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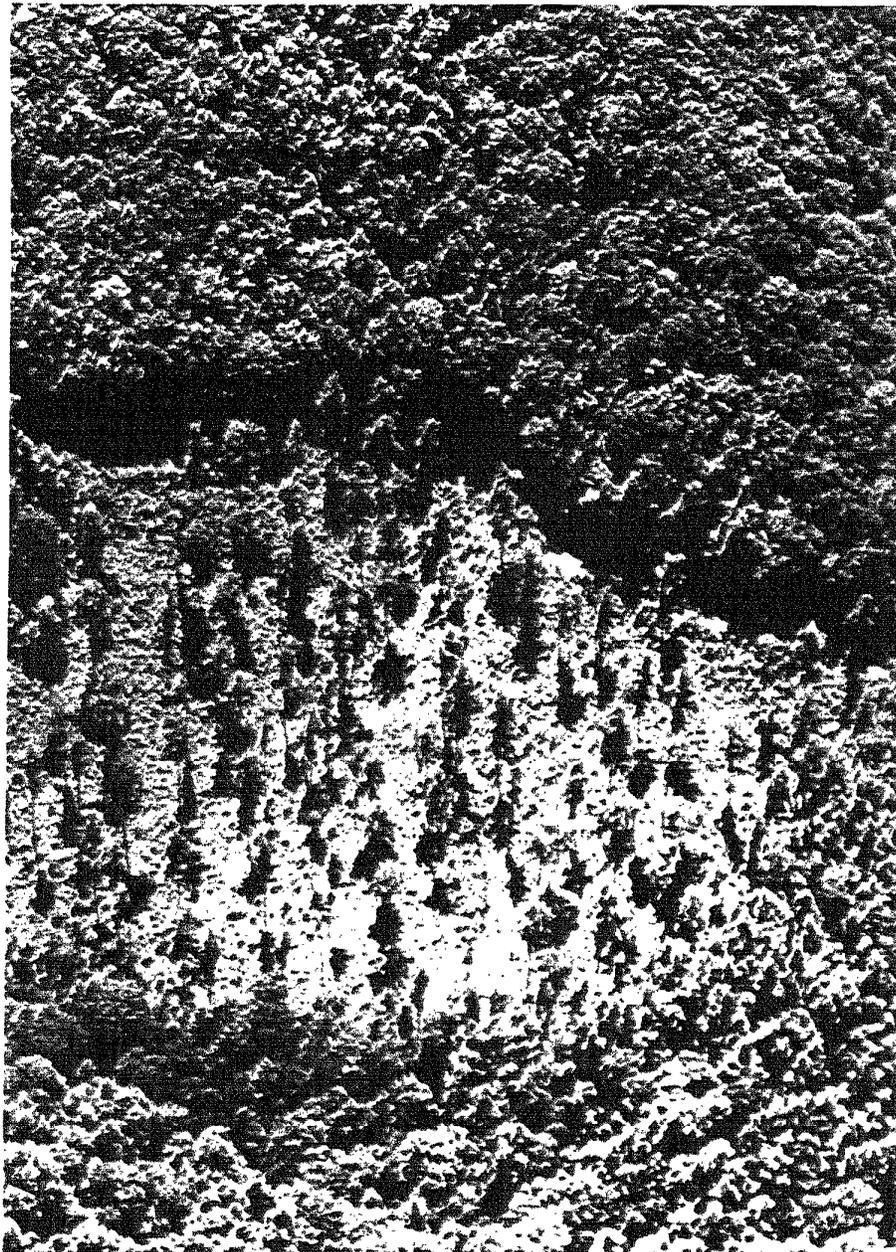
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Proceedings

10th Central Hardwood Forest Conference

Morgantown, West Virginia
March 5-8, 1995



CONTINUING FORESTRY EDUCATION

For attending this conference, each registrant was eligible for 12 hours of Continuing Forestry Education (CFE) credit offered by the Society of American Foresters.

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Cover Photo: This 1984 aerial photograph was taken from a helicopter three years after deferment cutting in 80-year-old central Appalachian hardwoods on the Fernow Experimental Forest near Parsons, West Virginia. (Photo by James N. Kochenderfer, USDA Forest Service.)

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10TH CENTRAL HARDWOOD FOREST CONFERENCE

Proceedings of a Meeting

Held at

Lakeview Resort and Conference Center

Morgantown, WV

March 5-8, 1995

Edited by

Kurt W. Gottschalk and Sandra L. C. Fosbroke

SPONSORED BY:

Division of Forestry, West Virginia University

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FOREWORD

This conference is the tenth in a series of biennial meetings that began in 1976 at Southern Illinois University. Other conferences have been hosted by Purdue University, University of Missouri, University of Kentucky, University of Illinois, University of Tennessee, Southern Illinois University with the North Central Forest Experiment Station (NCFES), Pennsylvania State University with the Northeastern Forest Experiment Station, and Purdue University with NCFES. The purpose of these conferences has remained the same: to provide a forum for the exchange of information concerning the biology and management of central hardwoods by forest scientists from throughout the Central Hardwood Region of the eastern United States. As with previous Proceedings, a wide range of topics that represent the broad array of research programs in this area is represented.

The social and biological characteristics of the Central Hardwood Region make it unique in comparison with other forest regions of the United States. For example, one-fourth of the United States human population resides in this region. Approximately 90% of the land is in private ownership and public lands tend to be small and fragmented with private inholdings. These and related conditions play critical roles in the practice of forestry in this region. The information presented in this Proceedings is important to the long-term management of the forest resources of this unique region.

REVIEW PROCEDURES

Each manuscript published in these proceedings was critically reviewed by at least two (usually three) scientists with expertise in disciplines closely aligned to the subject of the manuscript. Reviews were returned to the senior author, who revised the manuscript appropriately and resubmitted it in a diskette format suitable for printing by the Northeastern Forest Experiment Station, USDA Forest Service where they were edited to a uniform format and type style. Manuscript authors are responsible for the accuracy and content of their papers.

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

Donald J. Kaczmarek, Karyn S. Rodkey, Robert T. Reber, Phillip E. Pope, and Felix Ponder, Jr.¹

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 CO₂ 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 CO₂ 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 (m²/ha) and the second row under each species gives its relative dominance in each respective stand (%).

| Site Index | Site | | | | |
|---------------------|------------------------|-----------------|----------------|----------------|-------------------------|
| | Nelson-Stokes 85-90 | Feldun 75-80 | SIPAC 65-70 | Clark 55-60 | Jasper-Pulaski 55-60 |
| Species | | | | | |
| White Oak | 20.6 56.7 | 1.7 4.8 | 22.0 68.0 | 16.0 77.5 | 15.2 67.1 |
| Black Oak | 0.0 0.0 | 11.9 33.9 | 0.2 0.6 | 2.7 12.9 | 6.4 28.4 |
| Northern Red Oak | 3.5 9.6 | 3.1 8.9 | 2.4 7.4 | 0.0 0.0 | 0.0 0.0 |
| Hickory Spp. | 4.3 11.9 | 3.5 10.1 | 3.4 10.6 | 1.1 5.2 | 0.0 0.0 |
| Sugar Maple | 4.6 12.7 | 2.3 6.6 | 4.0 12.3 | 0.1 0.4 | 0.0 0.0 |
| Beech | 0.3 0.9 | 3.7 10.4 | 0.0 0.1 | 0.0 0.0 | 0.0 0.0 |
| Yellow Poplar | 0.5 1.3 | 7.5 21.4 | 0.0 0.0 | 0.0 0.0 | 0.0 0.0 |
| Misc. | 2.5 6.9 | 1.3 3.9 | 0.3 1.0 | 0.7 4.0 | 1.0 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 (m²) 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 Weibull 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 sieving 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 m². 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 m² 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. R² 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 H₂SO₄ in 50 ml Folin-Wu tubes. A mixture of K₂SO₄, CuSO₄, 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.

| Component | Site | | | | |
|---------------------------|------------------------|---------------------|---------------------|---------------------|-------------------------|
| | 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.

| Component | Site | | | | |
|---------------------------|------------------------|--------------------|--------------------|-------------------|-------------------------|
| | 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.

| Component | Site | | | | |
|---------------------------|------------------------|-----------------|----------------|----------------|-------------------------|
| | Nelson-Stokes 85-90 | Feldun 75-80 | SIPAC 65-70 | Clark 55-60 | Jasper-Pulaski 55-60 |
| Living Tree Wood | 1,947 (555) | 2,024 (360) | 1,416 (421) | 882 (125) | 867 (189) |
| Fine Roots (<3 mm) | 21 (13.3) | 24 (14) | 29 (11) | 25 (15) | 43 (20) |
| Medium Roots (3-10 mm) | 19 (19) | 41 (36) | 33 (21) | 25 (39) | 23 (22) |
| Coarse Roots (>10 mm) | 6 (21) | 26 (51) | 2 (6) | 7 (19) | 14 (44) |
| Root Total | 46 (32) | 91 (75) | 64 (26) | 59 (42) | 79 (55) |
| Annual Leaf-fall | 43 (4) | 47 (6) | 50 (4) | 35 (4) | 37 (7) |
| Non leaf Litterfall | 9 (6) | 9 (6) | 12 (6) | 11 (10) | 9 (7) |
| Total Litterfall | 51 (7) | 57 (11) | 62 (8) | 46 (12) | 46 (9) |
| Litter Layer | 47 (8) | 51 (13) | 44 (9) | 46 (11) | 36 (9) |
| Fermentation Layer | 154 (35) | 146 (64) | 215 (55) | 154 (29) | 316 (83) |
| Humus Layer | 67 (33) | 57 (32) | 89 (31) | 104 (27) | 257 (80) |
| Forest Floor Total | 268 (43) | 254 (85) | 348 (77) | 305 (50) | 609 (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 (Johanson 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 (McClougherty 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 (Meentemeyer 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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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 O₁, O₂, 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 (m²/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 56.7 | 1.7 4.8 | 22.0 68.0 | 16.0 77.5 | 15.2 67.1 |
| Black oak | 0.0 0.0 | 11.9 33.9 | 0.2 0.6 | 2.7 12.9 | 6.4 28.4 |
| Northern red oak | 3.5 9.6 | 3.1 8.9 | 2.4 7.4 | 0.0 0.0 | 0.0 0.0 |
| Hickory spp. | 4.3 11.9 | 3.5 10.1 | 3.4 10.6 | 1.1 5.2 | 0.0 0.0 |
| Sugar maple | 4.6 12.7 | 2.3 6.6 | 4.0 12.3 | 0.1 0.4 | 0.0 0.0 |
| Beech | 0.3 0.9 | 3.7 10.4 | 0.0 0.1 | 0.0 0.0 | 0.0 0.0 |
| Tulip poplar | 0.5 1.3 | 7.5 21.4 | 0.0 0.0 | 0.0 0.0 | 0.0 0.0 |
| Misc. | 2.5 6.9 | 1.3 3.9 | 0.3 1.0 | 0.7 4.0 | 1.0 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 ($\mu\text{g/g}$) | 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 m² 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 H₂O, stirred, and allowed to settle for 10 minutes. The floating fraction was removed, placed on a nest of two sieves (250 and 75 μm), 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 μm 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 μm sieve captures all components of "coarse sand" sized (2 mm-250 μm), and the 75 μm sieve captures all components of "medium sand" sized (250-75 μm). 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

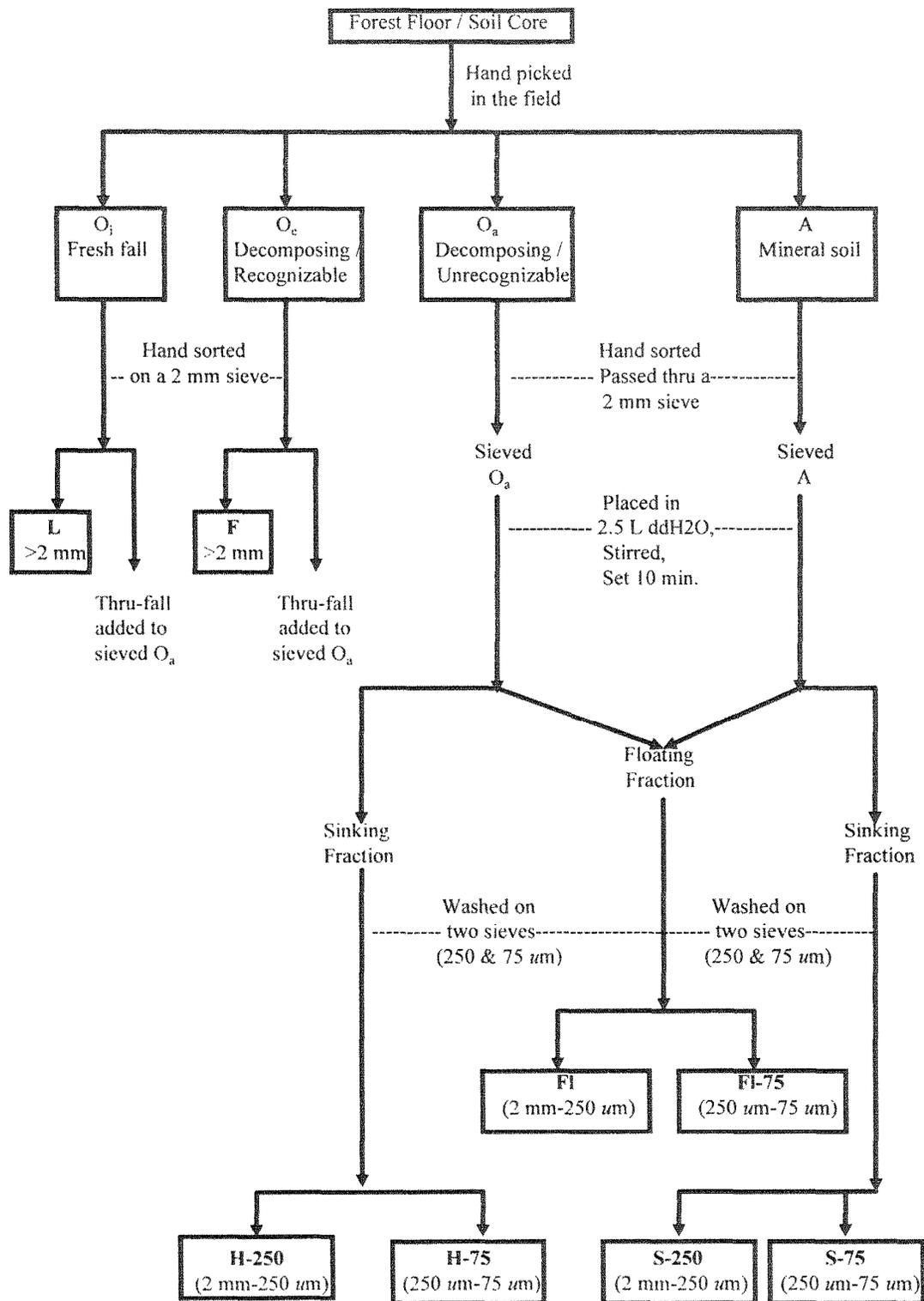


Figure 1. Forest floor fractionation.

called: L, corresponding with fresh fall O_i; F, O_e material > 2 mm; FI, floating material 2 mm-250 μm; FI-75, floating material 250 μm-75 μm; H-250, O_a material 2 mm-250 μm; H-75, O_a material 250 μm-75 μm; S-250, A horizon material 2 mm-250 μm; and S-75, A material 250 μm-75 μm. 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:

$$CF = (SaAFDM - A_1AFDM) / (LAFDM - A_1AFDM)$$

where:

CF is the fraction corrected for mineral soil contamination

SaAFDM is %AFDM of each respective fraction

A₁AFDM 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 FI-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):

$$CFNt = [SaNt - (FSI \times A_1Nt)] / CF$$

where:

CFNt is the nutrient concentration for the fraction corrected for mineral soil contamination

SaNt is the nutrient concentration for each respective fraction

FSI is the fraction of sample that is soil

A₁Nt 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 a 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, FI, FI-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 (CI) | 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 |
| FI | 2309 bc : C | 2412 c : C | 5281 b : AB | 3661 cde : BC | 6966 cd : A |
| FI-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 - FI-75) to the total of all fractions declines as site productivity declines, i.e. NS- 62%, Feld- 70%, SI- 64%, CI- 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 FI and FI-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 (CI) | Jasper-Pulaski (JP) |
|-----------------------|--------------------|---------------|--------------|-------------|---------------------|
| L | 0.88 f* : BC** | 0.98 cf : A | 0.97 cf : 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 |
| FI | 2.25 b : A | 1.85 b : B | 1.75 b : B | 1.71 a : B | 2.22 a : A |
| FI-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 FI forest floor fractions were significantly greater than the other fractions (Table 5). For a specific site, the P concentration was greatest for the FI fraction followed by the F fraction and tended to be followed by the L, H-75, H-250, FI-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.

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

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 (CI) | 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 |
| FI | 51.7 b : B | 45.9 b : B | 81.2 b : B | 62.5 b : B | 156.1 b : A |
| FI-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 (CI) | 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 |
| FI | 4.12 c : B | 3.57 bc : B | 6.46 b : B | 6.07 a : B | 13.54 bc : A |
| FI-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 (Meentemeyer 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 (Meentemeyer 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 (McClougherty 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 were 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_c 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_c 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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PLANT AND SOIL NUTRIENTS IN YOUNG VERSUS MATURE CENTRAL
APPALACHIAN HARDWOOD STANDS

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Abstract: Most models of forest succession and forest recovery following disturbance predict changes in nutrient availability. The purpose of this study was to compare soil and herbaceous layer plant nutrients between two young (~20 yr) and two mature (~80 yr) forest stands on Fernow Experimental Forest, Parsons, West Virginia. All sampling was carried out within 15 circular 0.04-ha sample plots per watershed, for a total of 30 plots for each age category. All vascular plants ≤ 1 m in height (herbaceous layer) were identified and estimated visually for cover in each of 10 circular 1-m² sub-plots. All above-ground portions of plants in the two sub-plots in each sample plot with the greatest herb layer cover were harvested and analyzed for nutrient content. In addition, a soil sample was taken to a 10-cm depth from each harvest sub-plot. Soils were analyzed for organic matter, texture, pH, and extractable nutrients. There were no significant differences related to stand age for soil pH, organic matter, cation exchange capacity, or any of the extractable nutrients. With the exception of significantly higher herb layer N for the young stands, there were few differences in herb layer tissue nutrients between young and mature stands. There were, however, differences in correlations among soil nutrients and other soil variables (e.g., texture and organic matter) which varied with stand age, with extractable nutrients more highly correlated with organic matter and texture in the young stands than in the mature stands. Furthermore, herb layer tissue nutrient concentrations were correlated significantly with soil organic matter for virtually all nutrients in young stands; in contrast, none were correlated with soil organic matter in mature stands. These results suggest minimal change in nutrient availability between 20 and 80 years of forest recovery from disturbance. Data in this study further emphasize the importance of soil organic matter decomposition as a source of available nutrients in these hardwood forests following disturbance and suggest that this importance might decrease with stand age. Finally, these results are consistent with the hypothesis that herb layer dynamics are controlled by nutrient availability early in succession, but that other factors, such as light, become more important later in succession.

INTRODUCTION

Most current models of secondary forest succession and forest response to disturbance predict measurable changes in nutrient availability over time (Bormann and Likens 1979, Vitousek and Reiners 1975). Although these patterns of change will vary among ecosystems and degrees of disturbance, it generally is accepted that nutrients will increase in availability and mobility immediately following a disturbance, such as forest harvesting, which usually results in ching increases and nutrient loss via streamflow. As regrowth occurs, however, plant root uptake increases rapidly, resulting in decreased nutrient leaching and increased nutrient storage in plant biomass. Thus, it is reasonable to generalize that nutrient availability increases for a short period following forest disturbance and that it decreases subsequently through time. Studies of stream chemistry response to forest harvests on montane watersheds of the eastern U.S. largely have supported these generalizations (Aubertin and Patric 1974, Bormann and Likens 1979, Kochenderfer and Wendel 1983, Swift and Swank 1981).

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Other research has focused on forest floor organic matter and its response to forest harvests (e.g., Covington 1981); fewer studies have looked directly at soil nutrients. Although forest successional changes in N are fairly well understood (Vitousek and others 1989), less is known about P and the base cations Ca, Mg, and K. These nutrients are not generally considered as frequently growth-limiting as is N, but limitations can occur, especially in forest soils developed from parent materials low in these nutrients (Jenny 1981), such as the highly weathered soils of the pine forests of the southeastern Coastal Plain (Gilliam 1991, Gilliam and Richter 1991), or the deep sands of the Adirondacks in New York (Stone and Kszystyniak 1977). In contrast to N change through time, which is tied into somewhat predictable changes in organic matter decomposition, it may be much more difficult to generalize about ecosystem changes in P and nutrient cations through succession because they are influenced both by decomposition rates of organic materials and by weathering rates of primary and secondary soil minerals.

Although difficult to assess empirically (Chapin and Van Cleve 1991), nutrient availability generally is defined in terms of amounts of nutrients present in the soil in chemical forms which allow for plant root uptake. Although N availability is often measured via incubation techniques, cation availability usually is measured as exchangeable amounts in soil extract solutions (Binkley and Vitousek 1991). Measurements of plant tissue concentrations also have been used to assess soil fertility and nutrient availability (Binkley and Vitousek 1991). This paper examines nutrient availability as both amounts of extractable nutrients from the mineral soil and tissue concentrations in plant material.

The herbaceous layer, defined here as vascular plants ≤ 1 m in height, is an important stratum of forest ecosystems, playing a significant role in initial competition among juveniles (seedlings and sprouts) of potential overstory canopy tree species (Gilliam and others 1994). Furthermore, the herb layer has been shown to be quite sensitive to a variety of forest disturbances, including gap openings (Moore and Vankat 1986) and forest management practices (Duffy and Meier 1992, Gilliam and Christensen 1986, Gilliam and Turrill 1993). Perhaps more important in the context of changes in nutrient availability, the herb layer also has been used as an indicator of edaphic factors and forest site quality (Cserep and others 1991, Pregitzer and Barnes 1982, Strong and others 1991). Reiners (1992) reported on 20 yr of vegetation recovery following deforestation and herbiciding on Watershed 2 at Hubbard Brook and found 6-8 fold increases in herb layer content of N, Ca, Mg, and K. In contrast, the shrub layer increased only 3-5 fold for these nutrients over the same 20-yr period (Reiners 1992).

The purpose of this study was to compare herbaceous layer and extractable soil nutrients (N, P, Ca, Mg, and K) between watersheds supporting young, clearcut (~20-yr old) vs. mature ~80-yr old stands of central Appalachian mixed hardwood forests. We were also interested in examining soil-plant nutrient interactions and how these interactions might vary with stand age.

METHODS

Study Site

Research was done on four contiguous watersheds of the Fernow Experimental Forest (FEF), a 1900-ha area of montane hardwood forests within the unglaciated Allegheny Plateau, located in Tucker County, West Virginia (39°03'N, 79°49'W). WS7 and WS3 support stands which were approximately 20 yr old and even-aged (following clearcutting) at the time of sampling and will be referred to as "young." These stands are dominated primarily by black cherry (*Prunus serotina* Ehrh.) and yellow poplar (*Liriodendron tulipifera* L.). WS13 and WS4 support stands which were older than 75 yr at the time of sampling and will be referred to as "mature." They are mixed-age, being dominated by sugar maple (*Acer saccharum* Marsh.) and northern red oak (*Quercus rubra* L.), and originated from natural regeneration from the heavy cutting which characterized the period of railroad logging from ~1880 to 1930 (Marquis and Johnson 1989). Herbaceous layer species have been described in previous papers (Gilliam and Turrill 1993, Gilliam and others 1994).

Field Sampling

Fifteen semi-permanent circular plots were established within each of the study watersheds, for a total of 60 sample plots for the study. Plots were established by locating plot centers throughout each watershed to include the extremes of elevation and aspect. A radius of 11.3 m was measured from each plot center for a total area of 0.04 ha per plot.

Methods of herbaceous layer and soil sampling also has been described in those papers, but is summarized briefly here. Within each sample plot all vascular plants within 10 1-m² circular sub-plots were identified to species and estimated visually for cover (total of 600 sub-plots for the study) using the technique of Gilliam and Christensen (1986). This method has been shown to be both reproducible and capable of accurate prediction of herb layer biomass (Gilliam and Turrill 1993). The two sub-plots with the greatest percentage of herb layer cover in each were chosen as "harvest" sub-plots, within which all above-ground herb layer material was collected. Harvesting was confined to only the two high-cover sub-plots in each plot to ensure enough herb tissue biomass for nutrient analysis of individual species. Although this criterion potentially confounds cover-nutrient relationships among watersheds, it allowed for a full range of cover values (from 1 to ~80%) for harvested species (Gilliam and Turrill 1993). Furthermore, there was a good correlation between the mean cover of the two sub-plots per plot and mean cover of the entire plot (based on all 10 plots). In other words, relatively high-cover sample plots had relatively high-cover harvest sub-plots, and visa versa. Therefore, using high cover as a selection criterion for herb layer harvests does not appear to create problems for comparison among watersheds. Finally, a sample of mineral soil was taken to a 10-cm depth from each of the two harvest sub-plots following removal of organic forest floor material.

Sample Analysis

Herb layer samples from each of the 120 harvest sub-plots were separated into species, oven-dried at 50°C, weighed, and ground in a Wiley mill to pass a 1-mm screen. Plant tissue (and soil--see below) samples were shipped to the University of Maine (U. M.) Soil Testing Service and Analytical Laboratory for macronutrient analysis (N, P, Ca, Mg, and K). Total plant N was measured as Kjeldahl N. All other nutrients were measured with plasma emission spectrophotometry after dry-ashing plant material and extraction with HCl and HNO₃.

Mineral soil samples were sieved to pass a 2-mm screen, air-dried, and shipped to the U. M. laboratory for analysis, including pH (1:1 w/v, soil/H₂O), 1N KCl-extractable Ca, K, Mg, and P (plasma emission), 1N KCl-extractable NO₃ and NH₄ (flow-injection colorimetry), and soil organic matter (loss-on-ignition). Particle-size (texture) was determined on each soil sample at the laboratory at Marshall University using the hydrometer method of Bouyoucos (1951).

Data Analysis

Data analysis for this study was based on mean plot values (i.e., not sub-plot values) of all soil and plant variables. Stand age class means of all variables were calculated as the average of 30 plots (15 plots in each of two watersheds per stand age class) and were compared (young vs. mature) using Student's t-test (SAS 1982, Zar 1984). Within each age class, relationships among soil and plant variables (soil vs. soil, plant vs. plant, and plant vs. soil) were determined with Pearson product-moment correlation analysis (SAS 1982).

RESULTS

There were no significant differences between stand age classes for any of the measured soil variables, including organic matter, cation exchange capacity, pH, and extractable nutrients (Table 1). There were also no differences between age classes for P, Ca, Mg, and K concentrations in the herbaceous layer (Table 2). However, the herb layer of the young stands was significantly higher ($P < 0.01$) in N than that of mature stands (Table 2).

Table 1. T-test comparisons of soil variables of young vs. mature stands of the Fernow Experimental Forest, WV. OM=organic matter; CEC=cation exchange capacity. NS indicates no significant differences between stand age classes at P<0.05. Values in parentheses are one standard error of the mean.

| Stand Age | OM (%) | CEC (meq/kg) | pH | NO ₃ | NH ₄ | P | Ca | Mg | K |
|-----------|---------------|---------------|----------------|-----------------|-----------------|--------------|---------------|--------------|--------------|
| | | | | -----mg/kg----- | | | | | |
| Young | 13.8 (0.7) | 45.5 (4.6) | 4.39 (0.06) | 1.3 (0.2) | 2.1 (0.2) | 0.8 (0.4) | 12.6 (5.0) | 2.1 (0.4) | 2.3 (0.2) |
| | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| Mature | 12.6 (0.4) | 40.1 (1.2) | 4.32 (0.05) | 0.9 (0.1) | 1.9 (0.1) | 0.4 (0.0) | 6.4 (1.1) | 2.4 (0.7) | 2.2 (0.1) |

Table 2. T-test comparisons of herbaceous layer tissue nutrients of young vs. mature stands of the Fernow Experimental Forest, WV. Significant differences (P<0.01) between stand age classes indicated by *. NS indicates no significant difference between age classes at P<0.05. Values in parentheses are one standard error of the mean.

| Stand Age | N | P | Ca | Mg | K |
|-----------|-----------------|----------------|----------------|----------------|----------------|
| | -----mg/kg----- | | | | |
| Young | 2.35 (0.07) | 0.16 (0.01) | 0.62 (0.08) | 0.22 (0.01) | 2.68 (0.26) |
| | * | NS | NS | NS | NS |
| Mature | 1.99 (0.09) | 0.15 (0.01) | 0.75 (0.06) | 0.24 (0.02) | 2.21 (0.19) |

Numerous significant correlations (nearly 60% of total possible combinations) existed among soil variables for the young stands (Table 3). Notable variables with which there were several significant correlations were texture classes (sand and silt) and organic matter. In contrast, neither extractable P nor extractable NH₄ were correlated with any other soil variables (Table 3). Soils of mature stands exhibited far fewer significant correlations (<20% of the total) compared to young stand soils (Table 4).

In contrast to differences between stand age classes in patterns of soil variable correlations, correlations among herb layer nutrient concentration were quite similar between young and mature stands. All plant nutrients were correlated significantly with each other for mature stands, and all but Ca:K were significant for young stands (Table 5).

In comparing plant vs. soil nutrients between stand ages, the young stand exhibited significant correlations for the nutrient cations, but neither N nor P; the mature stand had significant correlations for P, Ca, K, and plant N vs. soil NO₃ (Table 6). Finally, all plant nutrients except N were correlated significantly with soil organic matter in the young stands, whereas no plant nutrients were correlated with organic matter in mature stands.

Table 3. Correlations among soil variables of young stand plots. Values shown are Pearson product-moment correlation coefficients (r) significant at P<0.05.

| | Sand | Silt | Clay | OM | Ca | K | Mg | P | NO ₃ | NH ₄ | pH |
|-----------------|---------|--------|--------|--------|--------|--------|--------|-----|-----------------|-----------------|--------|
| Silt | -0.89** | | | | | | | | | | |
| Clay | -0.70** | --- | | | | | | | | | |
| OM | 0.56* | -0.41 | -0.53* | | | | | | | | |
| Ca | 0.46 | -0.42 | --- | 0.66** | | | | | | | |
| K | 0.56* | -0.42 | -0.52* | 0.77** | 0.72** | | | | | | |
| Mg | 0.47* | -0.39 | --- | 0.73** | 0.97** | 0.76** | | | | | |
| P | --- | --- | --- | --- | --- | --- | --- | | | | |
| NO ₃ | 0.50* | -0.44 | --- | 0.78** | 0.68** | 0.76** | 0.73** | --- | | | |
| NH ₄ | --- | --- | --- | --- | --- | --- | --- | --- | | | |
| pH | 0.55* | -0.49* | -0.39 | 0.51* | 0.75** | --- | --- | --- | 0.40 | --- | |
| CEC | 0.44 | -0.37 | --- | 0.68** | 0.98** | 0.69** | 0.98** | --- | 0.72** | --- | 0.61** |

*indicates correlation coefficient significant at P<0.01.

**indicates correlation coefficient significant at P<0.001.

Table 4. Correlations among soil variables of mature stand plots. Values shown are Pearson product-moment correlation coefficients (r) significant at P<0.05.

| | Sand | Silt | Clay | OM | Ca | K | Mg | P | NO ₃ | NH ₄ | pH |
|-----------------|---------|-------|------|------|--------|-------|-------|--------|-----------------|-----------------|-----|
| Silt | -0.82** | | | | | | | | | | |
| Clay | -0.47* | --- | | | | | | | | | |
| OM | 0.38 | -0.42 | --- | | | | | | | | |
| Ca | --- | --- | --- | --- | | | | | | | |
| K | --- | --- | --- | --- | 0.59** | | | | | | |
| Mg | --- | --- | --- | --- | 0.61** | --- | | | | | |
| P | --- | --- | --- | 0.44 | --- | --- | --- | | | | |
| NO ₃ | --- | --- | --- | --- | --- | --- | --- | 0.67** | | | |
| NH ₄ | --- | --- | --- | --- | --- | --- | --- | --- | --- | | |
| pH | --- | --- | --- | --- | 0.42 | 0.48* | --- | --- | --- | --- | |
| CEC | --- | --- | --- | --- | 0.74** | --- | 0.46* | --- | --- | --- | --- |

*indicates correlation coefficient significant at P<0.01.

**indicates correlation coefficient significant at P<0.001.

Table 5. Correlations among herbaceous layer nutrient concentrations of young and mature stand plots. Values shown are Pearson product-moment correlation coefficients (r) significant at P<0.05.

| | N | P | Ca | Mg |
|---------------|--------|--------|--------|--------|
| Young stands | | | | |
| P | 0.63** | | | |
| Ca | 0.49* | 0.62** | | |
| Mg | 0.71** | 0.38 | 0.58** | |
| K | 0.56* | 0.38 | --- | 0.67** |
| Mature stands | | | | |
| P | 0.83** | | | |
| Ca | 0.53* | 0.48* | | |
| Mg | 0.88** | 0.64** | 0.54* | |
| K | 0.88** | 0.67** | 0.58** | 0.89** |

*indicates correlation coefficient significant at P<0.01.

**indicates correlation coefficient significant at P<0.001.

Table 6. Plant-soil nutrient interactions of young and mature stands of Fernow Experimental Forest, WV. Values shown are Pearson product-moment correlation coefficients (r) for indicated pairs significant at P<0.05.

| Plant | Variables | | Stand Age | |
|-------|-----------|-----------------|-----------|--------|
| | vs. | Soil | Young | Mature |
| N | vs. | NO ₃ | --- | 0.63** |
| N | vs. | NH ₄ | --- | --- |
| P | vs. | P | --- | 0.63** |
| Ca | vs. | Ca | 0.78** | 0.43 |
| Mg | vs. | Mg | 0.57* | --- |
| K | vs. | K | 0.44 | 0.42 |
| N | vs. | OM | --- | --- |
| P | vs. | OM | 0.48* | --- |
| Ca | vs. | OM | 0.75** | --- |
| Mg | vs. | OM | 0.50* | --- |
| K | vs. | OM | 0.37 | --- |

*indicates correlation coefficient significant at P<0.01.

**indicates correlation coefficient significant at P<0.001.

DISCUSSION

Based on soil and plant tissue nutrient comparisons alone, there appears to have been little long-term change in nutrient availability over time following forest disturbance at this site. Soil variables were virtually identical between young and mature stands. In general these forest soils were acidic, with moderate levels of organic matter (~13%) and a relatively low cation exchange capacity (~42 meq/kg). It should be emphasized that the extractable N data represent pools of available N and not fluxes. Current research using *in situ* incubations ("buried bag" technique) on many of these same plots indicate that fluxes (e.g., uptake) are >10-fold higher than available N pools (Gilliam and Adams, submitted manuscript).

Herb layer tissue nutrient data are indicative of small decreases in N availability with stand development over time. Because these data are for the herb layer as an entire stratum (i.e., all species combined), the significant difference in plant N may have resulted from stand age-related differences in herb layer species. However, these stands are remarkably similar with respect to herb layer species composition, regardless of stand age (Gilliam and Turrill 1993, Gilliam and others, submitted manuscript), with the possible exception of higher fern cover on WS7 (Gilliam and others 1994). Herb layer nutrient concentrations for FEF were similar to other hardwood forests for N and P, but lower for Ca, Mg, and K (Grigal and Ohmann 1980, Peterson and Rolfe 1982, Siccama and others 1970). These differences may be related to the sandstone parent materials of the FEF watersheds. Concentrations of herb layer nutrients at FEF are well within the range of values reported as adequate for crop plants (Chapin and Van Cleve 1991).

Although correlation analysis is more appropriate for generating hypotheses than for testing them, such analyses can be useful in describing general patterns of relationships of soil and plant nutrients. For example, the numerous significant correlations among soil variables of the young stand plots suggest that there may be a single factor determining, or controlling, overall soil fertility of these young stands. Furthermore, the general lack of correlations for the mature stand plots indicate that this factor is not as prevalent for the mature stands as it is for the young stands.

Soil organic matter is the variable which is consistently the most highly correlated with extractable soil nutrients in the young stands (Table 3), suggesting that organic matter is an important factor determining overall fertility of these soils. Indeed, it was significantly correlated ($P < 0.01$) with all other young stand soil variables except extractable P and NH_4 (Table 3). Significant correlation ($P < 0.001$) between organic matter and cation exchange capacity further support this contention, and indicate that exchange sites of these soils are dominated by organic colloids (Tate 1987). In sharp contrast in mature stand soils, among the nutrients organic matter was correlated only with extractable P, and it was not correlated with cation exchange capacity.

Surprisingly, there were numerous significant correlations among plant nutrients for both stand age classes. Other studies have reported fewer significant correlations among plant nutrients, but ones which suggest either biochemical or functional groups. For example, using nutrient data from 110 plant species, Garten (1978) found significant correlations for the following plant nutrient pairs: N:P, Mg:K, and Ca:Mg. He concluded that these pairings were related to biochemical functions within the plant, e.g., nucleic acids-proteins for N:P. Gilliam (1988) found significant correlations for most of these same nutrient pairs and for K:P. He concluded that the latter was the result of limitation of herb layer plant growth from both nutrients in the highly weathered soils of a southeastern U.S. pine forest. Thus, the numerous correlations found in the present study are certainly notable, though difficult to interpret.

Young and mature stands differed slightly from each other with respect to correlations between plant tissue nutrient concentrations and extractable forms of the same nutrients in mineral soil (Table 6). However, correlations between plant nutrients and soil organic matter varied greatly with stand age. Virtually all nutrients were correlated in young stands, whereas none were correlated in mature stands (Table 6). The numerous significant correlations in young stands further illustrates the importance of soil organic matter in mediating nutrient availability following forest disturbance. Organic matter serves both as a nutrient source via decomposition and a cation exchange source.

CONCLUSIONS

Although differences between stand age classes in soil organic matter/plant nutrient correlations might suggest that this importance decreases with stand age, this explanation is probably unlikely considering the nature of the soils of these watersheds (i.e., that they are derived from low-nutrient sandstone parent materials). Because soil organic matter plays such an important role in determining fertility of these sandy soils, stand age-related differences in correlations of herb layer nutrient concentration with organic matter may arise from successional changes in factors limiting herb layer dynamics. Significant correlations would suggest soil-mediated limitations (e.g., nutrient availability), whereas lack of correlation would suggest limitations from other sources. Gilliam and Turrill (1993) hypothesized that the herb layer of these forests are nutrient-limited early in succession when light availability is relatively high and uniform in the stand, and that the herb layer becomes more limited by light availability later in succession following canopy closure and stratification. Although certainly not conclusive, data presented in this paper are consistent with this hypothesis.

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NUTRIENT BUDGETS OF TWO WATERSHEDS ON THE FERNOW EXPERIMENTAL FOREST

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Abstract: Acidic deposition is an important non-point source pollutant in the Central Appalachian region that is responsible for elevated nitrogen (N) and sulfur (S) inputs to forest ecosystems. Nitrogen and calcium (Ca) budgets and plant tissue concentrations were compared for two watersheds, one that received three years of an artificial acidification treatment and an adjacent reference watershed, both located on the Fernow Experimental Forest, West Virginia. Treatments consisted of ammonium sulfate fertilizer applied aurally three times per year at an annual rate of 61 kg S ha⁻¹ and 54 kg N ha⁻¹. Trees of four species (*Betula lenta* L., *Prunus serotina* Ehrh., *Acer rubrum* L. and *Liriodendron tulipifera* L.) were harvested for biomass and nutrient determinations. Some tree species on the treated watershed showed elevated N and decreased Ca levels in some tissues, particularly foliage, but no consistent pattern for any species or tissue component was found. Compared to other watersheds in the central and southern Appalachians, Fernow watersheds are losing more N in streamflow. This loss is almost solely in the form of NO₃, which appears to bring about increased leaching of Ca from watersheds.

INTRODUCTION

During its initial 10-year existence, the National Acid Precipitation Assessment Program (NAPAP) supported a great deal of air pollution research, primarily related to acidic deposition, and its effects on structures, human health, and ecosystems. Although much was learned through NAPAP, many unanswered questions remain, and acidic deposition continues. Nitrogen (N) deposition is expected to increase, despite recent Clean Air legislation (Aber and others 1993), and although reduced sulfur (S) deposition has been reported in some parts of the U.S. (Baier and Cohn 1993), in other regions no change has been detected. The effects of acidic deposition on central Appalachian hardwood forests are not well-understood. Hypothesized effects include nitrogen saturation, altered susceptibility to pests and pathogens, increased tree mortality, and increased growth. None of these hypotheses have been adequately tested, however. Ecosystem level studies can improve our ability to make predictions regarding the effects of acidic deposition on the health and long-term sustainability of central Appalachian forests.

One method to evaluate acidic deposition effects on forest ecosystems is whole-watershed manipulation, i.e. applying a potentially acidifying agent to one watershed and comparing the results with an untreated reference watershed. Because of their expense, whole-watershed experiments are not often replicated. Comparisons between watersheds are therefore based on pseudoreplicated measurements (Hargrove and Pickering 1992). Nonetheless, much can be learned with careful interpretation, and numerous paired watershed studies have been the basis for meaningful ecosystem research (Likens and others 1977, Swank and Crossley 1988). The objective of this paper is to describe and compare nutrient and biomass budgets on two experimental watersheds on the Fernow Experimental Forest, and to evaluate the early effects of an artificial acidification treatment on nutrient cycling. This paper will focus on N and calcium (Ca) because of the recent concerns about N saturation of forest ecosystems (Aber and others 1993) and potential Ca deficiencies, and implications for forest health.

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METHODS

Description of Watersheds

Two experimental watersheds were used for this study. Watershed 3 (WS3) is the treatment watershed, and watershed 7 (WS7) serves as a control or reference watershed. The watersheds are located on the Fernow Experimental Forest near Parsons, West Virginia, USA (39° 3' 15" N, 79° 49' 15" W). The Fernow is located on the unglaciated Allegheny plateau of the Appalachian mountains and is characterized by steep slopes and shallow soils (<1m). Precipitation is distributed evenly between dormant and growing seasons and is among the most acidic in the United States. Average annual pH is 4.20, but pH values below 4.0 are common in summer (Edwards and Helvey 1991). The predominant soil type on the experimental watersheds is Calvin channery silt loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) underlain with fractured sandstone and shale of the Hampshire formation (Losche and Beverage 1967). The experimental watersheds are drained by intermittent, second-order streams. Stands on both watersheds have similar species composition and originated at the same time (1969). Prior to 1969, WS7 was maintained barren with herbicides (Patric and Reinhart 1971), while WS3 was clearcut and permitted to regrow without interference. Other watershed characteristics are given in Table 1.

Table 1. Characteristics of two experimental watersheds on the Fernow Experimental Forest, West Virginia.

| | Watershed | |
|---|--|---|
| | 3 | 7 |
| Age (yr) | 24 | 24 |
| Stand density (trees ha ⁻¹) | 537.5 | 376.8 |
| Basal area (m ² ha ⁻¹) | 3.87 | 3.27 |
| Area (ha) | 34.3 | 24.2 |
| Aspect | S | ENE |
| Minimum elev. (m) | 735 | 725 |
| Maximum elev. (m) | 860 | 855 |
| Average annual precipitation (mm) | 1480 | 1417 |
| Average annual streamflow (mm) | 666 | 882 |
| Dominant tree species | Black cherry Red maple Black birch American beech | Black birch Red maple Sugar maple Black cherry |

Methods and Measurements

Ammonium sulfate fertilizer was applied to WS3 three times per year by helicopter beginning in 1989. March and November applications consisted of 33.6 kg of fertilizer per hectare, which corresponds to 8.1 and 7.1 kg ha⁻¹ of S and N, respectively. Each July we applied 100.8 kg fertilizer per hectare, or 24.4 and 21.2 kg ha⁻¹ S and N, respectively. Multiple applications per year were used to more closely mimic seasonal variations in chemical inputs. These application rates were approximately double the amount of S and N deposited on the watersheds in throughfall, which we believe to be a good estimate of bulk deposition. Consequently, the total amount of S and N deposited annually on the treatment watershed was 60.5 kg S (ambient S + 40.6 kg from treatment) and 53.8 kg N (ambient N + 35.4 kg from treatment) per hectare, or approximately three times that received by the reference watershed.

In July 1991, total aboveground portions of five trees from each of four species (black cherry, red maple, black birch and yellow-poplar: *Prunus serotina* Ehrh., *Acer rubrum* L., *Betula lenta* L., and *Liriodendron tulipifera* L., respectively) were sampled from both WS3 and WS7. Only dominant and codominant trees were selected for nutrient

determinations. (For biomass determinations, an additional six trees per watershed per species were selected to insure representative sampling of smaller trees.) All leaves were removed from the felled trees, weighed, then subsampled for nutrient analysis and moisture content determination. Each tree was limbed and divided into stemwood (bole to bottom of live crown), top-wood (remainder of bole), and small and large branches (<1 cm diameter and >1 cm diameter, respectively); all constituent parts were weighed in the field. Subsamples were collected for nutrient analysis and moisture content determinations. Each subsample was weighed to the nearest 0.1 g, dried at 70° C and reweighed. Dead wood biomass was determined on 100 square-meter plots. On each plot, standing dead and down dead biomass were weighed separately and subsamples collected for nutrient and moisture content determinations. Soil nutrients and herbaceous layer biomass and nutrient methods were described by Gilliam and others (1994).

Aboveground biomass was measured on 0.004 ha (.01 A) plots and stand biomass for each watershed was calculated using biomass equations of Brenneman and others (1978). For those species for which Brenneman and others had no equation, an equation for a species of similar specific gravity was used. Watershed foliar biomass was estimated from litterfall collected from 25 1-m² litterfall traps per watershed. Root biomass was estimated from four root cores (45 cm depth) collected from each of 25 plots per watershed during May and September 1991. Roots were washed from the cores, separated into fine and coarse roots, dried (70°C) and weighed. Samples were composited by watershed, horizon and size class to provide sufficient tissue for nutrient analyses. Roots were not separated by species.

Tissue samples were analyzed at the Plant and Soil Analysis Laboratory at the University of Maine. Total N was determined by block digestion using a sulfuric acid-hydrogen peroxide solution, and analyzed using a Wescan 360 ammonia analyzer (Wescan Instruments, Santa Clara, CA)². To determine total Ca, ground tissue samples were ashed at 550°C for 5-6 hrs, dissolved in 50% HCl, and analyzed using inductively coupled plasma emission spectrometry.

Nutrient budgets were constructed using mean watershed nutrient concentrations, multiplied by estimated watershed biomass of each component. Soil nutrient pools were calculated for a 60 cm soil depth. Average root biomass (fine + coarse roots) was calculated for each watershed. Herb layer values were calculated from data of Gilliam and Turrill (1993) and Gilliam and others (1994).

Annual (water year, May 1 - April 30) nutrient exports in stream water were calculated from streamflow volume and weekly ionic concentrations of grab samples to relate to watershed nutrient pools. Streamflow measurement, sampling techniques and analytical procedures were described by Edwards and Kochenderfer (1993) and Edwards and Wood (1993). Effects of the acidification treatment on stream and soil water chemistry were reported by Edwards and Wood (1992) and Adams and others (1993).

Watershed nutrient budgets were calculated for treatment comparisons. Mean mass, concentration and content were also calculated for each of the 4 tree species on each watershed and compared using Student's t tests.

RESULTS AND DISCUSSION

Biomass and Nutrient Budgets

Tree biomass varied between the two watersheds (Figure 1). The treatment watershed, WS3, had greater aboveground woody biomass (stems, tops and large branches) than the control, WS7. Because of different pre-treatment histories, the difference in total tree aboveground biomass between WS3 and WS7 can not be attributed to the acidification treatment. The vegetation on WS7 originated mostly from seed, going through the grass - herbaceous - semi-woody - woody plant successional phases (Kochenderfer and Wendel 1983), while the vegetation that developed on WS3

²The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

originated mainly from stump sprouts, getting a "head start" on biomass accumulation. Moreover, it is unlikely that such a large treatment effect on woody biomass (approximately 12 of the 17 mt ha^{-1} difference between the two stands is in stemwood) would be evident after only three years of fertilization treatment. Changes in production of foliage or small branches have been reported as a short-term growth response to N fertilization (Auchmoody and Smith 1977, Brix and Ebell 1969, Carlson and Preisig 1981). However, foliar biomass did not differ between the two watersheds, and small branch biomass was slightly lower on the treated watershed. The total root biomass was less on WS3 than on WS7.

Total biomass of dead wood was greater on WS3 (Figure 1). Because WS7 was cut earlier (1964-67) than WS3 (1969) and then maintained barren for 5 years, surface temperatures were higher, resulting in greater rates of decomposition (Mattson and others 1989). Also, WS7 was cut several years prior to WS3, allowing more time for woody slash to decompose. Therefore biomass differences between the watersheds are not attributed to fertilization.

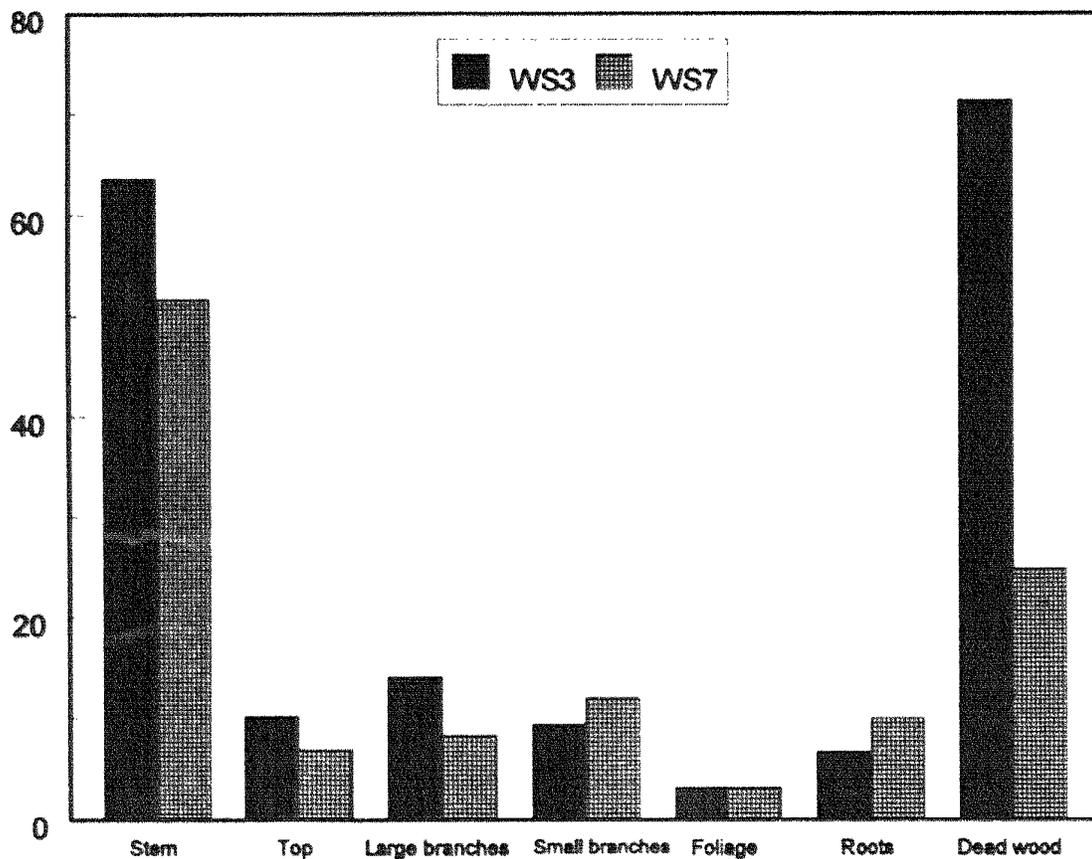


Figure 1. Biomass (mt ha^{-1}) by tree component for 2 experimental watersheds on the Fernow Experimental Forest, West Virginia.

Despite these confounding factors, some observations about the acidification treatment can be made. Aboveground N content was greater for WS3, except in the herb layer (Figure 2). The large herb layer N content in WS7 is due to a large fern community on WS7 which results in twice the herb biomass of WS3 (Gilliam and others 1994). Tissue N concentrations for the herb layer did not differ significantly between the two watersheds, nor did soil extractable N pools or pH differ significantly (Gilliam and others, 1994). Aspect did not significantly affect the response of small stands/watersheds to fertilization (Edwards and others 1991), therefore this is not an alternative explanation. Overall, it did not appear that the treatment had much effect on soil N and vegetation N levels at the watershed scale. Three years after the initiation of treatment, streamwater export of N from WS3 was not significantly different from WS7, although nitrate export from WS3 was significantly greater than that of another reference watershed (Adams and others 1993). This can be explained by examining the differences in pre-treatment N export (Figure 3). For six years prior to treatment, WS3 export of N was consistently less than that from WS7. Within 3 years of initiation of treatment, N export from WS3 increased to a level equal to that of WS7. Because of high variability, this change in trend is not statistically significant, but does agree with results of Adams and others (1993) and Edwards and others (1991) that report significant changes in soil water N and stream water N.

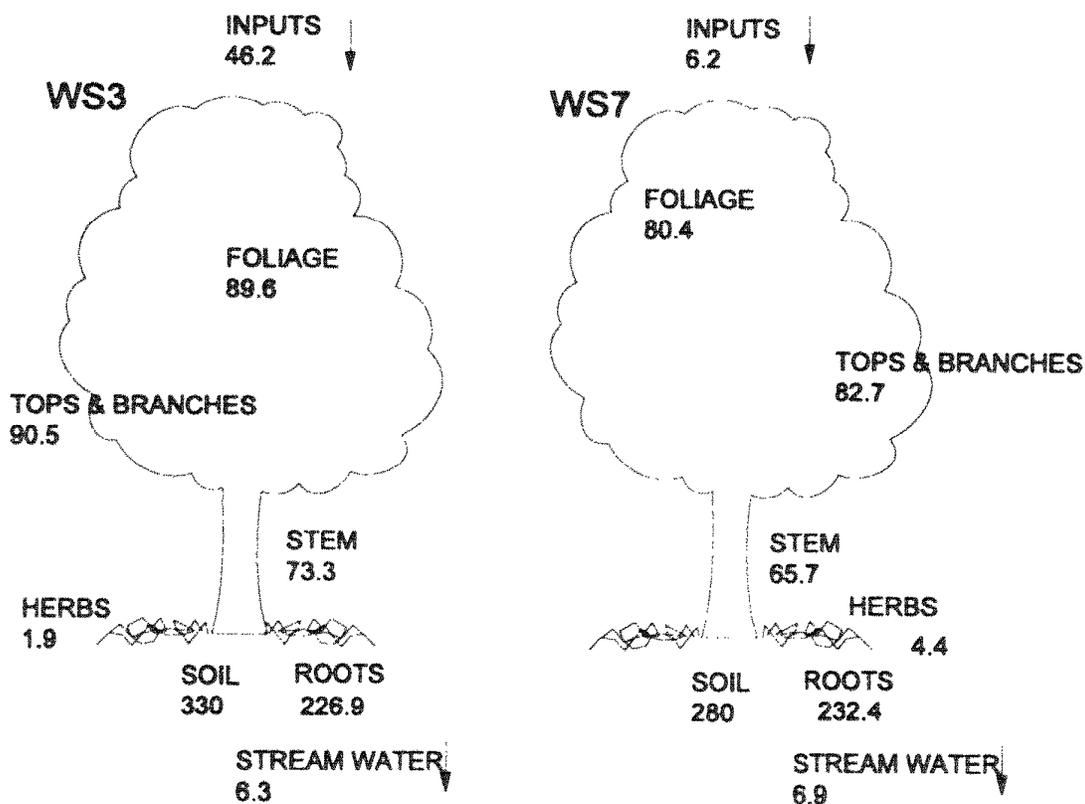


Figure 2. July nitrogen budgets for WS3 (treatment watershed) and WS7 (control watershed), Fernow Experimental Forest. Values are kg ha⁻¹.

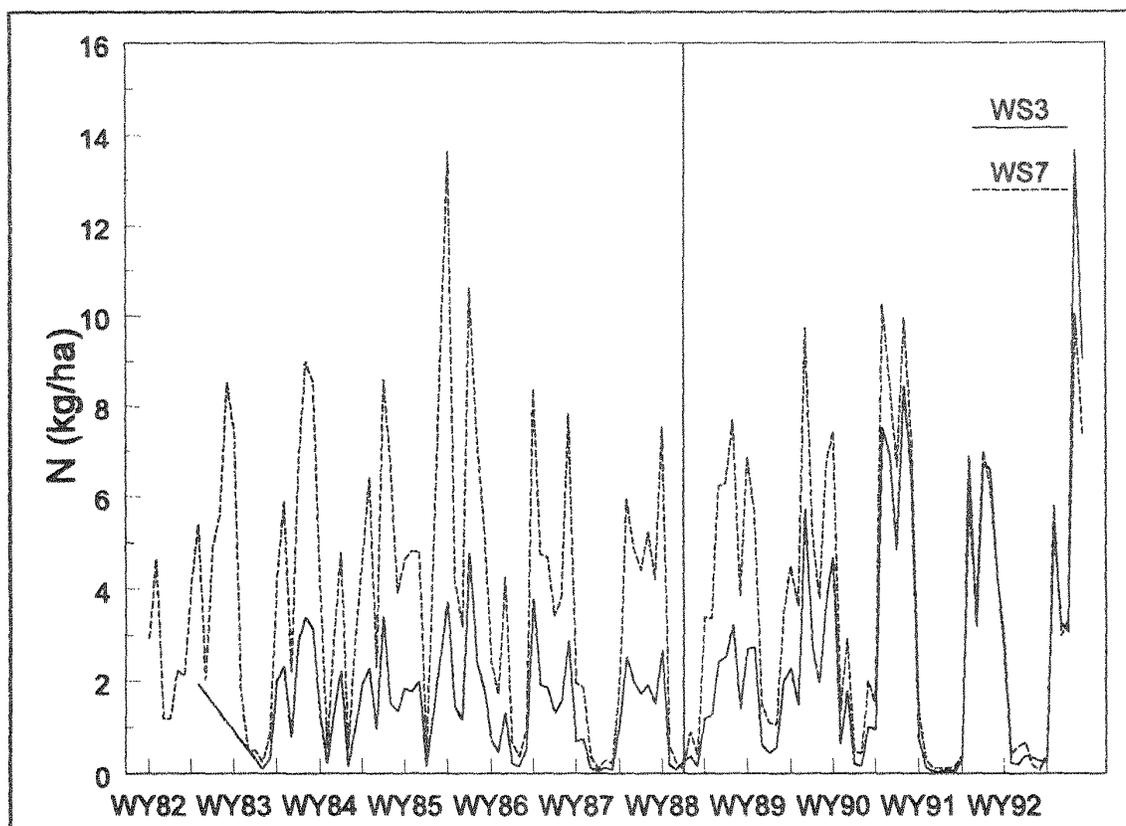


Figure 3. Mean monthly nitrogen export (kg ha^{-1}) from WS3 (treatment watershed) and WS7 (control watershed) on the Fernow Experimental Forest during water years 1982-1992. Vertical line indicates initiation of treatment.

Foliar Ca levels were lower on WS3 than WS7 (Figure 4), reflecting significant differences in foliar Ca concentrations for most species (Tables 3,4). Stemwood Ca did not differ between the two watersheds. Herb layer Ca concentrations for WS3 were twice as high as for WS7, a significant difference (Gilliam and others 1994). However, the difference is masked in the whole watershed budget because of differences in herb layer biomass described previously. Edwards and Kochenderfer (1993) reported ion pairing of Ca and NO_3^- in soil and stream water export from WS3. This observation suggests increased availability of Ca on WS3, as Ca is removed from soil exchange sites during export of the mobile NO_3^- . Although soil Ca levels appear lower on WS3 than WS7, Gilliam and others (1994) found no statistically significant differences in Ca concentrations of soil between the two watersheds, due to high variability. Annual streamwater Ca export from WS3 and WS7 did not differ significantly (Figure 5).

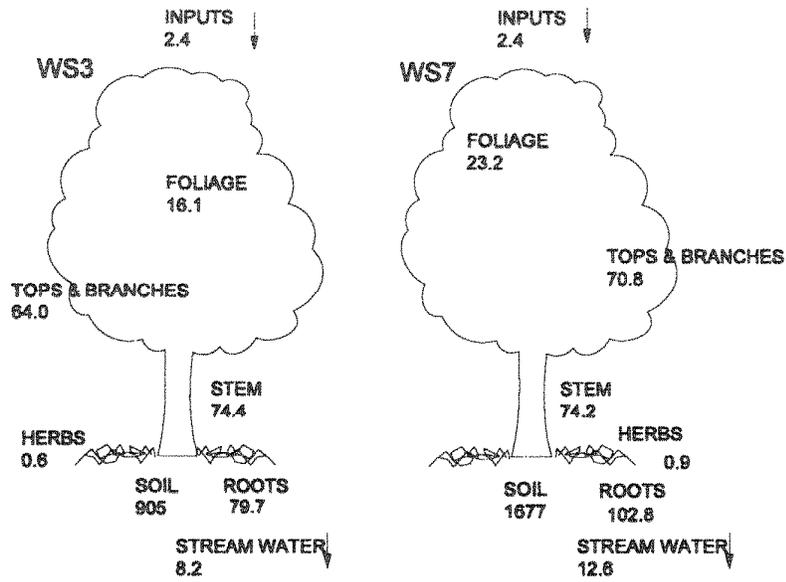


Figure 4. July calcium budgets for WS3 (treatment watershed) and WS7 (control watershed), Fernow Experimental Forest. Values are kg ha⁻¹.

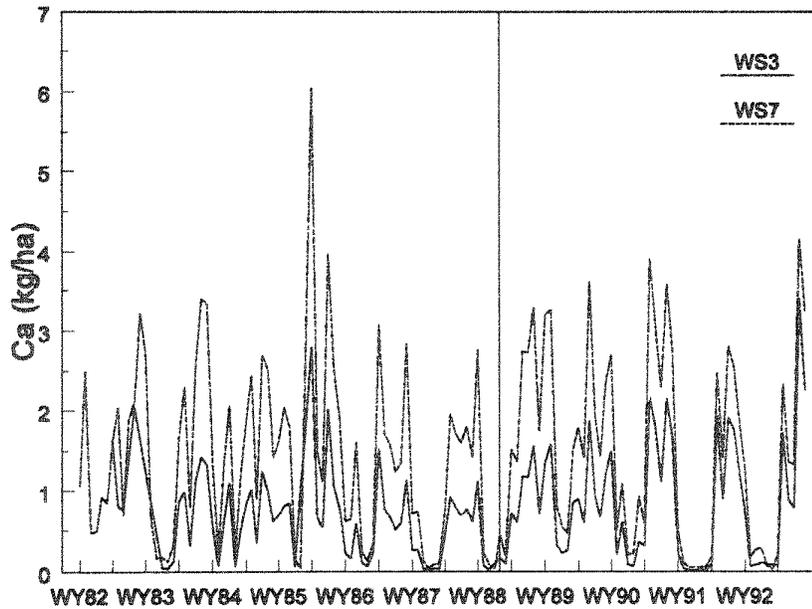


Figure 5. Mean monthly calcium export (kg ha⁻¹) from WS3 (treatment watershed) and WS7 (Control watershed) on the Fernow Experimental Forest during water years 1982-1992. Vertical line indicates initiation of treatment.

Nitrogen and Ca budgets for WS7 (reference watershed) were compared with those of Coweeta's Watershed 18 (Swank and Crossley 1988) and the Walker Branch Watershed in Tennessee (Johnson et al. 1988), both untreated reference watersheds (Table 2) to provide context for the observations from the acidification treatment. It was reasoned that if the three untreated controls showed similar nutrient levels, then the effects of the acidification experiment might be more obvious. The Fernow aboveground vegetation values appear low relative to the other two watersheds. This can be attributed mostly to differences in stand age -- stands on both the Coweeta Watershed 18 and Walker Branch Watershed were approximately 60 years old, while stands on WS3 and WS7 were 24 years old and had not accumulated biomass or nutrients for as long. Nutrient inputs in precipitation are similar among the three sites. However, it should be noted that the 6.2 kg N ha⁻¹ reported here for the Fernow for 1991 is below the average value of 13.7 kg N ha⁻¹ reported by Helvey and Kunkle (1986), who also reported average Ca inputs of 7.9 kg Ca ha⁻¹. This is attributed to lower precipitation in 1991 (125 cm compared with the long-term average of 380 cm). Even during this year of relatively low deposition, N exports were much greater from WS7 than from the Coweeta Watershed 18 or Walker Branch Watershed. Younger, more vigorous stands are normally more conservative of N than older stands, thus this seems a contradiction. For this same year, the export from an 85 year old reference watershed on the Fernow for the same year was 3.45 kg N ha⁻¹. Therefore, N export from the Fernow watersheds does appear elevated, relative to Walker Branch and Coweeta.

Table 2. Comparison of N, P, and Ca budgets for three reference watersheds in the central and southern Appalachian Mountains. (NM=not measured).

| | Fernow WS7 | Coweeta ¹ | Walker Branch ² | |
|-----------------|------------------|----------------------|----------------------------|-------------------|
| | | kg ha ⁻¹ | YP ³ | OH ⁴ |
| Nitrogen | | | | |
| Input | 6.2 | 8.8 | 9.8 | 9.8 |
| Aboveground | 233.2 | 563.2 | 450 | 353 |
| Soil | 467 ⁵ | 6803 | 5730 | 2873 |
| Output | 6.9 | 0.09 | 0.056 ⁶ | 0.20 ⁶ |
| Calcium | | | | |
| Input | 2.4 | 4.0 | 8.6 | 8.6 |
| Aboveground | 168.2 | 550.8 | 922 | 1283 |
| Soil | 2796 | 514 | 1445 | 668 |
| Output | 12.58 | 7.1 | 28.1 ⁶ | 4.81 ⁶ |

¹ Monk and Day (1988)

² Johnson and others (1988)

³ Yellow-poplar stand, mean of 2 values

⁴ Oak-hickory stand, mean of 2 values

⁵ Extractable soil N, Coweeta and Walker Branch are total soil N

⁶ Calculated from soil flux values of Johnson and others (1985)

Nutrient concentrations by species

Nutrient concentrations varied among the four species sampled, and among tree components. Foliar nutrient concentrations appeared the most responsive to treatment (Tables 3, 4). Foliar N concentrations were higher on WS3 for all four species studied, but were only significantly higher ($P \leq 0.10$) for black cherry and red maple. No significant differences in foliar mass were observed for these two species between the two watersheds. Foliar Ca was higher for all species on WS7 and was significantly different ($P < 0.10$) between the two watersheds for black birch, yellow-poplar and red maple. Some differences in foliar micronutrient concentrations also were detected, most notably for boron (data not shown). Overall, yellow-poplar showed the most differences, with significant differences in macro- or micronutrient concentrations for all components except small branches, suggesting that this fast-growing species may be more responsive to changes in nutrient supply than the other species examined.

Table 3. N and Ca concentrations by species, watershed and tissue type, from trees from two experimental watersheds on the Fernow Experimental Forest, WV. N is expressed in % and Ca as mg kg⁻¹. Watershed 3 = treatment, watershed 7 = control.

| Species | Watershed | Tissue Type | N | Ca |
|---------------|-----------|-------------|-------|-------|
| Black birch | 3 | Foliage | 2.720 | 3985 |
| | | Lg.branches | .198 | 1994 |
| | | Sm.branches | .462 | 2634 |
| | | Top | .180 | 1123 |
| | | Stem | .104 | 1000 |
| | 7 | Foliage | 2.540 | 5580 |
| | | Lg.branches | .170 | 2480 |
| | | Sm.branches | .448 | 3809 |
| | | Top | .130 | 1118 |
| | | Stem | .154 | 1195 |
| Yellow-poplar | 3 | Foliage | 3.002 | 6996 |
| | | Lg.branches | .212 | 2405 |
| | | Sm.branches | .475 | 3725 |
| | | Top | .193 | 1579 |
| | | Stem | .125 | 1294 |
| | 7 | Foliage | 2.750 | 11457 |
| | | Lg.branches | .222 | 2717 |
| | | S.branches | .435 | 4221 |
| | | Top | .230 | 1973 |
| | | Stem | .134 | 1915 |
| Black cherry | 3 | Foliage | 2.990 | 4354 |
| | | Lg.branches | .192 | 930 |
| | | Sm.branches | .508 | 1723 |
| | | Top | .180 | 776 |
| | | Stem | .126 | 1066 |
| | 7 | Foliage | 2.682 | 5899 |
| | | Lg.branches | .185 | 1042 |
| | | Sm.branches | .510 | 2413 |
| | | Top | .185 | 840 |
| | | Stem | .120 | 1071 |
| Red maple | 3 | Foliage | 2.310 | 4536 |
| | | Lg.branches | .172 | 1588 |
| | | Sm.branches | .448 | 3710 |
| | | Top | .183 | 1202 |
| | | Stem | .107 | 1306 |
| | 7 | Foliage | 2.070 | 6102 |
| | | Lg.branches | .178 | 2151 |
| | | Sm.branches | .446 | 4244 |
| | | Tops | .153 | 1486 |
| | | Stem | .101 | 1555 |

Table 4. Probability of >/t/, WS3 compared to WS7 for tissue biomass and nutrient concentrations, by tree component and species. Statistically significant values ($P \leq .10$) are underlined.

| | Mass | N | Ca |
|-----------------------|-------------|-------------|-------------|
| <u>Stem</u> | | | |
| Black birch | <u>.029</u> | .390 | .297 |
| Yellow-poplar | .035 | .750 | <u>.003</u> |
| Black Cherry | .848 | .780 | .974 |
| Red maple | .102 | .800 | .124 |
| <u>Top</u> | | | |
| Black birch | .340 | <u>.049</u> | .982 |
| Yellow-poplar | .455 | <u>.038</u> | <u>.063</u> |
| Black cherry | .162 | .746 | .520 |
| Red maple | .878 | .264 | <u>.067</u> |
| <u>Small branches</u> | | | |
| Black birch | .099 | .796 | <u>.027</u> |
| Yellow-poplar | .184 | .163 | .301 |
| Black cherry | .499 | .962 | .195 |
| Red maple | .984 | .970 | .132 |
| <u>Large branches</u> | | | |
| Black birch | .278 | .280 | .200 |
| Yellow-poplar | .052 | .732 | .282 |
| Black cherry | .395 | .720 | .578 |
| Red maple | .237 | .806 | <u>.089</u> |
| <u>Foliage</u> | | | |
| Black birch | .165 | .502 | <u>.040</u> |
| Yellow-poplar | .090 | .298 | <u>.082</u> |
| Black cherry | .285 | <u>.030</u> | .136 |
| Red maple | .300 | <u>.011</u> | <u>.013</u> |

Differences in nutrient concentrations were detected in the overstory trees, but not in the herb layer (Gilliam and others 1994). We predicted treatment effects first in the herb layer, particularly in response to N. It may be that the herb layer was limited by factors other than nutrition (e.g., light) (Gilliam and others 1994), and was unable to take advantage of the elevated N inputs. Gilliam and others (1994) reported significant changes in Fe and Al concentrations in herbaceous vegetation which they attributed to increased mobility of these ions in the soil due to the acidification treatment. Differences between watersheds in Al concentrations were significant only for yellow poplar and black cherry stemwood, but no significant differences in Fe concentrations were detected. Thus, the short-term response of these and other ecosystem components is variable and our ability to detect effects of acidic inputs also varies.

CONCLUSIONS

Whether observed differences in plant nutrient content reflect pretreatment differences between the watersheds is unknown. However, the lack of a consistent pattern of N enrichment for any tree species or tree tissue component suggest that plant nutrient status has been only minimally affected by three years of treatment. Soil acidification was not observed, but changes in stream water export of N were measured. The increased export of N from the treatment watershed suggests changes in N cycling at the watershed level. Nitrogen export may be elevated on the control watershed as well, suggesting ambient deposition may be causing effects, though more subtle, to those observed on the treated watershed. This research is ongoing, and will continue to evaluate the changes in nutrient cycling and other processes that result from acidic inputs, and consider implications for long-term sustainability of these important ecosystems.

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THE EFFECTS OF DOUBLING ANNUAL N AND S DEPOSITION ON FOLIAGE AND SOIL CHEMISTRY
AND GROWTH OF JAPANESE LARCH (*LARIX LEPTOLEPIS* SIEB. AND ZUCC.) IN
NORTH CENTRAL WEST VIRGINIA

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Abstract: Atmospheric deposition has been recognized as a significant environmental problem for several decades, but its impact on forest ecosystems in North America remains controversial. In an effort to further elucidate the impacts of atmospheric deposition to forested watersheds in the Mid-Appalachian region, several related watershed studies have been initiated by the U.S. Forest Service in Parsons, WV over the past decade. One of the experiments involved doubling the annual ambient rate of N and S deposition by aerial application of ammonium sulfate to Watershed 9 which had previously been converted from low grade hardwoods to Japanese larch. We report here on the impacts of this treatment on soil and foliar chemistry, and height and diameter growth of the Japanese larch. Foliar samples were collected from treated and control trees and analyzed for Al, Ca, K, Mg, Mn, N, P and S. Soil sample analysis included Al, C, Ca, K, Mg, Mn, N and S. Treated soil had significantly greater exchangeable Al and Mn and significantly lower exchangeable Ca and Mg ($\alpha \leq 0.05$) compared to control soil. Treated larch had significantly higher ($\alpha \leq 0.05$) foliar N, Mn and Al concentrations and significantly lower ($\alpha \leq 0.05$) P and Mg concentrations. Height and diameter growth of treated larch were significantly ($\alpha \leq 0.05$) less. The reasons for these growth differences are as yet unclear; however, preliminary analysis indicated significant correlations with selected soil chemical variables, some of which have changed in response to the treatment.

INTRODUCTION

The debate continues over the effects of anthropogenic nitrogen and sulfur deposition on forest health, resulting in a shift in research emphasis away from direct impacts and towards predisposing and/or inciting stresses. The forest health perspective has broadened on the issue of acid deposition to include effects on forest soils, tree nutrition, accelerated soil base cation leaching and metals toxicity (Tomlinson and Tomlinson 1990). Nutrient budgets for forests, such as those on Walker Branch Watershed, Tennessee, and Bear Brook Watershed, Maine (Johnson and others 1985; Kahl and others 1993) have been studied carefully and the impacts of atmospheric deposition on the cycling of nutrients in these forest ecosystems documented.

Ulrich and Matzner (1986) characterized soil acidification by base cation loss from the soil and acidic cation accumulation. Selective cation exchange leads to accelerated leaching of exchangeable cations (VanMiegroet and Cole 1984). Federer and others (1989) reported that calcium was being leached from some eastern forest soils. For forest soils already low in base cations, a further decrease in these nutrients associated with acidic deposition leaching may be critical to plant growth.

Documented changes in soil characteristics due to acidic inputs under field conditions are few (David and others 1990). Elevated acidic loadings have been shown to increase cation leaching (including Al^{3+}), decrease soil pH and adversely affect biological processes (Fernandez and Rustad 1990). The loss of cations is dictated by the amounts of

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anions in solution, and concentrations of strong acids, such as H_2SO_4 and HNO_3 . Increased soil acidity also increases Al, Mn and Fe solubility (Johnson and Cole 1980). Soil solution electroneutrality is maintained, following base cation losses, by these potentially-phytotoxic elements. Thus, soil chemistry changes may influence vegetation adversely.

The objective of this study was to quantify soil and foliar chemical changes and the response of Japanese larch to inputs of strong acids as a part of a catchment-scale acidification project. The results reported in this paper relate the growth and nutritional status of larch trees that have received increased deposition of N and S to the changes in soil chemistry resulting from this treatment.

METHODS

Study Site

Watershed 9 is an 11.6-ha catchment located in the unglaciated Allegheny Plateau of north central West Virginia. Kochenderfer and Helvey (1989) provided a general description of the watershed and a history of past land use. Minimum and maximum elevations on the watershed are 744 and 878 m, respectively. The watershed has a southerly aspect, with a 25% average slope. The predominant soil is Calvin channery silt loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) weathered from the Hampshire formation. Agriculture was the primary land use until the early 1930s, when the watershed was abandoned and allowed to naturally revegetate with low grade hardwoods. The U.S. Forest Service obtained the land in 1939. A mechanical site preparation study was conducted on the watershed beginning in 1983, in which all vegetation was removed except for an undisturbed 1.42-ha buffer zone along the stream. Site preparation included root raking and windrowing brush. In the spring of 1984, the watershed (excluding the buffer zone) was planted with 2-0 stock Japanese larch at 1.8 by 1.8 m spacing.

Experimental Treatments

Prior to treatment, six 30.5 by 30.5 m control plots were randomly located in the watershed and permanently marked. To simulate inputs of double the ambient rates of N and S deposition, granular ammonium sulfate fertilizer (21-0-0-24, proportions of N, P, K and S) was applied to watershed 9 by helicopter beginning in April 1987. The entire watershed including the buffer zone but excluding the control plots received three ammonium sulfate treatment applications per year through August 1993 (for a total of 18 applications prior to the August 1992 sampling and 20 applications prior to the August 1993 sampling) in an attempt to mimic seasonal deposition patterns. Determination of treatment amounts were based on historical throughfall deposition in the area, accounting for seasonal variation. Double the deposition rate for the January-April period was applied in March, double the rate for the May-August period was applied in July, and double the September-December rate was applied in November. The rates corresponded to 8.1 kg S ha⁻¹ and 7.1 kg N ha⁻¹ for applications in March and November, and 24.4 kg S ha⁻¹ and 21.3 kg N ha⁻¹ for the July applications (Adams and others 1993).

Study Design

Access to the control plots on the watershed was restricted by dense vegetation; consequently, only one control plot was selected for study. Other control plots could not have been studied without severe disturbance to the plots. A northeastern control plot was selected, and a 25 by 25-m plot was surveyed and marked within the 30.5 by 30.5-m control plot to allow a treated buffer zone. One adjacent treated area of the same dimensions was surveyed and marked along the same contour 10 m east of the control plot. Four transect lines along a north-south orientation were selected at 5-m intervals for both the control plot and the treated plot (Figure 1). Starting at the southern boundary line, 6 Japanese larch trees were selected and brass tagged at 5 m intervals in a northern direction along each transect line. Three additional larch trees were tagged between transect lines 1 and 2 and between lines 3 and 4. The total of 30 sample trees per plot represents approximately 45% of the total number of larch trees on each plot.

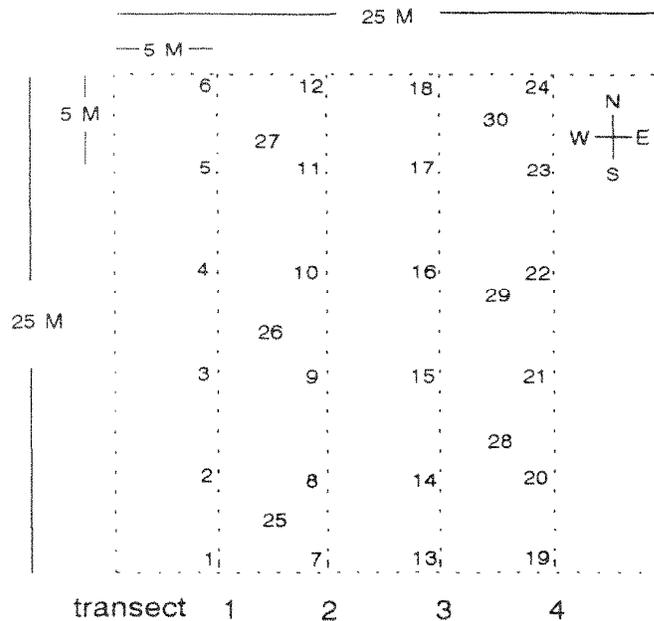


Figure 1. Transect and sampling design.

Sampling and Measurements

In August of 1992 and 1993, a telescoping pole was used to measure tree height to the nearest 0.1 cm and a caliper was used to measure tree diameter to the nearest 0.1 cm on all sample control and treated trees. A foliar sample for chemical analysis also was obtained from each of these trees. All needle whorls from a breast-high lateral shoot immediately below the terminal shoot were removed. Samples were handled with vinyl gloves, placed in paper bags, and kept cool until delivery for analysis (within 24 hours). Foliar analysis was performed by the Agricultural Analytical Services Laboratory, The Pennsylvania State University. Elemental analysis included Al, Ca, K, Mg, Mn, and P by inductively coupled plasma emission spectroscopy (Dahlquist and Knoll 1978), Kjehdahl N (Isaac and Johnson 1976) and sulfur (Huang and Schulte 1985).

In August 1992, 6 control and 6 treated soil pits (approximately 20 by 20 cm) were hand excavated near the sample larch trees along control transect 1 and treated transect 4. In August 1993, small pits were hand excavated by each sample larch tree on transect lines 1 and 4 for both the control and treated plots (12 pits per plot total). Soil samples were collected in the 0-2 cm layer (O horizon) and in the 2-10 cm layer (A horizon). These depths were chosen to represent the effective rooting horizons (Kochenderfer 1973). Samples were placed in paper bags and transported to the Environmental Resources Research Soil Chemistry Laboratory at The Pennsylvania State University. All analysis was conducted on air-dried soil sieved to 2 mm. Soil pH (1993 only) was determined in water with soil-to-solution ratios of 1:1 for both horizons (Black 1964). The base cations Ca, K, and Mg (K 1993 only) and metal cations Al and Mn (Mn 1993 only) were determined by atomic absorption spectrophotometry following 0.01 M SrCl₂ extraction and preparation as outlined by Joslin and Wolfe (1989). Soil carbon (Schulte 1991), NO₃-N (Isaac and Johnson 1976) and SO₄-S (Black 1964) 1992 analysis were performed by Agricultural Analytical Laboratory. In 1993, total C and N were analyzed by combustion using an organic elemental analyzer and for total S by combustion using the organic elemental analyzer with an electron capture detector (Baccanti and others 1993; Carlo Erba Instruments 1990) at the Timber and Watershed Laboratory, Parsons, WV.

Data Analysis

Statistical analysis followed a Model I two-treatment ANOVA for a fixed treatment. The SAS statistical package was used for data analysis, incorporating t-tests for mean comparisons (SAS Institute 1985). All significant differences are reported at $\alpha \leq 0.05$. Correlations using soil and tissue variables were performed using means for a particular treatment, soil horizon and chemical element. Quality assurance/control for all analysis included field duplicates, analytical duplicates, standard reference materials and blanks. Generally, duplicate analyses had relative standard deviation values below 10 percent.

RESULTS AND DISCUSSION

Larch Height and Diameter

Larch height and diameter growth were significantly greater for the control trees compared with treated trees for both 1992 and 1993 (Figure 2). Positive growth on both control and treated plots was evident, in that height and diameter measurements were greater in 1993 than 1992. However, control larch exhibited significantly greater height and diameter growth than treated larch in both years. Data for larch height growth on the entire watershed also indicate significantly greater height growth on the control plots compared to larch receiving the acidifying treatment (personal commun., J. Kochenderfer, U.S. Forest Service).

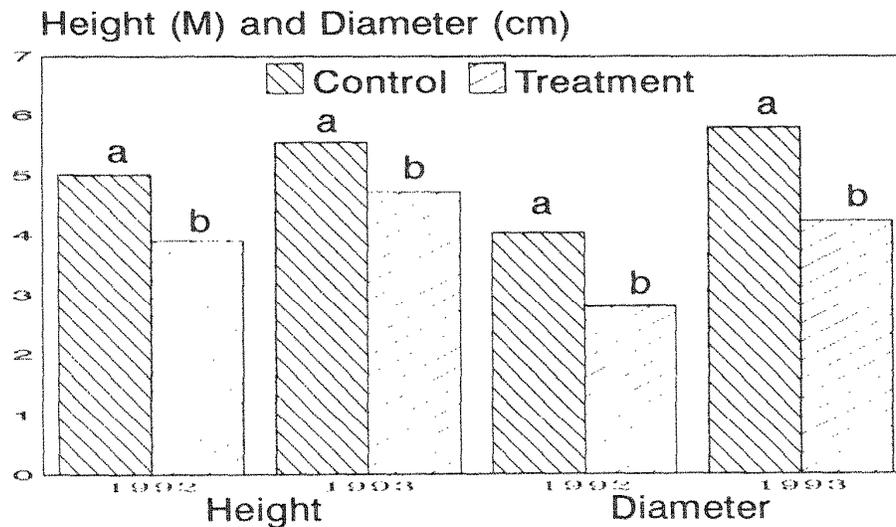


Figure 2. Larch height and diameter comparisons between control and treated plots; ($\alpha \leq 0.05$).

Soil Chemistry: Treatment Response (Within Horizon Comparisons)

Control and treated soil data comparisons were made for 1992 and 1993 by sample depth (O horizon or A horizon). In 1992, treated soil from the O and A horizon had greater values of $\text{NO}_3\text{-N}$ and C compared to soil from controls. The A horizon differences were statistically significant. Treated soil from the A horizon had significantly greater $\text{SO}_4\text{-S}$ than the control (Table 1).

Table 1. Soil SO₄-S, NO₃-N and C comparisons between control and treated samples collected in August 1992.

| | O HORIZON | | | A HORIZON | | |
|-----------|-------------------------------|---------------------------|----------|-------------------------------|---------------------------|----------|
| | SO ₄ -S (mg/kg) | NO ₃ -N (%) | C (%) | SO ₄ -S (mg/kg) | NO ₃ -N (%) | C (%) |
| Control | 148.83a | 0.965a | 16.9a | 29.50a | 0.113a | 1.9a |
| Treatment | 131.33a | 1.108a | 18.6a | 121.60b | 0.155b | 4.1b |

different letters within a soil parameter indicate significant difference at $\alpha \leq 0.05$ n=6

According to Stevenson (1986), net mineralization leading to an increase in mineral N levels occurs at C:N ratios below 20. For the 1992 soil data, the O-horizon C:N ratio was 17:1 and the A-horizon C:N ratio was 15:1, in both the control and the treated soil. Control O- and A-horizon total C and N were positively correlated with one another (O horizon: $r=+0.89$, $p < 0.05$, A horizon: $r=+0.97$, $p < 0.01$), as was treatment O-horizon C and N ($r=+0.96$, $p < 0.05$). Mineralization of N under these C:N ratios may be enhanced with N addition. Elevated humus layer N and increased organic matter in the Germany's Solling forest has been attributed to litter decomposition retardation, due to declining microbial activity under increasing acidic inputs (Robarge and Johnson 1992). The potential for N saturation is indicated by the low C:N ratios (Kahl and others 1993). The possibility of N saturation and the increase in N and S in treated soils provided the potential for SO₄²⁻ and NO₃⁻-induced leaching and increased soil acidification. In 1993, soil pH was significantly lower in the treated soil (O-horizon pH 4.47, A-horizon pH 4.91) compared to control (O-horizon pH 4.98, A-horizon pH 5.38), indicating increased soil acidification in the treated soil.

Exchangeable Al values in the treated soils were significantly greater and exchangeable Ca and Mg values significantly lower compared to control, for both years and at both depths (Table 2). In 1993, Mn was found to be significantly greater in the treated soil at both depths. Robarge and Johnson (1992) described increased solubility and mobility of Al as a potential effect of increased N and S inputs to forest soils. Soil acidification also can induce the loss of exchangeable cations such as Ca and Mg and increase exchangeable Al and other metals such as Mn (Schlegel and others 1992). Because the growth of larch is not stimulated by N and the Ca demand of larch foliage is relatively high, N-induced acidification and consequent Ca leaching may be contributing to the observed growth reduction of the treatment trees (Tyrrell and Boerner 1987; VanGoor 1953).

Table 2. Chemical comparisons (0.01 M SrCl₂ exchangeable) between control and treated soil sampled in August of 1992 and 1993.

| | O HORIZON | | | | | | A HORIZON | | | | | |
|-----------|-----------|--------|--------|--------|--------|-------|-----------|--------|-------|--------|-------|-------|
| | Al | Ca | K | Mg | Mn | pH | Al | Ca | K | Mg | Mn | pH |
| | ----- | ----- | -mg/L | ----- | ----- | | ----- | ----- | -mg/L | ----- | ----- | |
| 1992 | | | | | | | | | | | | |
| Control | 2.63a | 175.5a | NA | 22.48a | NA | NA | 2.02a | 170.7a | NA | 12.29a | NA | NA |
| Treatment | 6.21b | 104.0b | NA | 13.04b | NA | NA | 17.23b | 30.8b | NA | 3.96b | NA | NA |
| 1993 | | | | | | | | | | | | |
| Control | 4.11a | 160.8a | 13.45a | 18.08a | 9.07a | 4.98a | 1.54a | 123.5a | 5.89a | 8.33a | 0.87a | 5.38a |
| Treatment | 12.95b | 96.5b | 21.63b | 10.18b | 21.41b | 4.47b | 10.66b | 65.3b | 5.14a | 3.64b | 1.76b | 4.91b |

different letters within a soil parameter indicate significant difference at $\alpha < 0.05$

1992 n = 6 1993 n = 12 NA = not analyzed

Soil Chemistry: Within Horizon Observations

Control and treated soil N was significantly greater in the O horizon than the A horizon in 1992 and in 1993. Sulfur showed a similar, non-significant trend in 1992. Analysis of S for 1993 is ongoing. For the control soil sampled in 1992 and 1993, Mg was significantly greater in the O horizon than the A horizon. In 1993, O-horizon Al, K, Mn and N were all significantly greater than A-horizon levels, while pH was significantly lower in the O horizon. These differences may be due to greater leaching losses in the A horizon or to greater nutrient inputs (needle-fall) in the O horizon or both.

For the treated plots in 1992 and in 1993, O-horizon Mg was also significantly greater than A-horizon Mg. This may be a reflection of initial, pretreatment soil status, as the control O horizon also had significantly greater Mg than the A horizon. Therefore, although the control and treated soil comparisons showed that the treated soil had lost more Mg in both horizons compared to the control, the losses may be more severe in the A horizon as a result of its inherently lower Mg status compared to the O horizon.

There were no significant differences between control and treated soils for Mg in the O horizon between 1992 values and 1993 values, although both treatments had a trend of decreasing Mg values. However, for the control A horizon, the Mg level in 1993 was significantly less than that for 1992, and a similar trend (non-significant) was observed in the treated plots.

In 1992, treated plot Al and Ca levels were significantly greater in the O compared to the A horizon, but these differences were not significant in 1993. In 1993 the O horizon had significantly greater K and Mn and significantly lower pH compared to the A horizon.

Overall, there are more nutrients found in the O horizon compared to the A horizon on both the control and the treated plots. Carbon and N were also greater in the O horizon. These differences may be due to greater leaching losses in the mineral horizon or to greater nutrient inputs (needle-fall) in the O horizon. Larch allocate a small proportion of total annual C gain below ground (Gower and Richards 1990). Fine roots growing in the nutrient-rich O horizon are also exposed to elevated Al levels in the treated soil. Joslin and Wolfe (1989) showed root branching sensitivity in northern red oak (*Quercus rubra* L.) to Al in acidification treatments. Larch, which has been planted extensively on harsh sites, would not be expected to be very sensitive to Al toxicity; however, it is possible that Al toxicity may have decreased nutrient uptake and contributed to decreased growth.

Foliar Chemistry: Treatment Response

Foliar samples from the larch on the treated plot collected in 1992 and 1993 had significantly greater Mn and Al levels and significantly lower P and Mg levels compared to the control (Figure 3). Foliar K values were not significantly different between control and treatment larch. The treated larch had significantly greater foliar N (23000 mg/kg) compared to the control (21300 mg/kg) in 1993. Also, the 1993 values of treated larch for Mn, N, P and S were significantly greater than its 1992 values (1993 values: Mn=3443.8 mg/kg, N=23030 mg/kg, P=1330 mg/kg, S=2120 mg/kg; 1992 values: Mn=2427.2 mg/kg, N=20960 mg/kg, P=1040 mg/kg, S=1860 mg/kg). Lower foliar P in treated larch may be due to the formation of an Al-PO₄ precipitate, possibly contributing to lower P availability (McCormick and Borden 1974). VanGoor (1953) reported the existence of a N/P antagonism in Japanese larch. The lower the availability of soil P the more quickly this antagonism develops with added N. VanGoor (1953) reported that the optimum range of N/P in needles was 4 to 5. The ratios in this study were 17 and 15 for the treated and control larch, respectively. Both soil and foliar Mn were elevated in the treated larch compared to the control. Studies with agronomic crops have shown that Mn can become elevated in acidic soils and reach toxic levels, impairing Ca and Mg uptake, disturbing physiological processes and reducing growth (Elamin and Wilcox 1986; Smith and others 1983). A greenhouse study designed to evaluate larch growth under elevated soil Mn found no height or diameter depressions in soils with Mn levels ranging from 12.8 to 150 mg/L and foliar Mn from 1655 to 5550 mg/kg (Unpublished data, C. Pickens, The Pennsylvania State University).

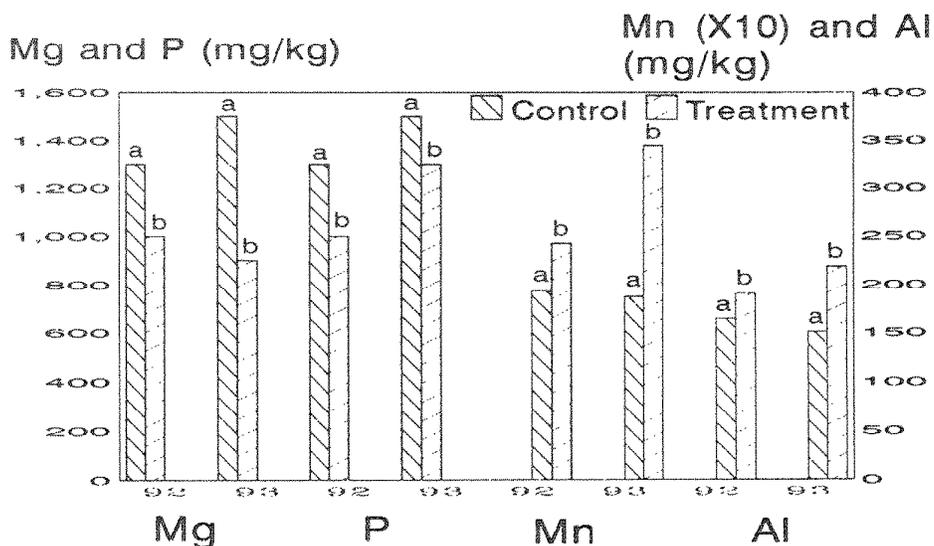


Figure 3. Foliar chemical comparisons between control and treated larch.

The patterns of foliar Al, Mg, Mn, N and S in the treated larch foliage compared to the control were somewhat similar to the patterns observed for soils. A general trend was that the treated plot had lower foliar and soil Mg levels, while Al, Mn, N and S were greater in treated soils and foliage compared to control values. The link between increased deposition of strong acids and an increase in soil Al has been made (Ulrich and others 1980), as has the antagonistic relationship between Al and the uptake and transport of Ca and Mg (Joslin and others 1988). Prior farming on watershed 9 included the addition of burned lime (personal comm., J. Kochenderfer, U.S. Forest Service) One possible explanation for the lack of Ca response (leaching) to acidic inputs may be due to these Ca additions, which still provide adequate Ca. However, Mg levels appear to be affected by the acidification treatment, with Mg levels reduced in the treated soil and foliage, possibly as a consequence of Mg leaching losses with mobile SO_4^{2-} and NO_3^- ions. Magnesium content of sandstone derived soils is low relative to Ca and, thus, it might be expected that the available pool of Mg might be affected before that of Ca. Magnesium deficiencies have been reported in declining Norway spruce (*Picea abies* L.) in Europe (Tomlinson and Tomlinson 1990) and in the eastern US (Ke and Skelly 1994), and Tomlinson and Tomlinson (1990) attributed these deficiencies to excessive leaching as a consequence of acidic deposition. Bergmann (1992) gives an adequate Mg range for European larch (*Larix decidua* Mill.) of 1200-3000 mg/kg. The treated plot larch had less than 1200 mg/kg of Mg in both 1992 and 1993 suggesting a possible deficiency.

Foliar and Soil Chemistry Correlations

Foliar Mg consistently correlated with a number of soil chemistry parameters. In the treated samples, foliar Mg was positively correlated with A-horizon Ca ($r = +0.86$, $p < 0.05$) and Mg ($r = +0.82$, $p < 0.05$) (1992) and O-horizon Ca ($r = +0.58$, $p < 0.05$) (1993). In 1992, soil values for treated A-horizon Ca and Mg were correlated positively with larch height (Ca: $r = +0.83$, $p < 0.05$; Mg: $r = +0.84$, $p < 0.05$) and diameter (Ca: $r = +0.91$, $p = 0.01$; Mg: $r = +0.83$, $p < 0.05$). Negative correlations were observed between O-horizon N and larch height ($r = -0.81$, $p < 0.05$) and diameter ($r = -0.84$, $p < 0.05$), and A-horizon Al and diameter ($r = -0.81$, $p < 0.05$). In 1993, A-horizon N again was correlated negatively with diameter measurements ($r = -0.81$, $p < 0.05$). In 1993, foliar Mg in treated larch were correlated positively to both height ($r = +0.60$, $p < 0.05$) and diameter ($r = +0.67$, $p < 0.05$). Negative correlations existed between foliar Mg and O-horizon C in 1992 ($r = -0.97$, $p < 0.01$) and 1993 ($r = -0.63$, $p < 0.05$), and between foliar Mg

and O-horizon N ($r = -0.97$, $p < 0.01$) and A-horizon S ($r = -0.81$, $p < 0.05$) in 1992, and A-horizon Al ($r = -0.70$, $p < 0.01$) in 1993.

Based on correlations with foliar and soil chemistry, Mg appears to be the most important variable potentially influencing larch growth. The negative correlations between larch growth parameters and soil N support the hypothesis that larch has a low N requirement and responds adversely to increased N (Leyton 1957). Treated soil Ca and Mg were correlated positively with growth; deficiencies of these nutrients under acidification stress may be detrimental to larch growth. Heenan and Campbell (1981) demonstrated that increasing Mn supply reduced Mg uptake in soybean, and that Mn reduced Mg leaf concentrations by reducing the rate of Mg absorption. It also has been reported that a liberal supply of Ca can counteract Mn toxicity (Ouellette and Dessureaux 1985). Plant available Mn was elevated in the treated soil, and such an increase along with a decrease in exchangeable Mg may have interfered with larch growth. The negative correlations between larch growth and soil Al also may implicate Al in the observed growth reduction.

SUMMARY AND CONCLUSIONS

After 18 (1992) -20 (1993) treatments (total applications) with ammonium sulfate fertilizer over 5 yrs/8 mos (1992) and 6 yrs/8 mos (1993), the larch trees growing on watershed 9 have reduced height and diameter growth compared to control trees. Soil chemistry revealed greater levels of Al, C, Mn, N and S and lower levels of Ca, Mg and pH compared to control soils. Significantly greater foliar N in the treated larch indicates greater N availability on the treated areas. Earlier studies have shown high N/P ratios to be detrimental to larch growth, but the N/P ratios for foliage in control and treated larch were high and well above the reported optimums. Treated larch height and diameter were correlated positively with foliar Mg. Foliar Mg was reduced significantly on the treated plot. Reduced Mg availability also may have contributed to reduced larch growth, since foliar Mg concentrations of treated larch were less than adequate. It appears most likely that a change in Mg supply coupled with increases in available Al and Mn have contributed to nutrient deficiencies and imbalances and impaired growth of treated larch.

ACKNOWLEDGMENTS AND DISCLAIMERS

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TREE SURVIVORSHIP IN AN OAK-HICKORY FOREST IN SOUTHEAST MISSOURI, USA UNDER A
LONG-TERM REGIME OF ANNUAL AND PERIODIC CONTROLLED BURNING

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Abstract: Fire significantly altered survivorship in southeastern Missouri forests burned at annual and four-year (periodic) intervals since 1949 and 1951. In the ANOVA model tested, treatment, species, pretreatment diameter and the interaction between species and pretreatment diameter were highly significantly related to survivorship. Overall survivorship and survivorship of hickories (*Carya* spp.) and red oak group species, including scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), southern red oak (*Quercus falcata* Michx.), was greatest in control plots, less in annually burned and least in periodically burned plots. In contrast, the survivorship of post oak (*Quercus stellata*, Wangenh.) did not significantly differ among fire regimes. General fire survivorship rankings were post oak > red oak species > hickory. Logistic regression indicated that survivorship was significantly and positively correlated with diameter at breast height for post oak and red oak group species, but not for hickories. This relationship of DBH with survivorship was apparently attributable more to self-thinning and differential life-span of trees rather than fire treatment effects. However, survivorship of red oak species was more sensitive to burning regime at smaller pretreatment DBH. When using fire to maintain or increase the abundance of red oak species of oak-hickory forests, age, species life-span, stage of stand development and other environmental stresses should be considered.

INTRODUCTION

The role of fire in oak-hickory forests in the Eastern Deciduous Forest of North America varies across regions. These regional differences are due, in part, to differences in fire behavior which are strongly influenced by topography and fuel type (Pyne 1984). In addition, variation in climate, species composition of the forest itself, soil type and composition of the surrounding vegetation also contribute to regional differences in fire response of oak-hickory forests (Pyne 1984).

In the southeastern U.S., frequent low intensity fires favor the dominance of southern pines, such as shortleaf (*Pinus echinata* Mill.), longleaf (*Pinus palustris* Mill.) and slash pine (*Pinus elliottii* Engelm.) over species of oaks (Garren 1943). In this region oak-hickory forests exist in areas protected from fire, such as in ravines (Garren 1943). Oaks are better adapted to fire than associated hickory species (Harlow and others 1991). As a result of these differential responses and the frequency of fire in this region, oak species can co-exist with pine better than hickories, forming oak-pine forests over much of the southeastern United States (Braun 1950).

Fire helps to maintain the composition of oak-hickory forests through selective mortality, or by creating conditions which alter growth rates of surviving trees (Curtis 1959, Bazzaz 1979, Crow 1988). However, fire also may kill and damage oaks (Stickel 1935). Fire may have both short- and long-term effects on tree mortality. The immediate danger fire poses is high temperature. Cells are killed between 50 and 64°C depending on cellular water content and species (Byram 1958, Hare 1961, Levitt 1980, Rouse 1986). Longer term risks posed by fire result from cambial injury and associated increased susceptibility of the stem to insect attack and diseases (Hedgecock 1926, Johnson 1974, McCarthy and Sims 1935, Stickel 1935, Stickel and Marco 1936).

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Fuel loading and moisture content determine both the maximum temperatures reached and duration of elevated temperatures during a fire (Byram 1958, Pyne 1984, Smith 1986, Vines 1968). In controlled burns at University Forest, southeastern Missouri, periodic burns, conducted every four years since about 1950, were more intense and caused greater mortality by 1964 than annual burns because of the accumulation of a deeper and more continuous litter layer in plots burned periodically (Paulsell 1957, Scowcroft 1966).

Many plant characteristics influence survival and growth after fire. Differential development of these characteristics explains much of the variation among species in post-fire survival and growth (Hare 1961, Kimmins 1987). Thick bark can insulate vital tissues, such as the cambium, which would otherwise be killed by high temperatures (Hare 1961, Vines 1968). Sufficient starch reserves and an ability to resprout allow some trees to survive despite experiencing topkill after fire (Johnson 1974, Kozlowski and others 1991, Little 1974, Malanson and Trabaud 1988). Thus, larger diameter trees may survive fire better than small diameter trees because they have thicker bark and greater starch reserves and because there is a lower probability that complete girdling will occur (Greene and Shilling 1987, Maslen 1988, McCarthy and Sims 1935, Paulsell 1957, Stickel 1935).

Previous field studies and observations have shown that species can be ranked according to fire tolerance. Hickory species are noted for their sensitivity to fire due to their thin bark. Fire sensitivity of oak species varies according to bark thickness, susceptibility to decay and ability to sprout. *Quercus coccinea* and *Q. falcata* both have thin bark and low resistance to decay after being wounded, making them quite sensitive to fire (Belanger 1990, Johnson 1990, Harlow and others 1991). Although more fire resistant because they have thicker bark, fire scars create entry points for decay organisms in both *Q. alba* and in *Q. velutina* (Sander 1990, Rogers 1990). Other oak species, such as *Q. stellata* and *Q. marilandica* survive fire better because they possess thick bark and can sprout after top-kill to form scrub thickets on sites subject to frequent fires (Harlow and others 1991, Stransky 1990, Vines 1968).

White oak group species (Subgenus *Leucobalanus*) generally live longer than red oak group species (Subgenus *Erythrobalanus*, Harlow and others 1991). Hence in young or near mature forests, white oak group species should have inherently lower mortality rates than red oak group species and, other factors held constant, should thus have greater survivorship. These differential fire and life history traits suggest that species differences in survivorship should be observed in the oak-hickory forests of southeastern Missouri.

Specific hypotheses addressed in this paper focused on factors affecting fire survivorship in these forests that have been subjected to three different long-term burning regimes: (1) annual and periodic burning decrease survivorship, (2) periodic burns reduce survivorship more than annual burns, (3) survivorship increases with DBH, and (4) fire survivorship differs among species.

METHODS

Experimental Design

In 1949 and 1951 two replicates of burning treatments were established about one mile apart from each other at the University State Forest in Wapapello, Missouri (36° 55' N, 90° 15' W). Replicate 1 had a site index of 65 on a Typic Fragiudalf while Replicate 2 had a site index of 56 on a Typic Fragiudult (Godsey 1988). Prior to establishment of the two study sites, fire had been excluded since 1930 and there had been no grazing permitted for 15 years. Each replicate contained two unburned control plots, two annually burned plots and two periodically burned plots for a total of six plots randomly arranged in a two by three grid. Each plot was 40 m by 40 m with 10.1 m buffer strips between plots. The burning schedule was staggered between replicates. Treatment of burn plots began in 1949 in replicate 1 and in 1951 in Replicate 2. Prescribed fire was conducted every four years after treatments began in periodically burned plots. Burning was conducted in the spring between March to May. The dates of the spring burns were chosen so that conditions in the late afternoon, when the burns were conducted, fell within moderate to high fire danger conditions (Paulsell 1957). The dates of prescribed burning always coincided with the occurrence of local fires (Paulsell 1957).

Stand Characteristics

Experimental plots had initial basal areas prior to treatment ranging from 12.49 to 15.25 m²/ha in Replicate 1 and from 15.56 to 17.34 m²/ha in Replicate 2. By 1984 total basal area, including ingrowth, had increased for all plots. Species of oak and hickory were predominant in tree-sized individuals (≥ 4.06 cm DBH). Hickories reported at the sites include shagbark hickory (*Carya ovata* (Mill.) K. Koch), mockernut hickory (*Carya tomentosa* (Poir.) Nutt.) and black hickory (*Carya texana* Buckl.). Hickory basal area ranged from 1.82 to 6.07 m²/ha. Measurements of all species of hickory were pooled in this study. White oak group species were *Quercus alba*, ranging in basal area from 0.00 to 1.18 m²/ha before treatments, and *Quercus stellata* ranging in basal area from 2.79 to 10.00 m²/ha in plots before treatment. Red oak group species were *Quercus falcata*, *Q. coccinea*, *Q. marilandica* and *Q. velutina* ranging in basal area before treatment from 3.59 to 8.15 m²/ha. Other trees on the plots were flowering dogwood (*Cornus florida* L.), common persimmon (*Diospyros virginiana* L.), ash (*Fraxinus* spp.), plum (*Prunus* spp.), sassafras (*Sassafras albidum* (Nutt.) Nees) and winged elm (*Ulmus alata* Michx.). Data from these last species were eliminated before calculations (see below).

In the original inventory, a j-shaped DBH distribution was observed in all plots, as was shown when plots were grouped by treatment for each replicate (Figure 1). Replicate 1 plots had a greater density of red oak group species, but fewer *Q. alba* or *Q. stellata* trees than Replicate 2. In addition, Replicate 1 plots had fewer hickories than replicate 2.

Statistical Analysis

Only individuals of the 1949 (1951) cohort were included in the analysis. In contrast with Godsey (1988) who analyzed plot frequencies, mean percent survivorship was calculated by plot, in 4 cm pretreatment diameter classes for each species. Separation by size was performed to increase the sensitivity of the statistical analyses (see below). Trees in diameter classes larger than 20 cm DBH were removed before analysis in order to ensure that there were observations for every species and pretreatment diameter class combination in all plots. No hickories larger than 20 cm were observed on the plots before treatments were started. In addition, observations of large oaks were not consistent among large diameter classes and were generally a small proportion of the cohort (Figure 1). Because the number of white oak trees and trees of "other species" were low, plot survivorship means of these species categories also were removed from the analysis.

Mean survivorship of each plot for each species group and diameter class combination was then arcsin transformed before analysis of variance to normalize error as described by Box and Cox (1964). Least square means of transformed 1984 survivorship were calculated by employing a nested ANOVA model with pretreatment diameter as a covariate and using the SAS General Linear Models procedure (Table 1). Least square means were then back-transformed into percentages.

In a second model, logistic regression (Harrell 1986) was used to develop functions describing the probability of an individual of a species or species group (hickory, post oak or red oak) surviving from 1949 (or 1951) until 1984 using the binary data of individual survivorship with DBH treated as a continuous independent variable. Pretreatment DBH was included as both linear and squared terms in logistic regression because a curvilinear relationship between survivorship and DBH² has been observed for other species of oak (McCarthy and Sims 1935). The Wald-Chi square values calculated for each logistic curve were used to determine the significance of DBH and DBH² coefficients for all combinations of species groups and treatments for which both sufficient numbers of observations were present and convergence was achieved in the logistic regression. Significant differences are reported at $p \leq 0.05$ unless otherwise noted.

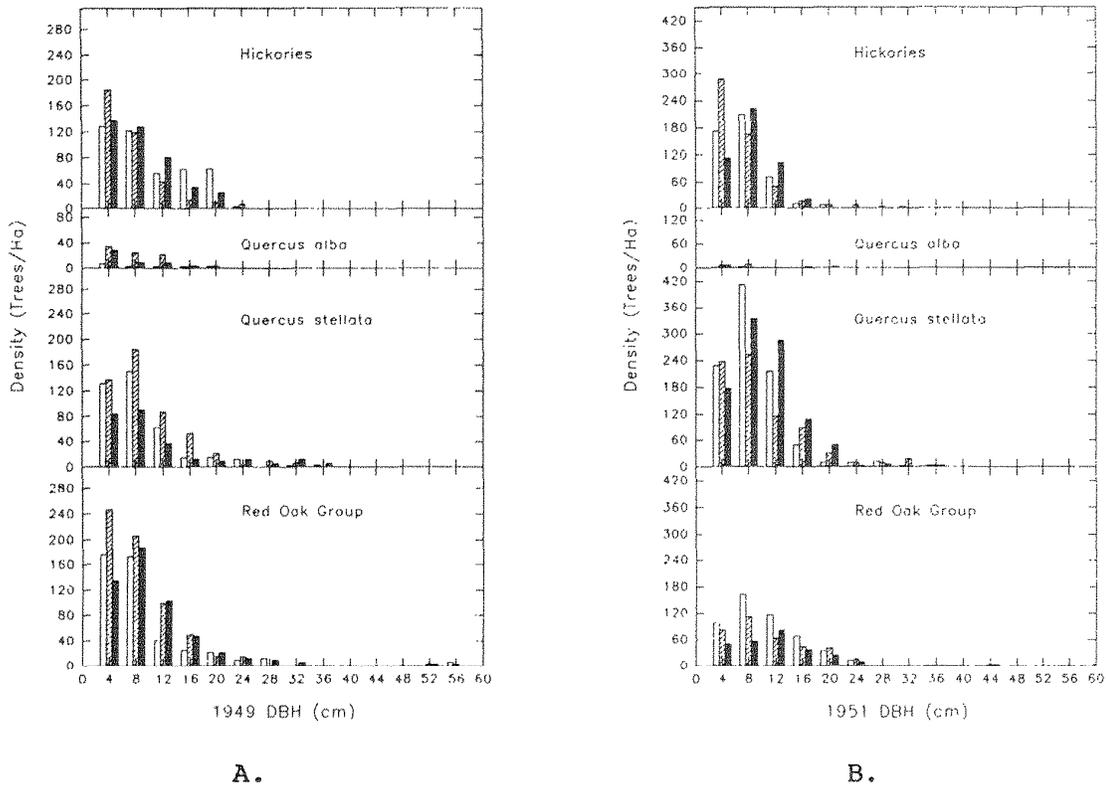


Figure 1: A - Density-diameter relationship in 1949 in Replicate 1 of species of hickory, white oak and red oak. B - Density-diameter relationship in 1951 in Replicate 2 of species of hickory, white oak and red oak. Open bars - control plots; cross hatched bars - annually burned plots; solid bars - in periodically burned plots. In Replicate 1, total densities were 1544 trees/ha in control plots, 1601 trees/ha in annually burned plots, and 1147 trees/ha in periodically burned plots. Density-diameter relationship Open bars - control plots; cross hatched bars - annually burned plots; solid bars - in periodically burned plots. In Replicate 2, total densities were 1872 trees/ha in control plots, 1631 trees/ha in annually burned plots, and 1616 trees/ha in periodically burned plots.

Table 1: Effects and their associated p-values from the ANOVA model used to calculate least square means of transformed 1984 plot survivorship.

| Effect | Degrees of freedom | Associated p-value |
|-----------------------|--------------------|-----------------------------------|
| DBH | 4 | <0.01 |
| Species | 2 | <0.01 |
| Species*DBH | 8 | <0.01 |
| Treatment | 2 | <0.01 |
| Treatment*DBH | 8 | 0.43 |
| Species*Treatment | 4 | 0.22 |
| Species*Treatment*DBH | 16 | 0.63 |
| Error | 44 | (Replicate*Species*Treatment*DBH) |

RESULTS

Statistical and Logistic Regression Models

In the complete ANOVA model, effects of pretreatment diameter, species, treatment, and the interaction between species and pretreatment diameter all were highly significant ($p \leq 0.001$, Table 1). Neither the interactions between treatment and pretreatment diameter, nor the interaction between species, treatment and pretreatment diameter were significant. Although the F-test of the interaction between species and treatment was not significant ($p = 0.22$, Table 1) statistically significant differences existed between least square means (Table 2).

Except for the DBH^2 term for post oak on control plots, all terms of the logistic regression models (intercept, DBH and DBH^2) were highly significant ($p \leq 0.01$) for post oak and red oak group trees in all treatments. In contrast, only the intercept term was significant in all logistic regression models for hickory species. In periodically burned plots DBH and DBH^2 approached statistical significance in relation to survivorship of species of hickory ($p = 0.071$ and 0.084 , respectively).

Species Differences in Survivorship

Both the effects of species and the interaction between species and pretreatment diameter were highly significant in the ANOVA model tested (Table 1). Differences among species in percent survivorship in all treatments were significant. Post oak showed the highest mean survivorship (55.6%), red oak species showed the next highest mean survivorship (26.1%) and the hickories showed the lowest mean survivorship (4.8%). The effect of burning regime was highly significant with mean survivorship in control plots (37.9%) being significantly greater than those in either annually burned plots (24.7%) or periodically burned plots (16.2%) (Table 2).

Although the interaction between species and treatment was not significant ($p = 0.22$, Table 1), there were differences among species/groups in response to fire regime. For example, both hickories and red oak species exhibited significant reductions in survivorship in periodically burned plots compared with control plots (Table 2). In addition, the survivorship of hickories in periodically burned plots was significantly lower than that of either control plots or annually burned plots (Table 2). In contrast, post oak showed no significant decrease in percent survivorship in annually burned or periodically burned plots compared with control plots.

The 1984 diameter distribution illustrated two ongoing population processes in the experimental plots. First, as the cohorts are followed through time, the form of the distribution based on the total number of living individuals changed from a j-shaped into a bell-shaped curve, reflecting stem exclusion resulting from competition (cf. Figures 1 and 2). Second, growth of hickories was slower than that of either post oak or the red oak group species. The largest diameter of hickories was 28 cm in Replicate 1 and 20 cm in Replicate 2 (Figure 2). In contrast, the largest diameter of post oak was 52 cm in Replicate 1 and 44 cm in Replicate 2. Likewise, the largest diameter of the red oak group was 48 cm in Replicate 1 and 44 cm in Replicate 2. Peaks of the diameter distributions appeared to be shifted among treatments. However, it was not possible to ascertain whether this shift in diameter distribution was due to the treatments or to differences in pretreatment size-class distributions among plots (cf. Figures 1 and 2).

Although the probability of hickory survivorship increased slightly with increasing DBH in control and annually burned plots (Figure 3), its significance is questionable because of the small numbers of surviving hickory trees in 1984. In contrast with hickory species, both post oak and the red oak group species had sizable surviving populations that had grown into larger DBH classes (cf. Figures 1 and 2). The estimated probability of survival of trees of post oak increased with DBH (Figure 3) with most trees with a pretreatment DBH 12 cm or larger surviving until 1984. Additionally, burning treatments had little effect on the relationship between DBH and the probability of survivorship in the post oak (Figure 3). Like post oak, pretreatment diameter had a noticeable effect on the probability of survivorship in the red oak group (Figure 3). However, the effect of pretreatment DBH on survivorship of red oaks differed from that of post oak in two respects.

Table 2: Percent survivorship from 1949 (1951) to 1984. Least square means with different letters are significantly different ($p \leq 0.05$).

| Treatment | Species Group | % Survival in 1984 |
|---------------------------|-----------------|--------------------|
| CONTROL PLOTS | | |
| | Hickory | 17.9 c |
| | Post Oak | 57.3 ab |
| | Red Oak Species | 40.9 b |
| ANNUALLY BURNED PLOTS | | |
| | Hickory | 2.4 d |
| | Post Oak | 62.1 a |
| | Red Oak Species | 23.0 bc |
| PERIODICALLY BURNED PLOTS | | |
| | Hickory | 0.5 d |
| | Post Oak | 47.2 ab |
| | Red Oak Species | 16.2 c |

First, survivorship of red oak species showed distinct peaks at about 18 cm in both control and periodically burned plots rather than simply increasing monotonically with DBH as was observed in post oak. Second, the peak in the probability of survivorship changed with burning regime for red oak group species. Below a pretreatment DBH of 20 cm, the probability survivorship of red oaks was greatest in control plots, followed by annually burned plots, and then periodically burned plots (Figure 3). Above a pretreatment DBH of 20 cm the probability of survivorship of red oaks was greatest in periodically burned plots, less in control plots, and least in annually burned plots (Figure 3). In contrast, the relationship between DBH and estimated survivorship probability differed little among treatments in post oak.

DISCUSSION

The relationships of survivorship with burning regime and pretreatment size depended on species. Burning reduced survivorship of hickory and red oak group species in both annually burned plots and periodically burned plots, but had little effect on survivorship of post oak. Reductions in the survivorship of hickory and red oak species were greater in periodically burned plots than in annually burned plots. Overall, the hickories had low survivorship rates which were further reduced with burning; the red oak group had intermediate survivorship rates that were sensitive to both burning regime and initial tree size; the post oaks had the highest survivorship rates that were relatively insensitive to burning regime and increased monotonically with initial tree size.

Because environmental stresses interact synergistically to increase susceptibility of trees to attack by insects and disease (Houston 1987), other stresses such as drought may account for some of the variation in survivorship among species. There are reports of decline symptoms in oaks in the Missouri Ozarks, particularly in the red oak group, that have been attributed to drought stress occurring in the 1980's (Jenkins 1992). The conservative growth strategy of post oak (Harlow and others 1991) and its high drought tolerance (Ni and Pallardy 1991, 1992) may have given post oak an advantage during and/or after this period of drought. However, while the species of hickory found in the study sites are somewhat sensitive to water stress, red oak group species are noted for being drought tolerant (esp. *Q. coccinea* and *Q. falcata*) (Belanger 1990, Johnson 1990, Sander 1990).

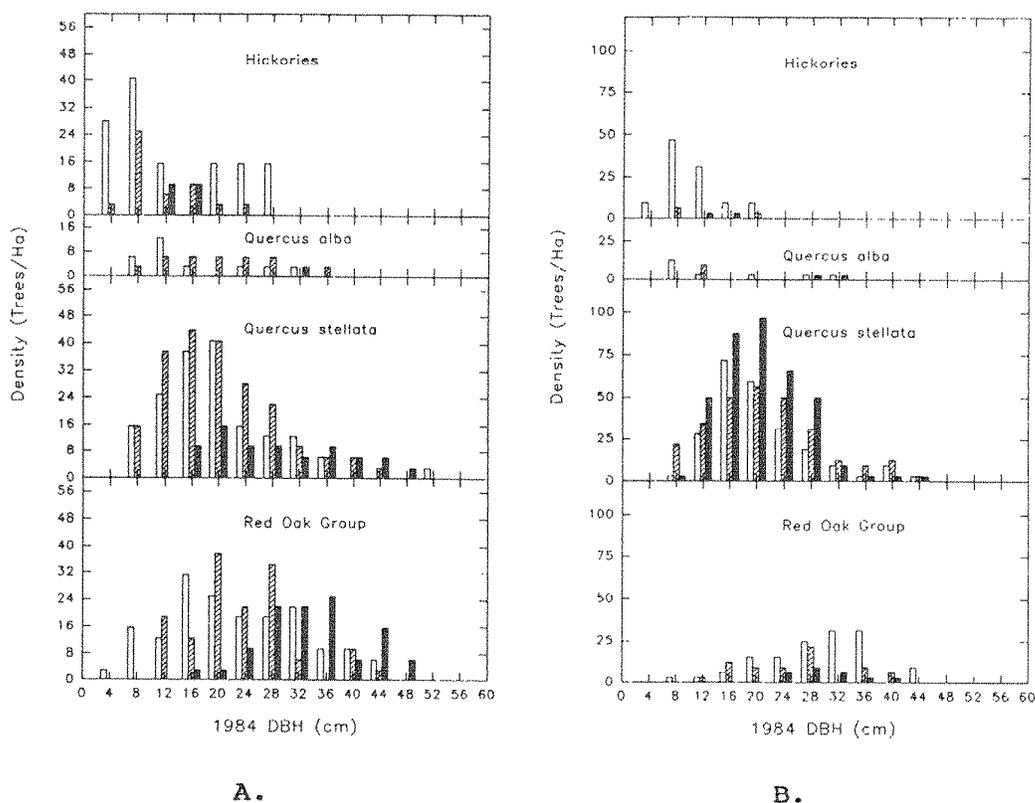


Figure 2: A - Density-diameter relationship in 1984 DBH distribution of species of hickory, white oak and red oak in Replicate 1. B - Density-diameter relationship in 1984 DBH distribution of species of hickory, white oak and red oak in Replicate 2. Open bars - control plots; cross hatched bars - annually burned plots; solid bars - in periodically burned plots.

Because forests at University Forest are between 80 and 90 years old (Jenkins 1992), the effects of differential average life-spans also may have influenced survivorship. White oak group species may live an average of 300-400 years while red oak group species generally live an average of 200 years or less (Harlow and others 1991). Logistic regressions supported the hypothesis that differential life-span accounts for at least some of the higher mortality observed in red oak species compared with post oak. Probability of post oak survivorship increased monotonically with DBH and hence showed no decline in larger, presumably older, trees. In contrast, the red oak group species in two of these burning regimes showed a distinct peak in survivorship probability with respect to DBH indicating mortality of older, larger trees as well as small trees.

As both the DBH*treatment and species*treatment*DBH interaction effects were not significant, while both DBH and species*DBH interaction were, most of the observed species difference in relationships between survivorship and DBH appeared to be the result of self-thinning and senescence-related mortality rather than the result of differential fire response. However, the logistic curves do suggest some species differences in survivorship response to fire regimes. For hickory species, DBH had little effect on survivorship. However, for red oak group species, the relationship between DBH and survivorship predicted by logistic regression differed among burning regimes. The curves suggest that survivorship of red oak group species was sensitive to burning, particularly for smaller diameter

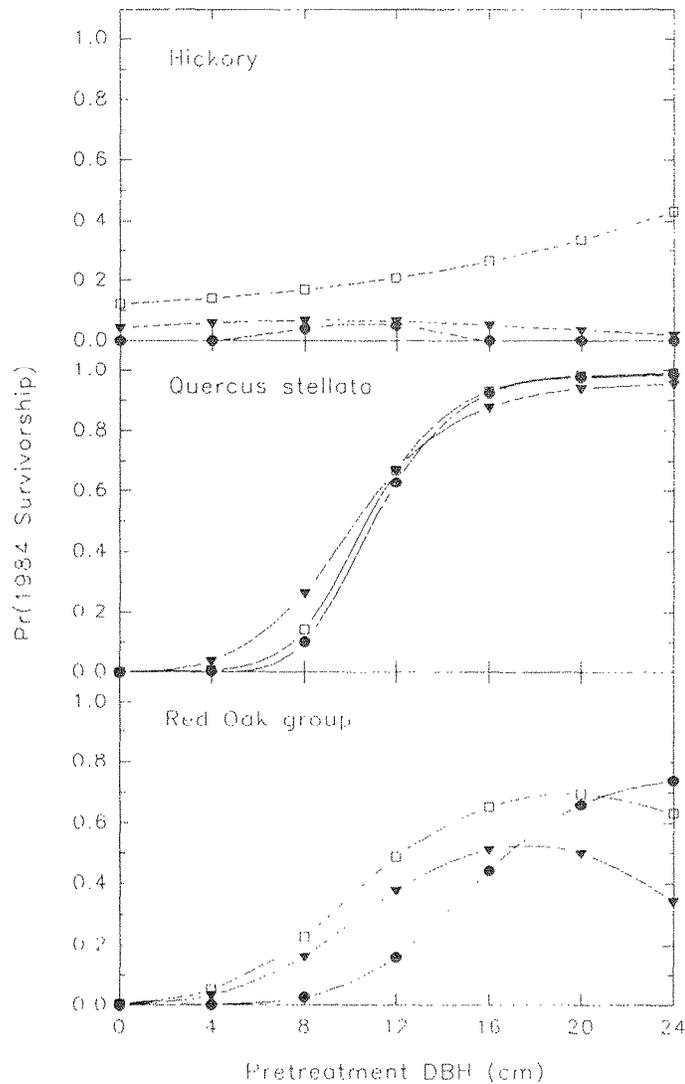


Figure 3: Probabilities of survivorship until 1984 given pretreatment DBH for hickory species, *Q. stellata* and the red oak group. Curves calculated from logistic equations using DBH and DBH² terms using all 1984 survivorship data. □ denote survivorship of control plots; ▾ denote survivorship in annually burned plots; ● denote survivorship in periodically burned plots.

trees. The considerable shade tolerance of hickory species (Graney 1990, Harlow and others 1991, Smith 1990) may account for the lack of significance of DBH terms in logistic regression for this species. Burning regime also had little effect on survivorship of post oaks which increased monotonically with DBH. These results suggest that post oak may become more important in oak-hickory forests of the Ozarks because of its longevity and/or superior fire adaptation. Red oak group species, on the other hand, appear to be somewhat more susceptible to fire and inherently shorter-lived. Thus, if a forest is reaching maturity, recruitment and protection of regeneration is important if maintenance of species, particularly short-lived species, is a management objective.

CONCLUSIONS

Annual and periodic burning regimes decreased survivorship of hickory and red oak group species, but had little impact on survivorship of post oak. Reductions in survivorship of hickory and red oak group species were greater in periodically burned plots than in annually burned plots. Survivorship increased with DBH for post oak and peaked at an intermediate DBH for the red oak group species. The relationship between DBH and survivorship appeared more likely associated with self-thinning and life-span of trees rather than with fire treatment effects. However, in red oak species there was some evidence of preferential fire mortality in small diameter trees. Results suggest that when using fire, age, species life-span, stage of stand development and other environmental stresses must be considered if maintaining or increasing the red oak component of an oak-hickory stand is an important management objective.

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CHEMICAL RELEASE OF POLE-SIZED TREES IN A CENTRAL HARDWOOD CLEARCUT

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Abstract: Our study evaluated the effectiveness of tree injection and full basal bark treatments using three herbicide formulations at reduced or standard practice rates to release crop trees in an overstocked pole-sized Central Hardwood stand. Herbicides tested included glyphosate (Accord), dicamba only (Banvel CST), and dicamba+2,4-D (Banvel 520). The study was conducted in a mixed hardwood stand in southern Illinois that regenerated following a clearcut harvest 18 years earlier. A highly significant interaction occurred among the six herbicide treatments and the method of application. Full basal bark treatment with any of the three herbicide formulations at either rate produced only light (8 to 25%) crown reduction at 45, 90, and 360 days after treatment (DAT). Tree injection with the high and low rate of glyphosate (4 and 8% ai), the ready-to-use dicamba (10.6% ai), and the registered rates of dicamba+2,4-D (1.7 and 2.4% ai, respectively) caused severe (64 to 78%) crown reduction on the treated trees and shrubs. The shrubs as a group were the most susceptible to the herbicide treatments, while sugar maple was the most herbicide-tolerant tree species. The elms, ashes, low-value hardwoods, and high-value hardwood groups were intermediate in response. Non-treated (crop) trees showed no visible crown reductions or reduced diameter growth following chemical release. We conclude tree injection application of glyphosate or dicamba can be an acceptable method for chemical release of crop trees in mixed hardwood stands.

INTRODUCTION

Forest inventories for the Central Hardwoods indicate that the amount of young hardwood growing stock has continued to increase following planting of abandoned agricultural lands and sapling regeneration in clearcuts. Many of the resulting stands are now overstocked with young pole-sized trees of little or no commercial value. Inexpensive, environmentally acceptable methods need to be developed if landowners are going to manage these stands to meet their objectives for wildlife habitat improvement, recreational opportunities, and timber production (Miller and Glover 1991).

Chemical release is a relatively inexpensive method of removing unwanted shrubs and trees when methods are identified that prevent ground water contamination, pose little risk to non-target organisms, and are not labor intensive. In the past, hardwood stands were thinned mechanically by cutting or girdling or chemically released using tree injection and, to a lesser extent, full basal bark treatments. Limited information exists on the effectiveness of several broad-spectrum herbicides developed for agricultural use on hardwood shrubs and trees. This includes using

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both tree injection and basal bark treatments (Griswold et al. 1989). Ideally, these broad-spectrum herbicides should exhibit low toxicity to non-target organisms and would be quickly adsorbed by soil, thus preventing ground water contamination.

Another advantage of chemical release of hardwood stands over mechanical methods would be less drastic changes in stand density as trees slowly die out. The partial crowns of treated trees would provide side shade to the non-target trees reducing chances of epicormic sprouting. In addition, upright decaying stems could provide improved wildlife habitat over a longer time interval.

Label recommendations for chemical release are usually established as the maximum amounts needed to achieve a nearly complete kill of all treated trees and shrubs within a single growing season while still protecting the environment, the user, and the chemical company. Substantial differences in tolerance can exist among different species depending on the herbicide, its formulation, and method of application (Gjerstad and Nelson 1986; Norris 1981). The effectiveness of reducing rates by one-third to one-half are usually not given on the herbicide label. Potentially reduced rates could cause partial crown reduction of treated trees leading to reduced growth and subsequent entrance to a less competitive canopy position.

This study was designed to evaluate the effectiveness of tree injection and basal bark treatments with three herbicide formulations applied at standard practice and reduced rates to chemically thin an 18-year-old mixed hardwood stand. Secondly, we wanted to determine if differences in tolerance exist among different tree species to these herbicides and/or their methods of application. Finally, we wanted to learn if these herbicides affected growth of the adjacent untreated hardwoods.

METHODS

We initiated the study in 1990 on a mixed hardwood stand on a small watershed at the Dixon Springs Agricultural Research Center in southern Illinois. The stand originated following a clearcut harvest 18 years earlier. Stand composition was approximately 35% sugar maple, 10% red bud, 9% slippery elm, 6% sassafras, 6% winged elm, 5% white ash, 4% hickory, 4% black cherry, 4% devil's walking stick, 3% northern red oak, 3% mulberry, 3% yellow poplar, 3% white oak, and 5% other minor trees and shrubs. Soils were primarily Grantsburg silt loams (fine-silty, mixed, mesic Typic Fradiudalfs) with slopes between 3 and 7%, southerly aspect, a pHw of 5.7, and an organic matter content of 5.1%.

In 1989 the stand had been marked to retain approximately 400 non-treatment trees per hectare. These included primarily high-value timber and mast-producing hardwoods (white oak, northern red oak, white ash, hickory, black cherry and tulip poplar). For this study we divided the watershed into forty-eight 8- x 16-m rectangular plots containing 2.8 ± 1.9 ($n = 48$) non-treatment trees each. Twenty-four plots outside the riparian zone were randomly assigned for treatment by the tree injection and 24 additional plots for full basal bark treatment. Plots contained an average of 24.5 ± 13.9 ($n = 48$) treated trees or shrubs and 6.2 ± 1.5 ($n = 48$) different species.

All chemical treatments were applied during the last week of May 1991. For tree injection (hack-and-squirt), we made a series of 4.5-cm-long incisions or frills 3 cm apart into the sapwood conductive tissues with a hand ax approximately 1 to 1.5 m above the ground. Approximately 1 ml of test solution was immediately applied to each incision using a squirt bottle. We tested glyphosate (Accord) at below recommended rate by diluting it with water to give a 10% or 20% (ai) solution. We applied ready-to-use dicamba (Banvel CST) at the recommended rate using an 11.0% solution. We also tested a dicamba+2,4-D mix (Banvel 520) diluted with oil (Androc) containing either 1.3% or 3.9% dicamba and 3.4% or 10.2% isooctyl ester of 2,4-D, respectively. Trees in the control plots were treated with 1 ml of water per incision. Four replications of each herbicide treatment were randomly assigned to the 24 plots marked for herbicide application by tree injection.

For full basal bark treatments, we wetted the lower 20 to 25 cm of the stem to drip-point using a backpack sprayer equipped with a cone tip. We applied glyphosate at reduced rates as either a 4% or 8% (ai) solution in water without the addition of oil or a surfactant. Dicamba only was applied directly as the ready-to-use aqueous formulation containing 10.6% ai dicamba. The dicamba+2,4-D mix was applied as a solution containing 0.7% or 1.3% ai dicamba and 1.7% or 3.4% ai 2,4-D diluted with oil. Trees in the control plots were sprayed with water only. Four replications of each herbicide treatment were randomly assigned to the 24 plots marked for basal bark treatment.

We visually estimated average plot crown reduction to within 5% for each shrub or tree species 45, 90, and 360 days after treatment (DAT). A percentage crown reduction of 0% indicated no visible dying leaves or defoliated branches while 100% indicated complete defoliation of the crown with no basal sprouts. To determine treatment responses by species, we divided the treated shrubs and trees into the following classes: maples (essentially all sugar maple), ash (mostly white ash), elms (nearly equal proportions of slippery and winged elms), mixed shrubs (redbud, sassafras, persimmon, sumac, and devil's walking stick), low-value hardwoods (persimmon, mulberry, and various hickories), and the high-value hardwoods (northern red oak, white oak, black cherry, black walnut, and yellow poplar).

The species and diameter at breast height (dbh) of each crop tree were determined in early March 1991 and again in early November 1992 (after two growing seasons). Visual estimations of crown reduction were made also on the non-treated trees 45, 90, and 360 days after application of herbicides to the adjacent hardwoods.

Percent crown reduction was calculated for each plot and subjected to a two-way analysis of variance for a completely random design with factorial arrangement of the five herbicide formulations and water control, the two methods of application, and their interaction (SAS Institute Inc. 1988). We used Fisher's protected LSD (5% t-test value) to determine where differences existed among treatment means for main effects or for their interactions. Terminology for degree of crown reduction (very light to severe) is according to Miller and Glover (1991). We subjected the 2-year dbh growth of non-treated trees to the same two-way ANOVA after excluding the small number of black cherry and tulip poplar crop trees with growth rates nearly double that of the other crop trees.

RESULTS AND DISCUSSION

We found a highly significant interaction among the six herbicide treatments and the method of application for the average percent crown reduction of treated mixed hardwoods (Table 1). This interaction was present at 45, 90, and 360 DAT. Basal bark treatment with glyphosate at both rates, dicamba+2,4-D at both rates, or dicamba ready-to-use resulted in light crown reduction of treated trees. Tree injection was a more effective method for applying glyphosate, dicamba, or dicamba+2,4-D than was full basal bark treatment. The standard practice rates of dicamba and dicamba+2,4-D plus both rates of glyphosate when injected resulted in severe crown reduction of the treated trees. In contrast, the reduced rate of dicamba+2,4-D resulted in light crown reduction compared to the severe crown reduction from the lowest rate of glyphosate. We suspect that severe crown reduction will cause many of these codominant trees to die or become part of the intermediate or suppressed canopy class in the treated plots.

With the full basal bark treatment, only one herbicide (dicamba+2,4-D) at the standard practice rates showed increasing amounts of crown reduction during the second growing season (Table 1). These results suggest that this oil-based herbicide once absorbed into the bark can remain active for more than one growing season. A similar, but less pronounced, pattern existed when the oil-based herbicide was injected. These results suggest expanded studies need to be done comparing injection vs. basal application of other highly effective basally applied herbicides such as triclopyr and picloram with and without 2,4-D. The test herbicides in this study were chosen because of their effectiveness when injected and low risks for environmental damage.

According to Miller and Glover (1991), herbicide treatments resulting in more than a 70% control of the treated trees with acceptable crop tree tolerance should be considered successful. Miller (1990) found that chemically treated hardwoods with over 80% crown reduction eventually died, while trees with less than 40% crown reduction usually recovered. Miller, however, did not indicate if recovered trees now occupied a lower canopy class resulting in less

Table 1.--Crown reduction (%) of treated hardwoods 45, 90, and 360 days after treatment (DAT) with six herbicide formulations using two methods of application.

| Method and Herbicide | Conc. Active Ingredient | Percentage Crown Reduction Treated Trees ¹ | | |
|------------------------------|-------------------------|---|--------|---------|
| | | 45 DAT | 90 DAT | 360 DAT |
| | % | --%-- | --%-- | --%-- |
| TREE INJECTION: | | | | |
| Glyphosate | 20 | 74 | 72 | 68 |
| Glyphosate | 10 | 63 | 64 | 69 |
| Dicamba+2,4-D | 3.9+10.2 | 64 | 69 | 74 |
| Dicamba+2,4-D | 1.3+ 3.7 | 23 | 25 | 27 |
| Dicamba only | 11.0 | 74 | 74 | 78 |
| Water | --- | 1 | 1 | 2 |
| BARK BASAL TREATMENT: | | | | |
| Glyphosate | 8 | 19 | 19 | 18 |
| Glyphosate | 4 | 11 | 10 | 5 |
| Dicamba+2,4-D | 1.3+3.4 | 14 | 18 | 31 |
| Dicamba+2,4-D | 0.7+1.7 | 1 | 1 | 1 |
| Dicamba only | 11.0 | 25 | 28 | 23 |
| Water | --- | 0 | 0 | 0 |
| 5% t-test value | | 19 | 18 | 21 |

¹Values deviate from those previously reported by Kai et al. (1992) because of method of calculation and correction of values for basal bark treatment with dicamba+2,4-D.

competition to the released trees. Thus, nearly all the herbicide treatments using the injection method would have qualified as being successful assuming no damage to the non-treated trees. Percent crown reduction averaged across all species, however, does not indicate if these treatments resulted in severe to very severe crown reduction of some hardwood species and light to moderate crown reduction for less susceptible species or groups of species.

When percentage crown reductions were analyzed by species groups, we found that the maples were least susceptible to most of the herbicide treatments (Table 2). At the standard practice rate for glyphosate, dicamba, or dicamba+2,4-D, the injection method only resulted in moderate crown reductions on the sugar maples. Basal bark treatment resulted in very light to light crown reductions from which most trees will probably quickly recover. This confirms earlier observations on the high tolerance of pole-sized sugar maples to herbicides (Brinkman 1970, Newton and Knight 1981).

As a group, the shrubs were more susceptible to the tested herbicides than most of the other hardwood species (Table 2). Injections using the reduced rates of glyphosate or dicamba+2,4-D resulted in severe to very severe crown reduction of most shrubs. Although basal bark treatments with reduced rates were ineffective for most of the species groups, they did result in moderate crown reductions for the treated shrubs. Typically, most shrubs have thin bark that may account for their increased susceptibility to these broad spectrum herbicides.

Only minor differences were found in susceptibility among the ashes, elms, and other tree species to the tested herbicide combinations (Table 2). In general, these hardwoods had severe to very severe crown reductions following injections of glyphosate, dicamba, or dicamba+2,4-D. Full basal bark treatments with standard practice rates for glyphosate and dicamba+2,4-D tended to produce light to moderate crown reduction. The response to basal bark application of ready-to-use dicamba gave mixed results. The number of treated trees within any species group never

Table 2.--Crown reduction (%) for each species class 360 days after treatment (DAT) with six herbicide formulations using two methods of application. Changes of more than 10% from percentages after the first growing season are marked with a + or -, respectively¹.

| Method and Herbicide | Conc. Active Ingredient | Hardwoods | | | | | |
|------------------------------|-------------------------|-----------|-------|-------|--------------|--------------|------------|
| | | Maple | Ash | Elms | Mixed shrubs | Lesser value | High value |
| | % | --%-- | --%-- | --%-- | --%-- | --%-- | --%-- |
| TREE INJECTION: | | | | | | | |
| Glyphosate | 20 | 41 - | 38 | 100 | 96 | 100 | 100 |
| Glyphosate | 10 | 48 | 82 | 69 + | 100 + | 81 + | 87 |
| Dicamba+2,4-D | 3.9+10.2 | 45 + | 92 + | 100 | 91 | 50 + | 89 + |
| Dicamba+2,4-D | 1.3+ 3.7 | 4 | 0 | 29 | 67 | 2 | 0 |
| Dicamba only | 11.0 | 38 | 100 | 100 | 100 | 100 + | 77 + |
| Water | --- | 0 | 2 | 0 | 0 | 0 | 0 |
| BARK BASAL TREATMENT: | | | | | | | |
| Glyphosate | 8 | 0 | 17 | 35 | 29 | 26 | 0 |
| Glyphosate | 4 | 1 | 0 | 0 | 13 - | 0 | 4 |
| Dicamba+2,4-D | 1.3+3.4 | 8 | 25 + | 27 + | 50 + | 25 | 33 + |
| Dicamba+2,4-D | 0.7+1.7 | 0 | 0 | 0 | 0 | 0 | 9 |
| Dicamba only | 11.0 | 7 | 100 | 15 | 65 | 40 | 19 |
| Water | --- | 0 | 0 | 0 | 0 | 0 | 0 |
| 5% t-test value: | | 19 | 37 | 33 | 39 | 39 | 36 |
| Number plots included: | | 46 | 28 | 43 | 42 | 39 | 41 |

¹Values for 45 and 90 DAT can be found in Kai (1993).

met the criteria of 30 to 50 test plants as recommended by Miller and Glover (1991) for herbicide efficacy determinations; thus, these observations will require further testing.

Visual inspection of the crop trees did not show any discolored or deformed foliage or deformed shoots. Similarly, we found no differences in stem diameter growth of the crop trees during the first two growing seasons after treatment (Table 3). This suggests that the non-treated trees had absorbed little if any of the herbicides through root grafts or from the soil. In addition, it also indicates the crop trees have not responded to any of the release treatments.

SUMMARY

Chemical release using tree injections of glyphosate, dicamba, or dicamba+2,4-D effectively removed most unwanted hardwoods, except sugar maple, in a mixed hardwood stand. Reduced rates of glyphosate were nearly as effective as the standard practice rates for dicamba-based herbicides. Reduced rates for dicamba+2,4-D were generally unsuccessful except on the thin-barked shrub species. For full basal bark application, ready-to-use dicamba was more effective than either glyphosate or dicamba+2,4-D solutions. Standard practice rates of dicamba+2,4-D in oil using either tree injection or full basal bark application consistently caused more crown reduction during the second growing seasons than during the first growing season. The non-treated or crop trees showed no visible crown reduction or reduced diameter growth in response to any of the herbicide treatments. In conclusion, tree injection application of dicamba or dicamba+2,4-D at standard practice rates or glyphosate at less than standard practice rates can be an acceptable alternative to release crop trees in mixed hardwood stands unless stands are dominated by sugar maple.

Table 3.--Average diameter growth of crop trees two years after chemical release using factorial combinations of six herbicide formulations and two methods of application¹.

| Release treatment | | Method of Application | |
|-------------------|------|-----------------------|-----------------|
| Herbicide | Rate | Tree Injection | Full Basal Bark |
| | | --cm-- | --cm-- |
| Glyphosate | High | 0.29 | 0.34 |
| Glyphosate | Low | 0.43 | 0.26 |
| Dicamba+2,4-D | High | 0.36 | 0.31 |
| Dicamba+2,4-D | Low | 0.33 | 0.32 |
| Dicamba only | RTU | 0.25 | 0.34 |
| Water | --- | 0.37 | 0.28 |
| 5% t-test value | | 0.16 | |

¹Crop trees in order of relative density include white oak, white ash, northern red oak, green ash, sugar maple, and black walnut.

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FOREST VALUES AND HOW TO SUSTAIN THEM

Leon S. Minckler¹

The forestry profession has the responsibility of managing forests for all of their values. In the past, this has usually not been done. Often, timber has been the only value considered. The emphasis has not been on practices that combine other values with timber production. Such forestry practices must consider forest types and conditions, site quality and characteristics, and the long time needs of the people. This will require a broad concept of economics and based on all values. These would include watershed protection, erosion control, recreation, aesthetics, wildlife habitat, wilderness management, and the survival of Earth as a home for humanity.

First, we need more foresters in the woods who understand the art and science of ecological management. This usually emulates nature but often on a different time scale. Most values can be obtained together in the same forest at the same time. We must also know the objectives and slant the actions toward them, but not at the expense of the natural ecological requirements of the forest involved. We must use a workable value system, not just "dollar economics".

Except for badly damaged and decadent forests, this means some form of selection harvest and improvement cutting. It requires practices to obtain new regeneration, such as knowledge of opening size to make, tree classes, stand structure and maturity guides are required for optimum residual stands. In the Central Hardwoods, the ecological method for high total values is group selection, not patch cutting or clearcutting.

A total of 42 references based on a 20-year compartment study on Kaskaskia Experimental Forest in Hardin County, Illinois, are given as the chief foundation of this article.

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CHANGES IN A MISSOURI OZARK OAK-HICKORY FOREST
DURING 40 YEARS OF UNEVEN-AGED MANAGEMENT

Edward F. Loewenstein¹, Harold E. Garrett¹, Paul S. Johnson², and John P. Dwyer¹

Abstract: Changes in basal area, density and average diameter were examined on a 156,000-acre privately owned oak-hickory forest in the Missouri Ozarks. The forest has been managed since 1954 using the single-tree selection method. Trees greater than five inches dbh were monitored on 486 one-fifth-acre permanent plots at five year intervals from 1962 through 1992. Seven species/species groups accounted for approximately 90% of both basal area and density throughout this 30-year period. Average basal area increased by 48% and average density by 69% during the study period. Quadratic mean diameter declined by 8.5% over the first 15 years and has since remained relatively stable.

INTRODUCTION

Silviculture is defined as the art and science of manipulating a forest to meet the landowners' objectives (Smith, 1986). Since traditional even-aged management has fallen into disfavor with a large segment of the general population in recent years, there is increased pressure to apply uneven-aged management in systems such as the oak-hickory type (Sander and Graney, 1993). However, little long-term information is available on the growth and compositional changes occurring in oak-hickory forests under uneven-aged management. By applying selection techniques to these systems at this time, the practice of silviculture becomes less of a science and more of an art.

The single-tree selection method has been successfully used to manage shade-tolerant species. Such species are able to develop beneath the continually present canopy of uneven-aged forests. In contrast, shade-intolerant species require a light intensity for their survival and recruitment into the overstory that is often lacking in uneven-aged forests (Oliver and Larson, 1990). It has even been suggested that single-tree selection will not regenerate the oak component of a forest (Sander and Clark, 1971; Sander and Graney, 1983). A major concern in using uneven-aged methods of management then centers on a compositional shift toward more shade-tolerant species, which may be of lesser commercial value (Johnson, 1977; Niese and Strong, 1992). However, most studies that have demonstrated a shift in tolerance were conducted in mesic systems where oak reproduction does not tend to survive and accumulate in the understory. In xeric, oak-dominated systems such as are present in the Missouri Ozarks, oak reproduction does tend to accumulate, so the possibility exists for sustained oak recruitment into the overstory (Johnson, 1992).

To improve our understanding of the long-term effects of uneven-aged management, this paper presents 30 years of data on changes in the composition and basal area of a predominantly oak-hickory forest managed by the single-tree selection method for 40 years. The information represents an initial assessment of uneven-aged management as applied in a xeric to dry-mesic oak-hickory forest in the Missouri Ozarks.

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Management Strategy

The management plan for this forest was developed to meet three objectives: (1) to obtain income from timber sales; (2) to maintain a continuous forest cover; and (3) to refrain from the use of clearcutting in managing the forest. Although maximization of income has not been a primary goal, the forest is required to be self-supporting.

To meet these requirements, the forest plan calls for an approximate 20-year cutting cycle. However, the timing of reentry coincides with the stand reaching 95 - 100 ft² of basal area per acre. Upon reentry, the stand is cut to about 65 ft² per acre. The operational unit on the forest is the equivalent of one section (640 acres) but topography rather than section lines are used to delimit section units. This reduces adverse site impacts when adjacent sections are harvested.

Only merchantable trees (hardwoods greater than 10 inches dbh and pine greater than 9 inches) are marked for harvest. Culls that suppress potential crop trees are marked and felled as a condition of a timber sale. Lack of markets and the length of time required to grow small diameter stems to merchantable size makes the cost of precommercial thinning prohibitive. Only where a market exists are smaller stems removed.

When a stand is marked for harvesting, the goal is to create or maintain a three-tiered condition comprised of an overstory, a midstory and a sapling/reproduction layer. If the time between entries is too great, small diameter trees are lost and a two-tiered stand results. During marking, each merchantable tree is examined for possible removal. Those deemed likely to die before the next entry are marked for removal. Healthy trees are also considered for harvest. Whenever crop trees are competing, one is removed. Vigor, potential value (e.g. branching patterns limiting merchantable height gain), slope position, aspect and species are used to determine trees to be removed.

Salvage harvests are also made. Marking is accomplished in a manner similar to that of a normal harvest with one exception. If after marking all dead and damaged stems it is determined that the stand will be understocked to the point where the next harvest will be significantly longer than 20 years, all stems of merchantable size are reevaluated as to their ability to survive to the next entry. Any trees deemed likely to survive are left.

METHODS

For forty years this forest has been monitored through the use of well-distributed permanent 0.2 acre continuous forest inventory (CFI) plots. The first inventory was conducted in 1952 with remeasurements made every five-years. In 1957, the current monitoring procedure was established. The number of CFI plots was doubled; one plot was installed for every 320 acres of land on the forest. On each 0.2 acre plot, all stems 5.0 inches dbh and greater, were permanently numbered. Species, dbh, merchantable height to the nearest two-foot class and percent soundness were recorded along with forest-specific product and mortality codes. During subsequent inventories, trees were remeasured, mortality since the last inventory noted and any ingrowth stems were assigned new identification numbers and tallied.

Description of the Forest

The forest covers over 156,000 acres in the Ozark Highlands of southern Missouri. Approximately 90,000 acres were purchased by the current owner in 1954. Additional land was purchased to bring the size of the forest to 134,000 acres by 1962 and to 150,000 acres by 1972. Additional CFI plots were installed as the size of the forest increased. As a provision of the original purchase, the previous owners retained the right to harvest white oak (*Quercus alba* L.) greater than 16 inches dbh. Harvesting of those trees occurred on selected areas of the forest into the early 1960's which left some stands with very low residual stockings. In 1962, 31.6% of the CFI plots supported less than 31 ft² of basal area per acre, 86% of the plots had less than 61 ft² (Figure 1).

Because of the size of the forest, site quality and vegetation vary widely. However, topography is generally steep with broad flat ridges. The soils are generally rocky and droughty, but range from deep gravel and rock outcrops to areas where the soil is over four feet deep. The soil is derived mainly from dolomitic limestone. Site index (base age 50-years) ranges from 50 to 90 for black oak (*Quercus velutina* Lam.). Although the forest is predominantly oak-hickory, shortleaf pine occurs throughout as scattered trees and as pure stands on upper south-facing slopes. Lower north-facing slopes and deep valleys typically support mixed mesophytic hardwoods.

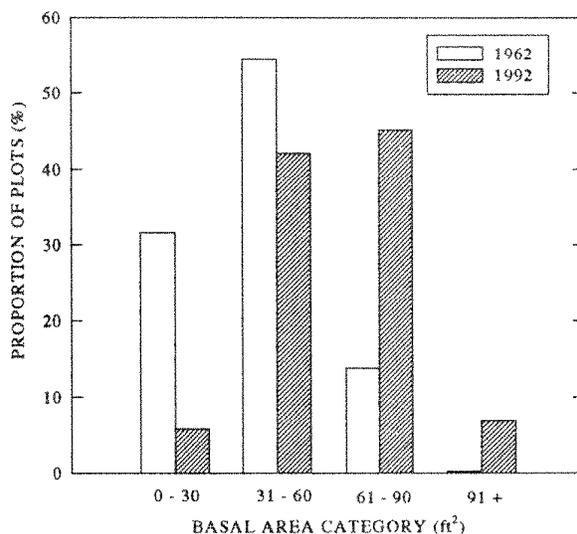


Figure 1. Breakdown of CFI plots, by basal area, at beginning and end of study period.

Analysis

Only the CFI data from 1962 to 1992 are presented in this paper. Basal area (ft² per acre), density (trees per acre), and quadratic mean diameter (QMD), were calculated by species for each measurement year. This information reflects a preliminary analysis of the dataset. Data from all available CFI plots have been included in the averages presented. Therefore, because additional property was added to the forest through time, of the landbase included in the 1992 data, 78% had been managed with single-tree selection for 40-years, 8% for 30-years, 10% for 20-years, 3% for 15-years and 1% for 10-years.

RESULTS

Seven principal species/species groups accounted for approximately 90% of both basal area and density throughout the 30-year study period from 1962 to 1992. These species include white oak, scarlet oak, black oak, northern red oak (*Quercus rubra* L.), post oak (*Quercus stellata* Wengen.), shortleaf pine and hickories (*Carya* spp.). During that time, total basal area on the forest increased by 48% and density by 69% (Table 1). However, of the primary species studied, only scarlet oak maintained the same proportion of basal area and density relative to the entire forest. White oak relative density increased by 12.8% while a similar percentage decline was observed in the remaining species. White oak and shortleaf pine have shown the strongest increase in relative basal area, 8.3 and 5.4% respectively.

Table 1. Average basal area, density and quadratic mean diameter, by year, averaged across species and CFI plots on the forest.

| Year | Basal Area (ft ² / acre) | Density (stems / acre) | QMD (inches) |
|------|--|---------------------------|-----------------|
| 1962 | 40.94 | 86.31 | 9.33 |
| 1967 | 44.57 | 97.77 | 9.14 |
| 1972 | 47.21 | 107.87 | 8.96 |
| 1977 | 49.58 | 124.72 | 8.54 |
| 1982 | 52.14 | 131.34 | 8.53 |
| 1987 | 54.03 | 134.32 | 8.59 |
| 1992 | 60.51 | 145.90 | 8.72 |

In absolute terms, five of the seven principal species have increased in density during the study period (Figure 2). Post oak (data not shown) and northern red oak, the two least common of the seven species, maintained relatively stable densities. The hickories, scarlet oak and black oak exhibited similar trends in density change, increasing from 1962 through 1977 and remaining stable thereafter. Density of shortleaf pine has been constant since 1972. Only white oak has continued to show substantial increases throughout the study period and accounts for 87% of the total gain in density occurring on the forest between 1977 and 1992.

The three red oaks (black, scarlet and northern red), exhibited similar trends for both basal area and quadratic mean diameter (QMD) through time (Figure 2). A steady decline was observed in QMD for the first 20 years followed by a recovery. Changes in QMD appear to be closely tied to changes in density. The decline in QMD was accompanied by an increase in density, northern red oak excepted, from 1962 - 1977. Stabilization and recovery of QMD for the red oak group has occurred since the density of black and scarlet oak leveled off. Basal area changes have shown an upward trend with scarlet oak exhibiting the greatest gain followed by black oak and finally northern red oak (Figure 2).

The pattern of change in QMD differed between the white and red oak groups. White and red oaks demonstrated the same initial decline in QMD; however, white oak QMD did not recover while red oak QMD did. Since 1977, white oak QMD has continued to decline, but at a greatly reduced rate. At the same time, white oak density and basal area have increased sharply.

For shortleaf pine, both basal area and QMD have steadily increased through time. The rate of change for these variables appears to have been effected when density peaked in 1977 with QMD increasing and basal area decreasing.

DISCUSSION

Indications are that the composition of this forest is not shifting toward shade tolerant species. The seven species found to be most prominent when single-tree selection was implemented in 1954, still comprise the same relative proportions of the forest today. Density for all species except white oak has been relatively constant since 1977 (Figure 2). White oak, which has high value both for timber and mast production, is increasing in prominence on the forest. Its density has increased over three-fold and its basal area has more than doubled during the 40-year monitoring period. As a proportion of the forest total, in 1962 white oak comprised less than 18% of the total basal area. In 1992, 26% of the basal area was in this valuable species.

Ingrowth and the harvesting of timber both have a suppressing effect on QMD. Since ingrowth is measured and averaged into the plot total when a tree reaches five-inches dbh, if QMD is larger than 5.0 inches any new ingrowth will bring about a reduction in QMD value. Likewise, if QMD is smaller than the ten-inch minimum harvest diameter, cutting any tree will lower the QMD. Only diameter increases of trees greater than five-inches dbh will increase the QMD.

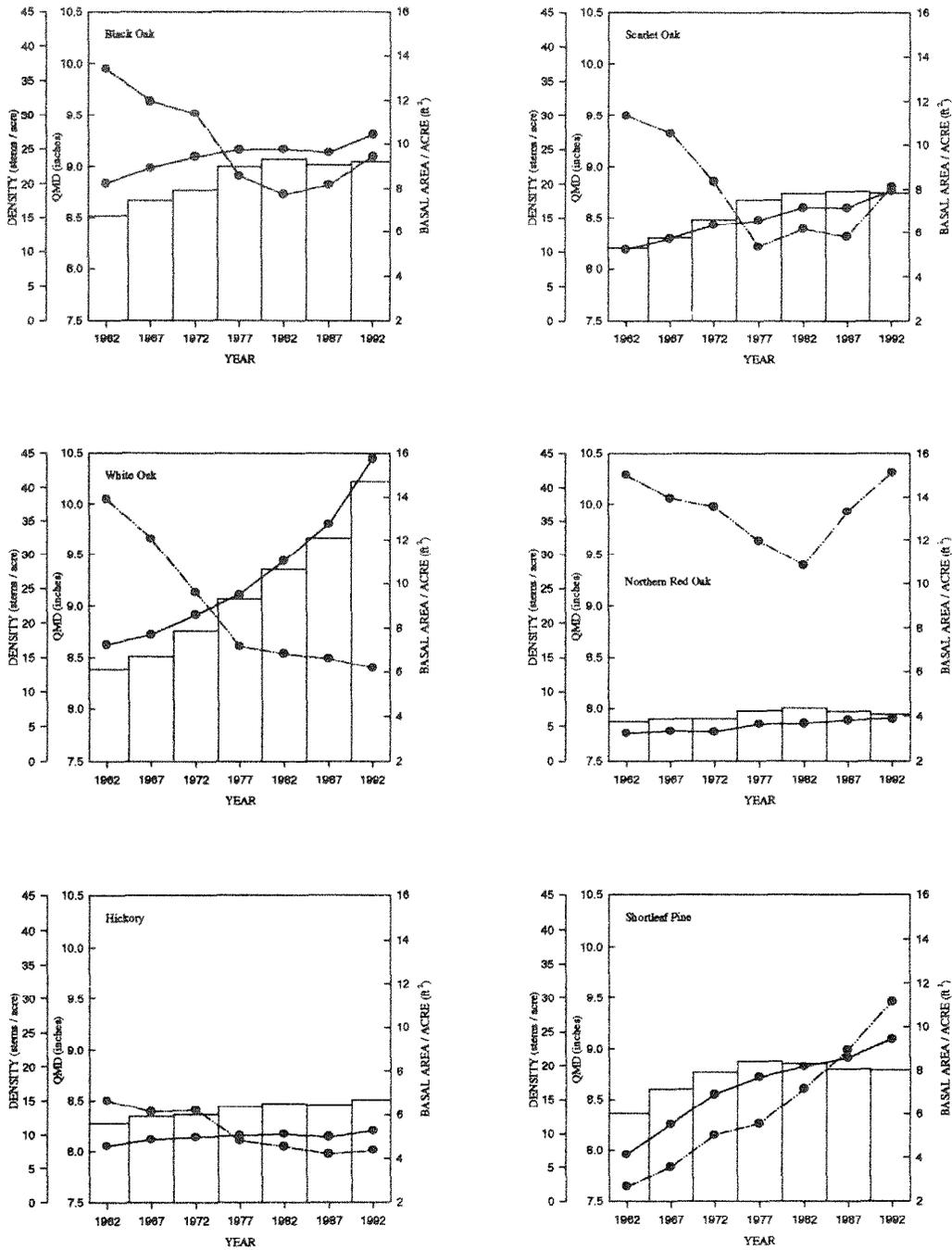


Figure 2. Changes in quadratic mean diameter (broken line), basal area per acre (solid line) and density per acre (hollow bars), for six species/species groups under uneven-aged management practices.

Average basal area has remained relatively stable for northern red oak and hickory, slowly increased for black oak and scarlet oak, markedly increased for shortleaf pine and increased exponentially for white oak (Figure 2). With black oak, scarlet oak and shortleaf pine, this increase in basal area mirrors the increase observed in QMD. Since the density of these species is stable (ingrowth equals the sum of harvest and mortality), both basal area and QMD will also likely stabilize when the growing capacity of the forest is reached.

The large increase observed in white oak basal area paralleled a similar increase observed in density. The fact that the QMD has declined only slightly since 1977 (0.2 inches) while density has continued to increase, indicates that considerable diameter development is occurring. Numbers and size of mortality and trees harvested were not available at the time of manuscript preparation; therefore, changes in density that are reported represent an extremely conservative estimate of ingrowth and its consequent effect on QMD suppression. The sharp early drop observed in white oak QMD is believed to be due to the ten stem per acre increase which occurred between 1962 and 1977, almost doubling the species' density (Figure 2). In this same 15-year period, basal area increased by 2.2 ft² per acre. Since ten, five-inch stems account for only 1.4 ft², the remaining 0.8 ft² (plus any basal area removed by mortality or harvesting) had to result from the growth of the remaining stems. Since 1977 the evidence for diameter development is even more dramatic. Again, almost a doubling of density was observed (23.5 to 41 stems per acre). However, during this time period the sharp decline in QMD observed earlier, did not occur. The 17 additional white oak stems tallied account for 2.4 ft² of the 6.2 ft² of basal area added since 1977.

As of the last remeasurement period (1992), the single-tree selection management approach appears to be maintaining a healthy, sustainable forest. Ingrowth into the five-inch diameter class is occurring at a rate sufficient to maintain or increase density for all of the principal forest species even after accounting for harvested stems. Diameter development is occurring as evidenced by the stabilization of QMD for the forest as a whole while average basal area and density are steadily increasing (Table 1). However, even though single-tree selection has been applied for 40 years, the forest can not yet be considered regulated. This is evidenced by the continuing increase in basal area and density which can only occur while there is available growing space. The forest is obviously still recovering from the low stocking levels which were present at the time ownership was transferred; as of 1992, approximately 45% of the forest still supported less than 60 ft² of basal area per acre (Figure 1). Despite the lack of full regulation, initial indications support Johnson's (1992) suggestion that under the conditions present in this xeric to dry-mesic, oak dominated ecosystem, selection silviculture may result in sufficient recruitment to perpetuate the oak-hickory type.

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