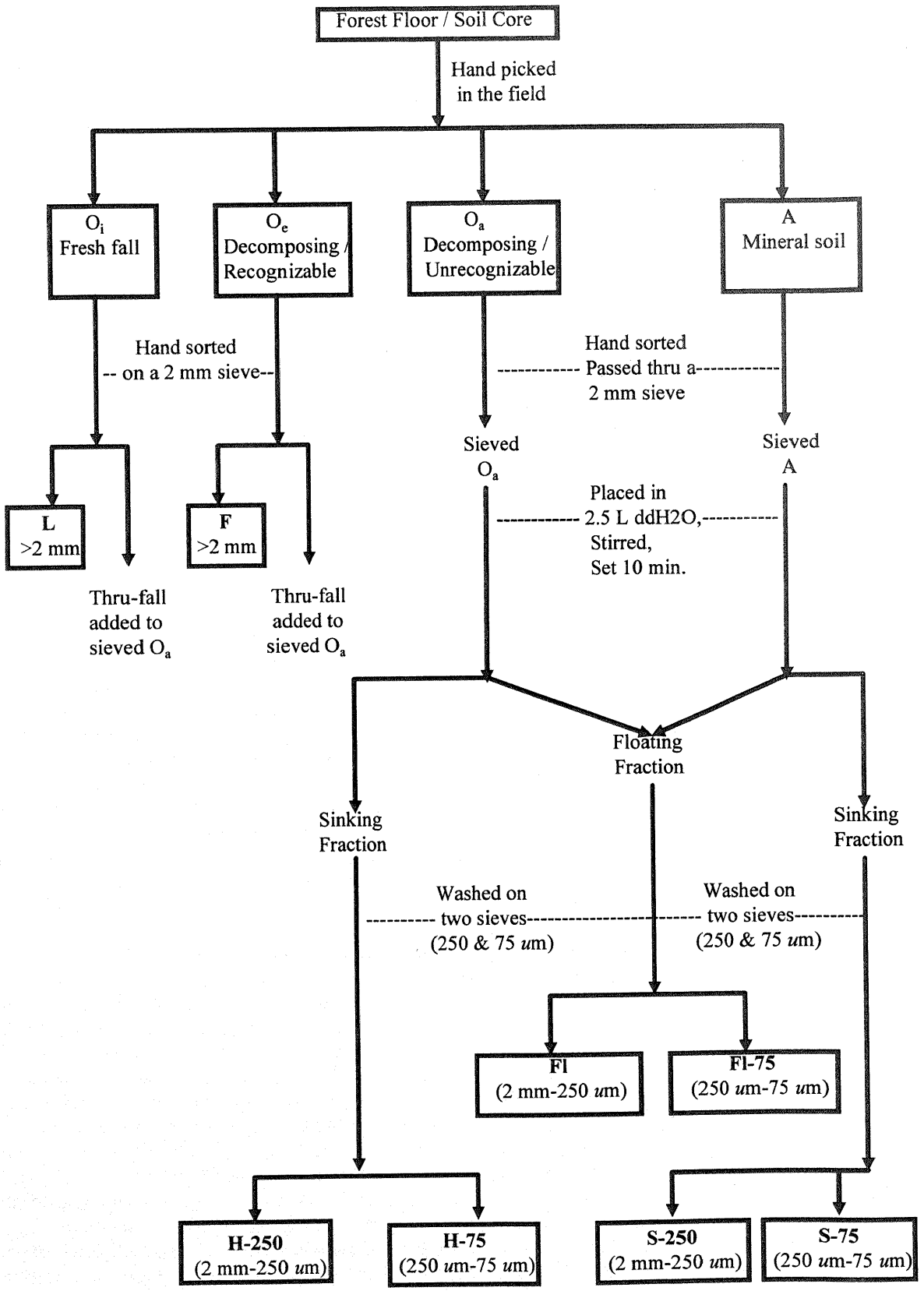

Figure 1. Forest floor fractionation.

called: **L**, corresponding with fresh fall O_i; **F**, O_e material > 2 mm; **Fl**, floating material 2 mm-250 *um*; **Fl-75**, floating material 250 *um*-75 *um*; **H-250**, O_a material 2 mm-250 *um*; **H-75**, O_a material 250 *um*-75 *um*; **S-250**, A horizon material 2 mm-250 *um*; and **S-75**, A material 250 *um*-75 *um*. The fractions could just as easily been numbered 1-8; however, these descriptive labels were chosen to aid the reader in identifying the original source of the material and the minimum size.

Analyses

Biomass was obtained for all eight fractions by placing a 500 mg subsample of each horizon in a 65°C oven until a constant weight was obtained, and correcting the wet weight for moisture. In this study, A horizon mineral soil was considered an organic matter contaminant. The freshly fallen leaves (O_i) were considered free of mineral soil contamination. Visual inspection would indicate that this assumption was true since sample collections were made immediately following leaf-fall and mixing of this layer (O_i) with other layers was minimal at this time of the year. The amount of mineral soil in each forest floor layer increased with increasing proximity to the mineral soil. To account for these differences among components, the mineral soil correction factors described by Blair (1988) were used to determine how much of each respective horizon was actually organic matter. While Blair developed this method to determine mineral soil contamination of litter in litter decomposition studies, this methodology is also applicable to our study. Over extended periods of time, as a single cohort of litter is produced, and the decomposition process proceeds, a portion of this litter gradually becomes stabilized soil organic matter. Thus, in our study the mineral soil was merely considered a contaminating component of the organic fraction. Subsamples of each respective fraction were dry ashed at 450°C for 4.5 hours to obtain % ash-free dry matter (AFDM) and the following equation was used to correct for mineral soil contamination:

$$CF = (SaAFDM - A_tAFDM) - (LAFDM - A_tAFDM)$$

where:
CF is the fraction corrected for mineral soil contamination
SaAFDM is %AFDM of each respective fraction
A_tAFDM is %AFDM of the A horizon
LAFDM is %AFDM of the litter.

This equation assumes that litter inputs are constant over time. That is, that the litter currently being produced on the site is similar in amount and composition to previously produced litter that contributed to the coarse organic fractions in the forest floor and mineral soil. Inherent in this correction factor is the implication that each respective layer is merely a more decomposed representation of the current litter inputs. Through the decomposition process mineral soil contamination will increase due to incorporation of the organic materials into the mineral soil. In addition, the equation also assumes that the A horizon mineral soil is the primary contaminant in each fraction. Based on visual inspection of the forest floor organic layers under natural field conditions and microscopic inspections of the fractionated components, these assumptions are valid.

Total nitrogen (N) was obtained by digesting a 100 mg or 500 mg oven dried subsample by the micro-kjeldahl technique (Nelson and Sommers 1973). One-hundred mg samples were used for highly organic horizons (L thru Fl-75) while 500 mg samples were used for samples that had lower organic matter contents (H-250 thru S-75). The nitrogen contents reported are for the corrected biomass values. Nitrogen concentrations of these fractions were corrected for mineral soil contamination again following the methods of Blair (1988) and Rustad (1994):

$$CFNt = [SaNt - (FSl \times A_tNt)] / CF$$

where:
CFNt is the nutrient concentration for the fraction corrected for mineral soil contamination
SaNt is the nutrient concentration for each respective fraction
FSl is the fraction of sample that is soil
A_tNt is the average conc. of nutrients in the A horizon
CF is the fraction of the sample that is organic.

Total phosphorus (P) was obtained by digesting a 100 mg subsample in perchloric acid and determining P by the phospho-molybdate blue method (Olsen and Sommers 1982). Results for P reported here are based on the fractions before the corrections for soil contamination were made. From these data, N and P concentrations and mass of each respective component on an per hectare a basis, total N and P contents were calculated on a per hectare basis.

Statistical analyses were performed with the general linear model (GLM) procedure contained in the SAS system (SAS institute 1985). In the analysis, plots were nested within sites. Two primary comparisons were made. Within each individual site, comparisons were made between all forest floor components. In addition, comparisons were made between individual forest floor components across sites (i.e. L layer at NS vs. SI vs. JP). Detection of significant differences were made with Duncan's Multiple Range Test at a 5% probability level.

RESULTS

Biomass

Across the site productivity gradient, biomass for the forest floor fractions shows two different trends (Table 3). As productivity decreases, the biomass of the L fraction decreases, with significant differences between the most productive site (NS) and the lowest productive site (JP). JP has consistently and significantly more biomass than NS for all organic fractions other than L. NS contains significantly low amounts of biomass in the F, Fl, Fl-75 fractions, however in the last four fractions (H-250, H-75, S-250, S-75) there are no significant differences between biomass and site.

Table 3: Biomass of forest floor fractions corrected for mineral soil contamination (kg/ha).

Forest Floor Fraction	Nelson-Stokes (NS)	Feldun (Feld)	SIPAC (SI)	Clark (Cl)	Jasper-Pulaski (JP)
L	5394 a* : A**	5152 b : AB	4507 b : BC	5646 bc : A	3887 e : C
F	6210 a : C	8063 a :ABC	10455 a : A	7013 ab : BC	9049 bc : AB
Fl	2309 bc : C	2412 c : C	5281 b : AB	3661 cde : BC	6966 cd : A
Fl-75	141 e : C	186 e : BC	435 d : B	394 f : BC	811 f : A
H-250	3263 b : B	2706 c : B	4749 b : B	9060 a : A	11822 ab : A
H-75	1180 d : B	945 de : B	1516 cd : B	1359 ef : B	2896 ef : A
S-250	2395 bc : B	2231 cd : B	3221 bc : B	4578 bcd : B	11976 a : A
S-75	1726 cd : B	1349 cde : B	2023 cd : B	2632 def : B	5274 de : A
Fraction Totals	22,618	22,044	32,187	34,343	52,681

* Column means with the same lower-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.
** Row means with the same upper-case letters are not significantly different at the 5% level using Duncan's Multiple Range Test.

The importance of each fraction within a site was calculated: i.e. the mass of a specific fraction / mass of the total of the eight fractions X 100. Organic material contained in the smaller size fractions tends to become increasingly important as productivity at the site decreases. Similarly, the percentage of the sum of the mass of the first four fractions (L - Fl-75) to the total of all fractions declines as site productivity declines, i.e. NS- 62%, Feld- 70%, SI- 64%, Cl- 49%, and JP- 40%.

Nitrogen Concentration

Nitrogen concentration of a particular forest floor fraction was not affected by site and showed no consistent trend with the site productivity gradient (Table 4). At each site, N concentration tended to be greatest in the Fl and Fl-75 fractions, followed by the H-250 and H-75 fractions, the L and F fractions, and the S-250 and S-75 fractions. The N concentrations for the A fractions represent total N in the A horizon (mineral soil and organic matter < 2 mm). Nelson Stokes, on the high end of the productivity gradient, and Jasper-Pulaski, on the low end of the productivity gradient were significantly different, and each was different from the sites representing the moderately high to moderately low productivity sites.

Table 4. Nitrogen concentrations (%) in forest floor layers corrected for mineral soil contamination.

Forest Floor Fraction	Nelson-Stokes (NS)	Feldun (Feld)	SIPAC (SI)	Clark (Cl)	Jasper-Pulaski (JP)
L	0.88 f* : BC**	0.98 ef :A	0.97 ef : A	0.82 c : C	0.93 d : AB
F	1.53 cd : A	1.23 de :B	1.24 cd : B	1.19 b : B	1.60 bc : A
Fl	2.25 b : A	1.85 b : B	1.75 b : B	1.71 a : B	2.22 a : A
Fl-75	2.60 a : A	2.44 a : AB	2.00 a : C	1.87 a : B	2.26 a : B
H-250	1.45 de : AB	1.54 c : AB	1.41 c : AB	1.24 b : B	1.80 b : A
H-75	1.75 c : A	1.40 cd : A	1.68 b : A	1.75 a : A	1.47 c : A
S-250	1.19 e : A	1.00 ef : ABC	1.06 de : AB	0.71 c : C	0.80 d : BC
S-75	1.81 c : A	0.89 f : B	0.80 f : B	0.63 c : B	0.77 d : B
A	0.24 g : A	0.19 g : B	0.19 g :B	0.21 c : AB	0.14 e : C

* Column means with the same lower-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.
** Row means with the same upper-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.

Phosphorus Concentration

At all sites, phosphorus concentrations in the F and Fl forest floor fractions were significantly greater than the other fractions (Table 5). For a specific site, the P concentration was greatest for the Fl fraction followed by the F fraction and tended to be followed by the L, H-75, H-250, Fl-75, and the S-250 and S-75 fractions.

Table 5. Phosphorus concentrations (%) in forest floor fractions not corrected for mineral soil contamination.

Forest Floor Fraction	Nelson-Stokes (NS)	Feldun (Feld)	SIPAC (SI)	Clark (Cl)	Jasper-Pulaski (JP)
L	0.077 c* : B**	0.069 c : C	0.062 c : C	0.050 cd : D	0.129 b : A
F	0.119 b : A	0.101 b : B	0.096 b : B	0.096 b : B	0.121 b : A
Fl	0.146 a : A	0.125 a : B	0.113 a : B	0.123 a : B	0.152 a : A
Fl-75	0.058 d : AB	0.040 e : BC	0.046 de : BC	0.036 de : A	0.077 c : A
H-250	0.055 d : A	0.055 cd : A	0.055 cd : A	0.044 de : A	0.060 c : A
H-75	0.090 c : A	0.065 c : B	0.062 c : B	0.062 c : B	0.064 c : B
S-250	0.043 d : A	0.044 de : A	0.020 f : B	0.037 de : AB	0.019 d : B
S-75	0.023 e : AB	0.031 e : A	0.032 ef : A	0.028 e : A	0.011 d : B

* Column means with the same lower-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.
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Nitrogen Content

Nitrogen contents of all of the forest floor fractions (Table 6) tended to follow a pattern similar to forest floor biomass, i.e. except for the L fraction, the JP site had significantly more total N in each fraction than the other sites including NS the highest productivity site. When the importance of each fraction is calculated against the total of all fractions, the F fraction at all sites except JP has significantly more N than the other fractions. Sites at the higher end of the productivity gradient have 65% of the N content in the first four fractions (L - Fl-75) whereas the lower productive sites have their N more evenly distributed through the profile.

Phosphorus Content

The P content of all forest floor fractions at the JP site was significantly greater than the P content of the same fractions at the other sites (Table 7). The P content in all fractions tended to decrease as site productivity increased. Similar to N content, within each profile, the F fraction has the highest P content for the more productive sites (NS, Feld, and SI), and at the lowest productivity site (JP) the P content of the O_a fractions (H-250, H-75) tended to be greatest. Although P is distributed through the profile, there is still a shift from the upper fractions (L - Fl-75) of 55-60% of the P at the higher productivity sites, to 40-45% in these same layers at the lower end of the productivity gradient.

Table 6. Nitrogen content (kg/ha) in forest floor fractions corrected for mineral soil contamination.

Forest Floor Fraction	Nelson-Stokes (NS)	Feldun (Feld)	SIPAC (SI)	Clark (Cl)	Jasper-Pulaski (JP)
L	47.3 b* : A**	51.0 b : A	43.9 cd : AB	46.7 c : A	36.3 d : B
F	98.5 a : B	94.9 a : B	125.6 a : A	84.0 a : B	141.0 b : A
Fl	51.7 b : B	45.9 b : B	81.2 b : B	62.5 b : B	156.1 b : A
Fl-75	3.7 d : B	4.7 c : B	7.7 f : B	7.4 f : B	18.7 d : A
H-250	47.7 b : B	43.3 b : B	64.9 bc : B	80.1 a : B	212.8 a : A
H-75	19.0 c : B	13.5 c : B	24.4 def : B	23.8 de : B	43.7 d : A
S-250	22.9 c : B	23.4 c : B	36.4 de : B	37.9 cd : B	88.5 c : A
S-75	23.3 c : AB	12.5 c : B	15.5 ef : B	14.5 ef : B	33.0 d : A
Fraction Totals	314.1	289.2	399.6	356.9	730.1

* Column means with the same lower-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.
** Row means with the same upper-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.

Table 7. Phosphorus content (kg/ha) in forest floor fractions not corrected for mineral soil contamination.

Forest Floor Fraction	Nelson-Stokes (NS)	Feldun (Feld)	SIPAC (SI)	Clark (Cl)	Jasper-Pulaski (JP)
L	4.15 c* : B**	3.56 bc : B	2.79 c : C	2.86 b : C	5.02 de : A
F	8.44 a : B	8.67 a : B	11.36 a : A	7.58 a : B	11.95 bc : A
Fl	4.12 c : B	3.57 bc : B	6.46 b : B	6.07 a : B	13.54 bc : A
Fl-75	0.13 d : B	0.15 e : B	0.28 d : B	0.25 b : B	1.14 e : A
H-250	5.80 b : B	4.66 b : B	6.89 b : B	7.18 a : B	22.11 a : A
H-75	3.23 c : B	2.12 cd : B	2.68 c : B	2.51 b : B	7.64 cd : A
S-250	3.54 c : B	4.37 b : B	2.61 c : B	8.49 a : B	14.93 b : A
S-75	1.18 d : B	1.93 d : AB	1.71 cd : AB	2.08 b : AB	2.50 de : A
Fraction Totals	30.59	29.03	34.75	37.02	78.83

* Column means with the same lower-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.
** Row means with the same upper-case letter are not significantly different at the 5% level using Duncan's Multiple Range Test.

DISCUSSION

The forest floor plays a critical role in nutrient cycling in forest ecosystems. It is the zone where plant organic materials are converted to stable soil organic matter. Understanding forest floor developmental processes is a major step toward understanding nutrient cycling in forest ecosystems. Forest floor development appears to be controlled by several prime factors. Among these are macroclimate variables such as temperature and seasonal moisture availability (Meentenmeyer 1978), microclimate site characteristics (Berg and others 1993, Paul and Clark 1989), and the chemical composition of the detrital inputs to the system (Aber and Melillo 1982, Blair 1988, Melillo and others 1982). The forest floor represents an integration of all these factors. The forest floor characteristics measured in our study represent many years of development. Federer (1984) found that it took approximately 50 years of development for forest floor organic layers to reach a steady-state following disturbance events in northern hardwood forest ecosystems. Thus, it would appear that the forest floor differences observed in these stands are the result of long-term differences in developmental processes observed at the various sites. Likewise, current developmental processes in these stands will be reflected in future forest floor characteristics. The interacting influences of these factors control decomposition rates of litter inputs to forest systems. The rate of decomposition in turn will affect nutrient mineralization/ immobilization patterns (Melillo and others 1989) and may directly affect the development of the forest floor.

The primary purpose of our study was to quantify differences in biomass and nutrients in forest floor organic layers in oak-hickory dominated stands distributed along a productivity gradient. The stands selected differed in soil water availability, and nutrient availability (Table 2). These factors subsequently interact to control the species composition of the stands. While the oak-hickory species group dominated the basal area and litter inputs in each stand, the importance of mesic site species such as sugar maple and yellow poplar increased as soil moisture holding capacity and nitrogen availability increased. Based on the results of previous studies, (Aber and Melillo 1982, White and others 1988) these differences in species composition between the five stands led to litter inputs of differing initial chemical characteristics. This study was designed to determine if the integration of these differing controlling factors subsequently affected forest floor development and N and P storage patterns.

Forest Floor Biomass

This study, and supporting data from previous work (Table 2), found that on an annual basis, the litter inputs into the systems were directly related to potential site productivity. As site quality decreased, annual leaf-fall also decreased in mass and returned a lower total quantity of nitrogen to the site. Below freshly fallen litter, however, biomass of the various layers of the forest floor have an inverse relationship to site productivity. These data are consistent with the conclusion that decomposition is slowed by conditions that do not promote microbial growth or activity (Swift and others 1979). As a result, organic materials tend to accumulate as decomposition rates are reduced.

Several factors may influence forest floor developmental processes. The inherently low soil water-holding capacity of the lower productivity sites would, over time, tend to limit the rate of litter decomposition and favor and accumulation of forest floor biomass (Meentenmeyer 1978). The lower productivity sites are dominated by oak species which produce litter characterized by high lignin/nitrogen ratios (Aber and Melillo 1982, White and others, 1988). The higher productivity sites, while still dominated by oak leaf-fall, have more of a mix of species which Seastedt (1984) hypothesized would stimulate the decomposition of adjacent recalcitrant litter types. On the xeric, nutrient poor sites, annual leaf-fall was composed almost entirely of oak foliage. At the Jasper-Pulaski and Clark sites, oak leaves accounted for 95% and 85% of the annual leaf-fall respectively. Litterfall on the more mesic sites i.e. Nelson-Stokes and Feldun , while still dominated by oaks, this component of the annual litterfall is lower and ranges from 52 - 60%. The differing chemical characteristics of the various species found in the stands may account for the differences in biomass accumulation observed in the forest floor at each site.

Studies conducted throughout the country have demonstrated the recalcitrant nature of oak litter. Oak litter is typically characterized by a chemical composition which leads to subsequent slow decomposition rates. Lignin concentrations in oak litter are usually between 20-25% of the dry weight (Aber and others 1990) while other

associated species such as yellow poplar (15%) (White and others 1988), sugar maple (12%) (Aber and others 1990), red maple (10%), or dogwood (5%) (Blair 1988) have much lower lignin concentrations. In all these studies, oak litter was found to decompose at much slower rates than the associated species with lower lignin concentrations. Although lignin can be degraded by soil microorganisms, the rate of lignin degradation is 1/10th to 1/20th the rate of cellulose degradation (Berendse and others 1987). The early stages of litter decomposition are characterized by rapid weight loss as cellulose is degraded by microorganisms. The late stage of litter decomposition is characterized by very slow rates of decomposition as microbial populations utilize the recalcitrant lignin fraction of the litter. The lignin in the decomposing litter may also serve as one of the primary building blocks of stabilized soil organic matter (Paul and Clark 1989). The combined effects of site environmental conditions that retard the decomposition process and litter inputs that are inherently more resistant to decay may be responsible for the increased forest floor biomass observed on the lower productivity sites.

The relative importance of the various forest floor layers changed with changes in site productivity. On the more productive sites, the litter and fermentation layers contained a higher percentage of the forest floor biomass than on the less productive sites. On the low productivity sites, the biomass of the H-250 and the S-250 were higher. These lower forest floor and mineral soil horizons are composed of organic materials that have progressed to a late stage of decomposition. The greater biomass in these layers may again be related to the chemical composition of the litter. Melillo and others (1982) found that the amount of humus formed from a litter material was directly related to the lignin concentration of the litter. This reinforces the observation that although inputs to the system are lower on the lower productivity sites, the slower decomposition rates on the more xeric sites offsets the lower inputs, and over time, leads to greater biomass accumulation in the lower soil horizons.

Nutrient Concentrations

The combination of the four lower fractions (H-250, H-75, S-250, and S-75), which represent latter stages of decomposition of the forest floor, had relatively more biomass than the combination of the upper forest floor fractions (L, F, Fl, and Fl-75)at the lower productivity sites, but the nitrogen concentrations of these fractions were not different. This result is consistent with Melillo and others (1989) who hypothesized that litter materials of differing initial chemical composition would be converted to a relatively homogenous material during the late stages of decomposition . The differing litter inputs did appear to be converted to a common substrate with a relatively constant nitrogen concentration. These data supported the idea that the fractionation technique presented in this paper was isolating fractions of similar "quality" or organic content across sites.

Nitrogen concentrations in the forest floor profile showed similar trends across all sites. Nitrogen concentrations increased through the first 4 forest floor organic layers (L, F, Fl, and FL-75). Initial litter inputs in these systems were characterized by relatively low nitrogen concentrations and high carbon concentrations (Kaczmarek and others 1994). Litter with high C/N ratios such as these may initially immobilize nitrogen. It is only after decomposition proceeds that a net mineralization of nitrogen occurs (McClaugherty and others 1985). Fractions representing later stages of decomposition (i.e. H-250 - S-75) , had decreased nitrogen concentrations. *In-situ* litter decomposition studies are currently in place in all five of these stands. In these studies mass loss and nutrient concentrations will be determined and these data used to determine the stage of decomposition at which nutrient immobilization/mineralization takes place in the litter. Explanation of the slight "peaks" in N concentration observed at the H-75 layer (at NS, SI, CL), and the S-75 layer (at NS) may come from studies in which particles of smaller sizes where shown to have higher nitrogen concentrations (Cameron and Posner 1979, Young and Spycher 1979). In these studies, all organo-mineral aggregates were dispersed and as particle size decreased from sand to clay, nitrogen concentration increased. Our study did not try to disperse microaggregates, and it is possible that the material that stayed on the 75 um sieve is made up of silt and clay sized microaggregates. These microaggregates would include soil organic matter (SOM), and/or microorganisms and microbial byproducts occluded on or trapped in silts and clays as described by Cameron and Posner (1979), and therefore, would show higher concentrations of nitrogen than the layer above.

Phosphorus showed no strong trends along the productivity gradient. Phosphorus concentrations increased at all sites through the first three fractions (L, F, and Fl) except at the JP site at which there was a slight drop from the L to the F

with further increases in phosphorus concentrations after that fraction. In short-term decomposition studies such as Blair (1988) and Rustad (1994), P was shown to initially decrease in litter. After approximately six months, phosphorus concentrations began to increase as phosphorus was immobilized. These data can be compared to our study in that the first three layers obtained through our separation technique are similar to the stage of decomposition achieved in a 24 month decomposition study . Our results are similar to the results by Blair (1988) and Rustad (1994) except that we did not detect an initial decrease in P concentrations at the higher productivity sites. The JP site is somewhat of an anomaly in that soil N availability is low, but soil P availability is high. Phosphorus concentrations in all plant tissues sampled at this site have always been very high (Kaczmarek unpublished data). In addition, foliage samples collected during the growing season and at autumnal leaf-fall have demonstrated very low P retranslocation at this site. Whereas white oak on the other sites sampled retranslocated 60-70% of their tissue P concentrations, white oak at the JP site retranslocated less than 20% of foliar P (Kaczmarek unpublished data). Dalla-Tea and Jokela (1994) found that P retranslocation in southern pines was inversely correlated with soil P availability. In addition, P dynamics during the decomposition process depended upon soil P availability upon which the trees grew that produced the leaf-fall. High soil P availability increased the inorganic P concentrations in the leaf-fall. This inorganic P was subject to rapid leaching losses early in the decomposition process (Polglase and others 1992). The high P availability at the JP site may be creating similar P dynamics in the litter produced at this site.

Nutrient Contents

Nitrogen and phosphorus storage in the various forest floor layers was dependent upon the biomass and nutrient concentration of the layer. Total nitrogen storage ranged from approximately 300 kg/ ha on the high productivity sites to over 730 kg/ ha at the low productivity sites. As site quality decreased, increasing percentages of the nitrogen in the forest floor are found in the lower fractions (H-250 - S-75), whereas on higher quality sites the trend is reversed. In addition, as site quality decreased, the relative percentage of nitrogen contained in the forest floor humus (represented by H-250) layer increases. This again reinforces the observation that the biomass and hence nitrogen storage capacity of this layer is enhanced under low productivity conditions.

Phosphorus content of all of the forest floor organic fractions at the Jasper-Pulaski site was 79 kg/ha. Phosphorus contents for all other sites were 29 to 37 kg/ ha and did not show any strong trends by site productivity. The high phosphorus content at Jasper-Pulaski was a function of the high biomass and elevated phosphorus concentrations in the organic material sampled. The majority of the phosphorus at these sites was contained in the fermentation, floating, and humus fractions.

SUMMARY

The results of this study indicate that forest floor organic layers in these stands contain appreciable pools of nitrogen and phosphorus. The results also indicate that forest floor development follows different patterns in sites of differing productivity. In mesic, nutrient rich stands, leaf and litterfall occur at high levels, but the stand environmental conditions that favor this high litter production also favor relatively rapid decomposition rates. As a result, relatively low quantities of biomass remain in the O_e and O_a layers. On the less productive sites, water and nutrient limitations favor almost complete stand domination by oak species. Annual litter inputs are low, but subsequent decomposition of these resistant materials is slow especially under the xeric, nutrient poor conditions characterized by our study sites. These conditions result in relatively high biomass in the O_e and O_a layers. Nitrogen and phosphorus concentrations also change throughout an individual forest floor profile. Beginning with freshly fallen litter material, nitrogen and phosphorus concentrations increase in the decaying tissues. It is only in the latter stages of decomposition that nutrient concentrations decrease. The potential impact of the forest floor organic layers should be considered when management decisions concerning these study areas are made. On the more productive sites, the forest floor layers contain relatively small amounts of nutrients. On the less productive sites however, the amount of these nutrients is relatively large. These results may indicate that the forest floor organic layers serve as a nutrient conserving mechanism and any catastrophic event that would destroy the forest floor organic layers could drastically alter nutrient recycling characteristics of these systems. It also appears that the rate of nutrient turnover in these systems

will outweigh the absolute pool size of nutrients in determining nutrient availability. While the sites with a lower potential site productivity have a greater pool of N in the forest floor, the site conditions may slow the turnover of this pool. *In-situ* N mineralization studies are currently in place in each of these stands to assess N mineralization and nitrification patterns across the productivity gradient. Future research on the forest floor layers will focus on the carbon and lignin they contain as well as assessing nutrient availabilities and microbial biomass contributions to nutrient cycling in these stands.

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