CARBON AND NITROGEN POOLS IN OAK-HICKORY FORESTS OF VARYING PRODUCTIVITY

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Abstract: Carbon (C) and nitrogen (N) storage capacities are critical issues facing forest ecosystem management in the face of potential global climate change. The amount of C sequestered by forest ecosystems can be a significant sink for increasing atmospheric CO_2 levels. N availability can interact with other environmental factors such as water availability or temperature to control potential forest productivity. This in turn, may determine the amount of C that can be sequestered in forest ecosystems.

This study was designed to quantify C and N pools in oak-hickory dominated forest stands of varying productivity. Sites selected were second-growth upland oak forests with site indices ranging from approximately 55 to 90 (base age of 50 years of white oak). This wide range of potential site productivities was selected to determine if patterns of C and N storage vary with changing site productivity. Carbon and N pools were determined for the following components: living aboveground biomass, root biomass, annual litterfall, forest floor layers, and the mineral soil. Results indicate that total C and N storage increases as site productivity increases, but that the relative importance of these components may vary with changes in site productivity. In addition, the annual nutrient inputs from the various pools may vary directly with changes in site productivity.

INTRODUCTION

Under changing environmental conditions, forest ecosystems become increasingly more important as both sources and sinks for nutrients. In particular, the role of forest ecosystems to serve as potential sinks for increasing atmospheric CO_2 concentrations has become increasingly more important to develop global carbon budgets. There has also been concern about the possible impacts of increasing atmospheric nitrogen deposition in forest ecosystems and the ability of forest ecosystems to adapt to potential increasing nitrogen inputs in highly industrialized regions. Conversely, as utilization and management of forest resources continue to increase, questions have arisen concerning the long-term sustainability of these practices. In particular, as intensive harvesting becomes more widely practiced, will these forest systems continue to be self-sustaining or will nutrient limitations become apparent? If the potential impacts of environmental changes and management activities are to be determined, the carbon and nitrogen storage characteristics of forest ecosystems under current conditions must be determined.

Most previous studies examining nutrient storage patterns in forest ecosystems have shown that the nutrient storage potential of the living biomass and the soil at a site are often high and that in the long-term, these pools may contain the majority of nutrients within a forest stand. In mature undisturbed forest stands, the short-term availability of nutrients within a site is determined by the annual inputs of nutrients via litterfall, fine root turnover, mineral weathering, symbiotic nitrogen fixation, and atmospheric inputs. In undisturbed old-growth forest stands, the addition and turnover of nutrients through the mortality and decay of senescent trees can represent a highly significant input of nutrients into these systems. However, in younger, aggrading forest ecosystems, the addition of organic matter and nutrients through tree death is usually a relatively minor component of inputs. Following large scale disturbance such as timber harvesting, extensive fires, or mortality caused by insects or disease, the potential nutrients

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returned to the site from the aboveground biomass can be significant in young stands. However, in young forest stands lacking catastrophic disturbance events, the yearly inputs of aboveground leaf and litter fall and belowground root production and turnover will be significant in determining the amount of nutrients available to the forest stand.

There have been a host of studies that have examined the carbon and nitrogen storage patterns of different forest ecosystems, but few studies have determined if nutrient storage patterns differ within a single ecosystem distributed along a productivity gradient. In this context, this study was designed to determine the carbon and nitrogen storage patterns of oak-hickory dominated forests distributed along a productivity gradient. The study concentrated on quantifying and determining the relative importance of pools in these forest stands. Greatest emphasis was placed on those pools that undergo relatively rapid turnover in these second-growth forest stands; therefore, sampling intensity was greatest for annual leaf-fall, forest floor organic layers, and fine root components.

METHODS

Five study sites distributed throughout the state of Indiana were selected for this study. All study locations were in second-growth oak-hickory dominated forests having overstory trees ranging from 80-120 years of age. The oak-hickory species group comprised at least 55% of the basal area in each stand, but associated species differed among the various sites. Sites were chosen that represented a broad range of potential site productivities ranging from xeric, nutrient poor to mesic, nutrient rich sites. On the two more xeric sites, the oak-hickory group comprised 95% of the total stand basal area, while on the more mesic sites, the oak-hickory group dominance decreased to 55-70% and mesophytic species increased in importance. Species composition, basal area by species, and relative dominance for each species is listed in Table 1. The study sites, all located in the state of Indiana, are described in order of productivity from highest to lowest productivity.

(1) 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) developed from moderately thick loess deposits overlying glacial till. The overstory vegetation is dominated by white oak, *Quercus alba*, northern red oak, *Quercus rubra*, assorted hickories, *Carya* spp., and has a subcanopy dominated by *Acer saccharum*, sugar maple. The site index for oak is approximately 85-90 feet at a base-age of 50 years.

(2) 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*, northern red oak, tulip poplar, *Liriodendron tulipifera*, and beech, *Fagus grandifolia*. The site index for oak is approximately 75-80 and the site index for tulip poplar is approximately 95.

(3) Southern Indiana Purdue Agricultural Center (SIPAC) is located in DuBois County 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 the subcanopy dominated by sugar maple. The site index for white oak is approximately 65-70.

(4) Clark State Forest is located 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 a subsoil derived from weathered shale. The heavy clay texture of the subsoil restricts water infiltration through the profile during the winter and early spring, but also has a low plant available water holding capacity when water becomes limiting during summer and early fall. During the growing season, soil water potentials typically become very low. The overstory vegetation is comprised primarily of white and black oak. The site index for oak on this xeric, nutrient poor site is approximately 55-60.

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 (%).

			Site		
Site Index	Nelson-Stokes 85-90	Feldun 75-80	SIPAC 65-70	Clark 55-60	Jasper-Pulaski 55-60
Species					
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	3.5	3.1	2.4	0.0	0.0
Red Oak	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
Yellow 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

(5) Jasper-Pulaski is located at the Jasper-Pulaski Fish and Wildlife Area in Jasper County. This area is in the Kankakee Sand Section of the Grand Prairie Natural Region (Homoya and others 1985). This 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 on this xeric site is composed almost entirely of white and black oak. The site index for white and black oak on this site is approximately 55-60.

At each site, three replicated blocks were established at random locations within the stand. Woody vegetation was sampled at each site using 5, 1/20 ha circular plots within each block. All woody vegetation with a diameter at breast height (DBH) of 5 cm or greater was identified and its DBH recorded. Vegetation less than 5 cm in diameter at breast height was not measured. The composite information from these 15 plots at each stand was used to determine the basal area/ha (m^2) and the relative dominance of each species.

Standing aboveground biomass for living trees was determined using equations developed by Hahn and Hansen (1991) and Smith (1985). These equations utilize species specific modified Wiebull volume regressions to determine the volume of the tree. The calculated volume is a function of the diameter of the tree and the site index for that species on the site. Once the volume for each individual tree is determined, this volume is converted to the oven dry weight of the standing aboveground biomass (Smith 1985).

Root biomass was determined by collecting 24 soil cores each measuring 6.3 cm in diameter and 30 cm in length from each stand. All fine root sampling was conducted in August and September. Previous studies utilizing soil pits at each of these sites demonstrated that the vast majority of fine and coarser roots were restricted to the upper soil horizons, therefore, root sampling was restricted to the upper 30 cm of the soil profile. Roots were separated from the soil in the cores by wet seiving on a 120 micron sieve. The roots were then separated into three size classes: fine (0-3 mm diameter), medium (3-10 mm diameter), and coarse (greater than 10 mm diameter). Root samples were then oven dried at a temperature of 65° C for 72 hours to obtain oven-dried weights. Values for each size class were converted to a kg/ha basis using appropriate conversion factors.

Biomass, nitrogen (N), and carbon (C) contained in the forest floor organic layers were determined from 12 randomly located cores from each forest stand. Each core measured 1/10 m^2. Each stand was sampled in the autumn after approximately 95% of leaf-fall had occurred. This protocol was followed to assure that accurate assessments of forest floor biomass and to minimize microbial decomposition of the litter material. Sampling began in the northern part of the state and progressed southward to follow natural leaf-fall patterns. Each core was separated to obtain litter, fermentation, humus layers, and A horizon mineral soil samples. Corrections for mineral soil contamination of the forest floor organic layers were made according to the method of Blair (1988) and Rustad (1994). More detail of the procedure used to make these corrections is available in Rodkey and others (1994). Subsamples of each layer were oven-dried at a temperature of 65° C and these values were converted to a dry weight kg/ha basis. Soil samples for soil horizons below the A horizon were obtained by excavating three soil pits at random locations within each site. Soils were fully described and samples collected from each respective horizon. Annual leaf-fall was determined by placing 15, 1/2 m^2 littertraps at each site. During autumnal leaf-fall, the litter from the traps was collected at approximately biweekly intervals, air dried, and subsamples oven-dried at 65°C to a constant weight to convert all biomass figures to an oven-dried basis.

Nutrient Analysis

Carbon and nitrogen concentrations in annual leaf-fall, standing aboveground biomass, root tissues, and soil samples were determined on a Leco 500 CHN elemental analyzer. Due to the large number of samples, several protocols were developed. The most intensive sampling was reserved for pools which were expected to show the greatest variability between sites and represent frequent turnover rates. Fine roots, forest floor organic layers, and annual litterfall were sampled most intensely. Several assumptions were made to determine carbon and nitrogen storage in aboveground biomass. First, it was assumed that the greatest differences in nutrient concentrations would be found in smaller diameter branches and limbs. Samples of these materials were taken from the dominant species at each site. It was further assumed that tree bole carbon and nitrogen concentrations would remain constant across sites. Inherent in this sampling scheme is some degree of uncertainty. Wood N concentrations will vary from species to species. Johnson and others (1982) found that wood bole nitrogen concentrations could vary as much as 20% between species. Therefore, our sampling likely has this degree of uncertainty in its estimate of aboveground N storage. Wood samples were taken from one site and these values used across sites. Sampling of woody boles and limbs was conducted in mid February to early March well before bud expansion began. Medium diameter roots (3-10 mm in diameter) were assumed to have carbon and nitrogen concentrations equal to branch samples, and coarse diameter roots (> 10 mm diameter) were assumed to have carbon and nitrogen concentrations equal to those found in woody boles.

Samples of forest floor organic layers were also analyzed for nitrogen and carbon concentrations using the Leco 500.

Following carbon analysis, these same samples were dry-ashed in a muffle-furnace at a temperature of 450° C for 4.5 hours. From this information (known carbon concentrations from analysis on the CHN analyzer and mass loss from dry ashing), regression equations were developed to accurately predict carbon concentrations by mass loss due to dry-ashing. R^2 values for these regressions ranged from 0.97-0.99. Nitrogen concentrations in these samples were determined by digesting 100 mg of tissue in 5 ml of concentrated H_2SO_4 in 50 ml Folin-Wu tubes. A mixture of K_2SO_4, $CuSO_4$, and Se in the ratio of 100:10:1 served as a catalyst for the digestion (Nelson and Sommers 1973). Following digestion, the samples were steam distilled, the distillate captured in a mixed boric acid indicator solution and back-titrated using 0.01 N HCl to determine the nitrogen concentration in the tissue.

RESULTS

Basal areas (m²/ha) increased with increasing productivity and ranged from 21 to 36 m²/ha (Table 1). There was also a slight change in species composition with changes in site characteristics. On the two most xeric sites, JP and Clark, the oak-hickory group made up at least 95% of the total stand basal area. The more mesic sites, while still dominated by the oak-hickory group, had a significant component of more mesophytic species such as sugar maple, tulip poplar, and beech.

The standing aboveground biomass varied widely among the five sites examined and was directly related to the site index. Standing aboveground biomass ranged from 124,000 kg/ha on low quality sites to over 245,000 kg/ha on highly productive sites (Table 2). This two-fold difference in standing biomass was due to greater stem density, greater average diameter, and greater average height on the more productive sites. The exclusion of small diameter (< 5 cm) stems from the sampling will have a minor effect on total aboveground biomass. Across the five sites, the number of 5.0-6.4 cm diameter stems ranged from 79-225/ha. These stems would contribute from 1300 to 3800 kg/ha and these stems are accounted for in our sampling methods. Stems less than 5 cm in diameter contribute little to aboveground biomass. Even if there are 1000 stems/ha less than 5 cm in diameter present in these stands, stems of this diameter class would contribute 1000-2000 kg/ha or at most 2% of the total aboveground biomass. These small diameter stems measuring less than 5 cm would however contribute to other processes occurring on the site such as root growth, turnover, and annual litter production and these processes are considered in our other measurements.

Root biomass followed a distinctly different trend from standing aboveground biomass. In contrast to aboveground biomass which increased as site quality increased, fine root biomass (0-3 mm) actually decreased as site quality increased. Fine root biomass demonstrated an approximate two fold difference ranging from 2100 kg/ha on higher quality sites to 3800 kg/ha on lower quality sites. These results would indicate that for these oak-hickory dominated forest stands, proportionally greater amounts of fine roots are needed to maintain the trees in the stand as site quality decreases. Accurate estimates of medium and coarse root biomass is more difficult due to their heterogeneous distributions throughout the stand and medium and coarse rooting in the deeper soil horizons. Biomass on a kg/ha basis for medium roots ranged from under 2000 kg/ha to almost 5000 kg/ha. Similarly, estimates of coarse roots (>10 mm diameter) were also highly variable with estimates ranging from 400 to 5,000 kg/ha (Table 2) indicating the difficulty in accurately assessing this component. Total root biomass, the sum of fine, medium, and coarse roots ranged from 6,300 to 12,400 kg/ha.

Annual inputs to the sites via annual litterfall increased as site productivity increased. Lower quality sites, Jasper-Pulaski and Clark, produced substantially lower autumnal leaf-fall than the more mesic, nutrient rich sites. Other litterfall in the form of seeds, twigs, and branches was similar across the five sites examined and contributed lower total biomass inputs than leaf-fall. These differences in annual leaf-fall are due to differences in stand basal areas which should result in significant differences in leaf area indices between the stands examined (Chapman and Gower 1991).

Forest floor biomass storage showed a distinct trend for greater total biomass on more xeric, nutrient poor sites (Table 2). Total forest floor biomass ranged from approximately 18,000 kg/ha at the mesic, nutrient rich sites represented by Nelson-Stokes and Feldun to over 35,000 kg/ha at the xeric Jasper-Pulaski site. Broken down into its individual

Table 2. Biomass of each respective component at the Nelson-Stokes, Feldun, SIPAC, Clark, and Jasper-Pulaski sites. Values are given in kg/ha. Standard deviations are in parentheses under each respective value.

			Site		
Component	Nelson-Stokes 85-90	Feldun 75-80	SIPAC 65-70	Clark 55-60	Jasper-Pulaski 55-60
Living Tree Wood	246,358 (57,620)	221,830 (40,215)	210,319 (61,951)	124,260 (17,849)	124,765 (27,126)
Fine Roots (<3 mm)	2,133 (1,348)	2,742 (1,475)	3,597 (1,331)	3,365 (1,828)	3,759 (1,662)
Medium Roots (3-10 mm)	2,930 (1,394)	4,784 (4,255)	3,782 (2,453)	3,434 (4,992)	1,877 (1,863)
Coarse Roots (>10 mm)	1,218 (4,244)	4,980 (9,585)	381 (1,180)	1,411 (3,801)	2,552 (8,331)
Root Total	6,281 (5,248)	12,391 (11,875)	7,610 (3,043)	8,146 (5,751)	8,032 (8,863)
Annual Leaf-fall	4,890 (519)	4,836 (589)	5,145 (423)	4,317 (493)	3,947 (721)
Non leaf Litterfall	1,003 (687)	967 (606)	1,207 (613)	1,312 (1,254)	972 (584)
Total Litterfall	5,893 (791)	5,803 (1,138)	6,352 (826)	5,628 (1,584)	4,918 (1,026)
Litter Layer	5,394 (879)	5,152 (948)	4,507 (923)	5,646 (828)	3,887 (731)
Fermentation Layer	8,660 (1,885)	10,661 (4,711)	16,171 (6,038)	11,068 (2,011)	16,826 (4,036)
Humus Layer	4,443 (1,486)	3,651 (1,308)	6,265 (2,946)	10,419 (8,024)	14,718 (3,800)
Forest Floor Total	18,496 (1,614)	19,464 (5,461)	26,943 (8,361)	27,133 (8,887)	35,431 (6,687)

components, the litter layer biomass comprised from 29 and 26 percent of the total forest floor biomass at the mesic Nelson-Stokes and Feldun sites respectively, but comprised only 11% of the total forest floor biomass at the Jasper-Pulaski site. The fermentation layer represented a large total proportion of the forest floor ranging from 41-60% of the total forest floor biomass. The humus layer biomass showed a wide disparity between mesic sites and xeric sites. In the more mesic sites, the humus layer represented a relatively small proportion of the total forest floor biomass (19 and 24% at the Feldun and Nelson-Stokes sites respectively) while the more xeric sites, the humus layer contained a relatively large proportion of the total forest floor biomass (38 and 42% of the forest floor biomass at the Clark and Jasper-Pulaski sites respectively).

Total carbon and nitrogen storage in each particular pool (i.e., living trees or annual leaf-fall) is a function of each individual pool biomass multiplied by the carbon or nitrogen concentration of that pool. Therefore, both the size of the pool and the nutrient concentrations of the pool become important in determining the carbon or nitrogen storage potential. It is possible for a particular component to have a high value for nitrogen high concentration, but if the biomass is low, the overall contribution may be small. Likewise, a particular component with a low nitrogen concentration may be highly significant if the biomass is large. In addition to determining the overall carbon or nitrogen storage and the potential for nutrient cycling at a site, the temporal aspects of changes in a specific pool are also important. Pools that turn over on a relatively frequent basis, i.e, a short term period, become more important to the overall cycling of nutrients than a much larger pool that turns over on a less frequent basis, i.e. over longtime period.

When static pool sizes are determined, it is clear that the aboveground biomass and mineral soil are the most significant storage components for carbon in these systems (Table 3). Carbon storage in the aboveground biomass in these systems is a function of the relatively large amount of biomass and high carbon concentrations (approximately 45%). The soil has a low carbon concentration, but its extremely high mass on a kg/ha basis makes this component a highly significant carbon storage pool. The forest floor follows these components as the third primary carbon pool in these systems. In comparison to the aboveground biomass and soil components, the forest floor contains smaller amounts of carbon. Still, this component can be extremely important in these sites. It represents a transition zone between the relatively decomposable organic carbon sources contained in the vegetation to the much more recalcitrant soil organic matter.

Inputs of carbon in these systems come primarily from aboveground litterfall and fine root turnover. While these represent a relatively small percentage of system carbon, the yearly additions of these sources are extremely important. Mortality of mature trees is relatively low and carbon returns from this source is low at the present stage of stand development. Therefore, carbon inputs to the systems come primarily from fixed atmospheric carbon that is returned to the site via leaf-fall, litterfall, and root turnover.

Nitrogen pools in these systems show somewhat different trends. The mineral soil contains the vast majority of the total nitrogen found in each stand. The aboveground biomass becomes the second most important nitrogen pool, with the forest floor organic layers ranking third in importance (Table 4). During decomposition of leaf and litter fall, nitrogen concentrations increase. The nitrogen concentration of the fermentation layer is higher than either the litter or humus layers. The high nitrogen concentration coupled with a relatively high biomass leads to the high total nitrogen storage in this pool. As site quality decreases, the nitrogen contained in the forest floor organic layers becomes increasingly more important. The nitrogen contained in the forest floor organic layers at the Jasper-Pulaski site is approximately 70% of the nitrogen contained in the aboveground biomass but the organic layers at Nelson-Stokes and Feldun contain only 15% and 13%, respectively. These results indicate that the forest floor becomes increasingly more important as site quality decreases. In the more productive stands examined, the total amount of nitrogen contained in the forest floor is relatively insignificant compared to that contained in the aboveground biomass. In the more xeric, less productive stands sampled, the nitrogen contained in the forest floor approaches the level of nitrogen contained in the aboveground biomass. This high nitrogen retention in the forest floor organic layers may be a significant nitrogen conservation mechanism in these stands and may become a critical issue in proper management of these stands.

Table 3. Carbon content of each component at the Nelson-Stokes, Feldun, SIPAC, Clark, and Jasper-Pulaski sites. Values given are in kg/ha. Standard deviations are in parentheses under each respective value.

			Site		
Component	Nelson-Stokes 85-90	Feldun 75-80	SIPAC 65-70	Clark 55-60	Jasper-Pulaski 55-60
Living Tree	114,265 (32,576)	98,892 (17,602)	99,692 (29,627)	61,496 (8,711)	57,180 (12,432)
Fine Roots (<3 mm)	988 (624)	1,202 (674)	1,582 (611)	1,504 (904)	1,726 (796)
Medium Roots (3-10 mm)	1,363 (1,394)	2,132 (1,896)	1,793 (1,163)	1,403 (2,172)	860 (854)
Coarse Roots (>10 mm)	515 (1,794)	2,106 (4,054)	160 (494)	547 (1,548)	1,080 (3,526)
Root Total	2,866 (2,298)	5,440 (5,104)	3,534 (1,425)	3,605 (2,529)	3,666 (3,785)
Annual Leaf-fall	2,258 (240)	2,214 (270)	2,370 (195)	1,989 (227)	1,891 (345)
Non leaf Litterfall	463 (296)	443 (271)	556 (281)	604 (568)	466 (329)
Total Litterfall	2,721 (355)	2,657 (503)	2,926 (380)	2,593 (707)	2.357 (477)
Litter Layer	2,490 (409)	2,339 (453)	2,076 (447)	2,601 (372)	1,862 (352)
Fermentation Layer	3,915 (884)	4,791 (2,181)	7,297 (2,780)	4,932 (906)	7,933 (1,871)
Humus Layer	1,148 (544)	1,031 (517)	2,035 (1,465)	1,803 (396)	4,312 (1,509)
Forest Floor Total	7,553 (966)	8,161 (2,493)	11,408 (3,983)	9,336 (1,167)	14,107 (2,305)
Mineral Soil	45,082	77,156	45,836	45,755	35,543

Table 4. Nitrogen content of each component at the Nelson-Stokes, Feldun, SIPAC, Clark, and Jasper-Pulaski sites. Values are given in kg/ha. Standard deviations are in parentheses under each respective value.

	Site				
Component	Nelson-Stokes 85-90	Feldun 75-80	SIPAC 65-70	Clark 55-60	Jasper-Pulaski 55-60
Living Tree Wood	1,947	2,024	1,416	882	867
	(555)	(360)	(421)	(125)	(189)
Fine Roots (<3 mm)	21	24	29	25	43
	(13.3)	(14)	(11)	(15)	(20)
Medium Roots (3-10 mm)	19	41	33	25	23
	(19)	(36)	(21)	(39)	(22)
Coarse Roots (>10 mm)	6	26	2	7	14
	(21)	(51)	(6)	(19)	(44)
Root Total	46	91	64	59	79
	(32)	(75)	(26)	(42)	(55)
Annual Leaf-fall	43	47	50	35	37
	(4)	(6)	(4)	(4)	(7)
Non leaf Litterfall	9	9	12	11	9
	(6)	(6)	(6)	(10)	(7)
Total Litterfall	51	57	62	46	46
	(7)	(11)	(8)	(12)	(9)
Litter Layer	47	51	44	46	36
	(8)	(13)	(9)	(11)	(9)
Fermentation Layer	154	146	215	154	316
	(35)	(64)	(55)	(29)	(83)
Humus Layer	67	57	89	104	257
	(33)	(32)	(31)	(27)	(80)
Forest Floor Total	268	254	348	305	609
	(43)	(85)	(77)	(50)	(127)
Mineral Soil	12,288	18,005	10,423	23,286	7,561

Nitrogen contained in the annual litterfall and fine root biomass is the primary pool which is recycled in these system. These pools turn over at relatively frequent intervals and while their pool size at any given point is relatively small, the turnover of these pools at approximately yearly intervals is highly significant. Assuming equal longevity and turnover rates of fine roots on all sites, the role of fine roots in the nitrogen cycle in these stands is most significant on the more xeric, nutrient poor sites. On the more mesic sites, the role of leaf-fall and litterfall potentially outweighs the role of root turnover. Current research is underway to determine the rates of fine root turnover in these forest stands and the environmental factors controlling fine root production and turnover. Once this research is completed, a more complete understanding of the role of C and N inputs via above and belowground production will be achieved.

DISCUSSION

The results of this study support previous studies which indicate that standing aboveground biomass, forest floor organic layers, and the mineral soil itself are the primary storage pools for carbon and nitrogen in forest ecosystems. Carbon and nitrogen storage in the five oak-hickory stands examined is a function of both the relative biomass of the pool and the nutrient concentration of the components in the pool. The selection of oak-hickory sites located along a productivity gradient demonstrates the wide differences that may exist within this forest type. In addition, it demonstrates that the relative importance of various pools may change as site quality changes.

Both biomass and nutrient concentration must be determined in order to determine the size of the carbon or nitrogen pool within a system. Biomass determinations of the various components reveal the wide differences that may be encountered in oak-hickory forests. This may be expected due to the broad ecological amplitude of these species, i.e., ranging from xeric, nutrient poor sites to mesic, nutrient rich sites. This wide variation in site quality is readily reflected in standing aboveground biomass of the five stands. The estimates of standing aboveground biomass ranging from 124,000 kg/ha to 246,000 kg/ha is within the range generally encountered in moderately low to high productivity hardwood forests. There are a wide variety of aboveground biomass estimates for hardwood forests ranging from a low of approximately 68,000 kg/ha for northern pin oak/bur oak forest on outwash sands in northwest Wisconsin (Bockheim and Leide 1991) to over 220,000 kg/ha for sugar maple/northern red oak stands in Michigan (Zak and others 1989). Aboveground biomass estimates for oak dominated stands in the same study range from 83,000 to 207,000 kg/ha (Zak and others 1989). Aboveground biomass estimates for mixed hardwood forests in eastern Tennessee range from 188,000-207,000 kg/ha (Johnson and others 1982). The estimates of aboveground biomass are within expected ranges for this forest type, and indicate its broad ecological adaptation.

Fine root biomass is the second component that is estimated in these stands. Our fine root biomass estimates are at the lower range of expected values for hardwood ecosystems. Comparisons between different studies are complicated by several factors. Fine root biomass often undergoes fairly wide seasonal variation (Edwards and Harris 1977, Hendrick and Pregitzer 1993). In addition, many researchers sample differing depths in the soil profile and have different definitions of fine roots (i.e., < 2 mm vs. < 3 mm). These confounding factors make direct comparisons difficult. At the higher range of fine root biomass estimates, Hendrick and Pregitzer (1993) estimate sugar maple stands in Michigan contain 7,900 kg/ha and 9,500 kg/ha of fine roots (<2.0 mm) in April and October respectively. Lower estimates of fine root biomass are also reported. Joslin and Henderson (1987) determine that white oak stands in Missouri contained 5,500 kg/ha of fine roots (<2 mm) in the upper 44 cm of the soil profile. Aber and others (1985) estimate fine root biomass measures ranging from 2,700 to 5,200 kg/ha for oak stands in the state of Wisconsin. Mixed hardwood stands in Massachusetts contain an average fine root (<3 mm) biomass of 5,100 kg/ha (McClaugherty and others 1982). All sampling in our stands is carried out during late summer to early fall during a time at which fine root biomass should reach peak levels (Edwards and Harris 1977). This sampling protocol should assure that the relative differences between fine root biomass in the five stands is accurately reflected in our measurements.

Determinations of medium and coarse root biomass become more problematic. Roots of these diameters exhibit a great deal of spatial heterogeneity. Sampling to determine these components must be intense to accurately access these components. This problem is magnified for coarse roots (> 10 mm). Few of the sample cores collected contained roots of this diameter. Estimates of these components is also complicated by the fact that roots of these diameters may have a distribution through the lower soil horizons. While examinations of medium and coarse root distribution in soil pits reveal that the majority of these roots are confined to the upper 30 cm of soil, there are medium and coarse roots in lower soil horizons which are not sampled. Therefore, our estimates likely underestimate this component due to their horizontal and vertical distributions in the soil profile. The exact magnitude of this underestimation is difficult to determine, but several other studies have examined root distribution in similar forest stands. Johnson and Risser (1974) report that mixed post oak/blackjack oak stands contained 39,000 kg/ha of total root biomass. Kelly and Joslin (1989) indicate that mixed oak stands in Tennessee contained from 30,000-35,000 kg/ha of total root biomass. Of this total, from 70-80% is contained in the upper 30 cm of the soil profile. In northern hardwood forests in New Hampshire, total root biomass is estimated at 27,000 kg/ha with over 80% of this total contained in the upper 20 cm of soil (Fahey and others 1988). Estimates of the standing crop of fine roots in the stands we examined is much less problematic. Excavations reveal that these roots are distributed much more evenly throughout the stand. In addition, the vast majority of these roots are contained in the upper 30 cm of the soil profile. Therefore, our estimates of this pool, which is the most active belowground in terms of turnover and its significant impacts, are less subject to error due to vertical and horizontal variability.

The trend for fine root biomass to increase as site quality decreases has been observed by other researchers. Binkley and others (1986) found that sites with high levels of nitrate had lower fine root biomass than lower quality sites where lower levels of ammonium were present. In addition, Harris and others (1977) found that belowground biomass increased relative to aboveground biomass as site quality of tulip poplar and loblolly pine stands decreased. The trend observed in our study supported this observation. On the more xeric, nutrient poor sites, fine root biomass was much higher than on the higher quality sites. When the standing aboveground biomass differences between the low and high quality sites was considered, the preferential allocation of fixed carbon belowground on the lower quality sites became more striking.

Inputs to the system via annual leaf and total litterfall were within the commonly reported figures for hardwood ecosystems. Zak and others (1986) reported that annual leaf-fall in Michigan ranged from 1,600 kg/ha for xeric oak ecosystems to 3,100 kg/ha for mesic sugar maple/northern red oak ecosystems. Total litterfall in Missouri oak ecosystems was 5,200 kg/ha (Joslin and Henderson 1987) while figures for oak forests in Wisconsin ranged from 3,000 kg/ha (McClaugherty and others 1985) to 5,900 kg/ha (Nadelhoffer and others 1985). The results of our study indicated that litter inputs in oak-hickory forests varied widely and were dependent upon the productivity of the site. The more productive sites had much greater annual leaf-fall than the lower productivity sites. Other litterfall (seeds, twigs, bark, etc.) was approximately equal across sites.

Differences in the forest floor organic layers were also apparent across this site productivity gradient. Our results indicated that the biomass of the forest floor increases as site quality decreases. This was due to factors other than strictly the input of detritus to the forest floor as inputs were greater on higher productivity sites than on lower productivity sites. Rather, it appeared that either site conditions or the chemical composition of the litter inputs themselves affected forest floor development.

It has been long-established that the rate of organic matter decomposition is moisture and temperature dependent. The highest rates of organic matter decomposition are observed under warm, moist conditions. Either drought, cold conditions, or oxygen limitations can reduce the rate of organic matter decomposition (Meentenmeyer 1978, White and others 1988). Conditions which limit organic matter decomposition are expected to increase forest floor biomass if other factors are held constant. Periodic monitoring of the five stands examined demonstrates little difference in soil temperature, but relatively large differences in soil moisture availability. The Clark and Jasper-Pulaski sites have limited plant available water holding capacity. Monitoring of the soil moisture status of these soils shows that water is rapidly depleted from these sites during relatively short-term midsummer drought events. Therefore, on the lower productivity sites, it is likely that decomposition rates during midsummer are lowered due to water limitations. This in turn may increase the amount of forest floor organic matter compared to that found on more mesic sites.

The second factor that may be significant in altering forest floor developmental patterns is the chemical characteristics of the litter inputs. Litter of different chemical characteristics is found to decompose at vastly different rates. In general, nitrogen and lignin concentrations are the prime chemical constituents controlling litter decomposition rates (Aber and others 1990, Berendse and others 1987, Berg and others 1993, Melillo and others 1989). The early stages of decomposition are characterized by the microbial utilization of cellulose (Melillo and others 1989). Late stages of decomposition are dependent upon microbial degradation of lignin and this process usually proceeds at much slower rates (Aber and others 1990). Further, lignin is often viewed as a precursor to stable soil organic matter formation (Paul and Clark 1989). The differing chemical characteristics of the litter inputs themselves may affect the forest floor development. The litter inputs at the Clark and Jasper-Pulaski sites are composed almost entirely of oak. Previous studies have demonstrated that oak species typically have high lignin concentrations of approximately 20-25% and typically exhibit slow decomposition rates (Aber and others 1990). Other species such as sugar maple (Aber and others 1990) or tulip poplar (White and others 1988) have much lower lignin concentrations and exhibit much more rapid decomposition rates. The leaf-fall at the more mesic sites is composed partly of oak litter, but also of a variety of other species which, based on previous studies, should have lower lignin concentrations and decompose at more rapid rates. Under these conditions, we would expect lower biomass in the forest floor in mesic stands where species other than oak contribute significant amounts of annual leaf-fall.

The total carbon and nitrogen pool size is a function of the biomass of that pool multiplied by its nutrient concentration. Carbon pool sizes follow slightly different trends than nitrogen. While the aboveground biomass, soil, and forest floor organic layers contain the majority of carbon and nitrogen in the oak-hickory forests examined, the frequency of inputs must also be considered to properly assess the true significance of nutrient inputs at any one point. In these second growth forest stands, tree mortality is at a relatively low level. Nutrients that are contained in trees that do die become very slowly available due to the very slow decomposition rates of tree boles and the strong immobilization of nutrients in decaying boles (Alban and Pastor 1993). On a short term basis in these stands, this pool of nutrients is cycled at a very slow rate.

The soil nitrogen and carbon pools are also very large in these systems, but there is a problem in defining the relative importance of this pool. While it cannot be argued that there is a huge reserve of carbon and nitrogen in this pool, the stable soil organic matter of this fraction appears to be relatively recalcitrant and undergoes relatively slow decomposition and nutrient release. The relative rates of turnover from these pools have been determined. Readily decomposable plant material has a half-life of 0.17 years. Plant material that is highly resistant to decay has a half-life of 23 years. In contrast, physically and chemically stabilized soil organic matter have half-lives of 50 and 2300 years respectively (Paul and Clark 1989). Figures such as these indicate that while the soil pools are very large, the turnover rates of the pools must also be considered to assess their true impacts.

Annual litterfall and fine root production and turnover are two pools that are constantly cycling C and N in these ecosystems. Although their pool sizes at any given point are small relative to the other pool sizes, their inputs are fairly steady and over time, can become highly significant. Clearly, the production rates of aboveground litter and fine roots become critical issues in determining the importance of each pool. We currently have good estimates of aboveground leaf and litter production, but standing fine root biomass is less desirable than root production rates. The second critical factor becomes the residence time of fine roots. Fine root longevity becomes a critical issue in these ecosystems. Estimates of fine root longevity can vary widely with estimates ranging from 0.6 years (Harris and others 1977) to 4.8 years (Joslin and Henderson 1987). Most estimates of the residence time of fine roots fall in the range of 0.5 to 2.0 years (Nadelhoffer and others 1985). If these estimates of root longevity hold true for our forest stands and root longevity is the same for the five stands examined, this would indicate that root turnover could be as important or more important than aboveground litterfall in supplying organic matter and nitrogen to these systems. The significance of belowground turnover may be greatest on the more xeric, nutrient poor sites. These stands had higher standing fine root biomass. In addition, on these sites, leaf and litter fall was lower than on the more fertile sites. These observations would indicate that fine roots become increasingly more important as site quality decreases if, in fact, production and turnover is equal across sites. Additional research is currently in place that will determine fine root production, turnover, and decomposition rates in each of the five stands examined. When this is completed, the relative importance of above and below ground pools in the nutrient cycles of these stands will become clear.

CONCLUSIONS

The results of this research support previous research that identified the soil, forest floor organic layers, and the aboveground biomass as the most significant pools of carbon and nitrogen in forest ecosystems. The relative importance of each pool can change as site characteristics change. The nitrogen contained in the forest floor pool becomes increasingly more important as site quality decreases. This suggests that these forest floor organic layers may serve as important nutrient conserving mechanisms in these less productive ecosystems. The research also suggests that while the absolute pool size may be important, the temporal aspects of the turnover of the pool must also be considered. In the forests we examined, most inputs to the systems come from annual litterfall and root turnover. Estimates of annual litterfall is easily obtained, but root production, turnover, and decomposition is much more difficult to estimate. Current research is focusing on quantifying these factors in the five stands described. In addition, more stands have been sampled to develop a greater understanding of the processes taking place in oak-hickory dominated stands found on a wide variety of site types.

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