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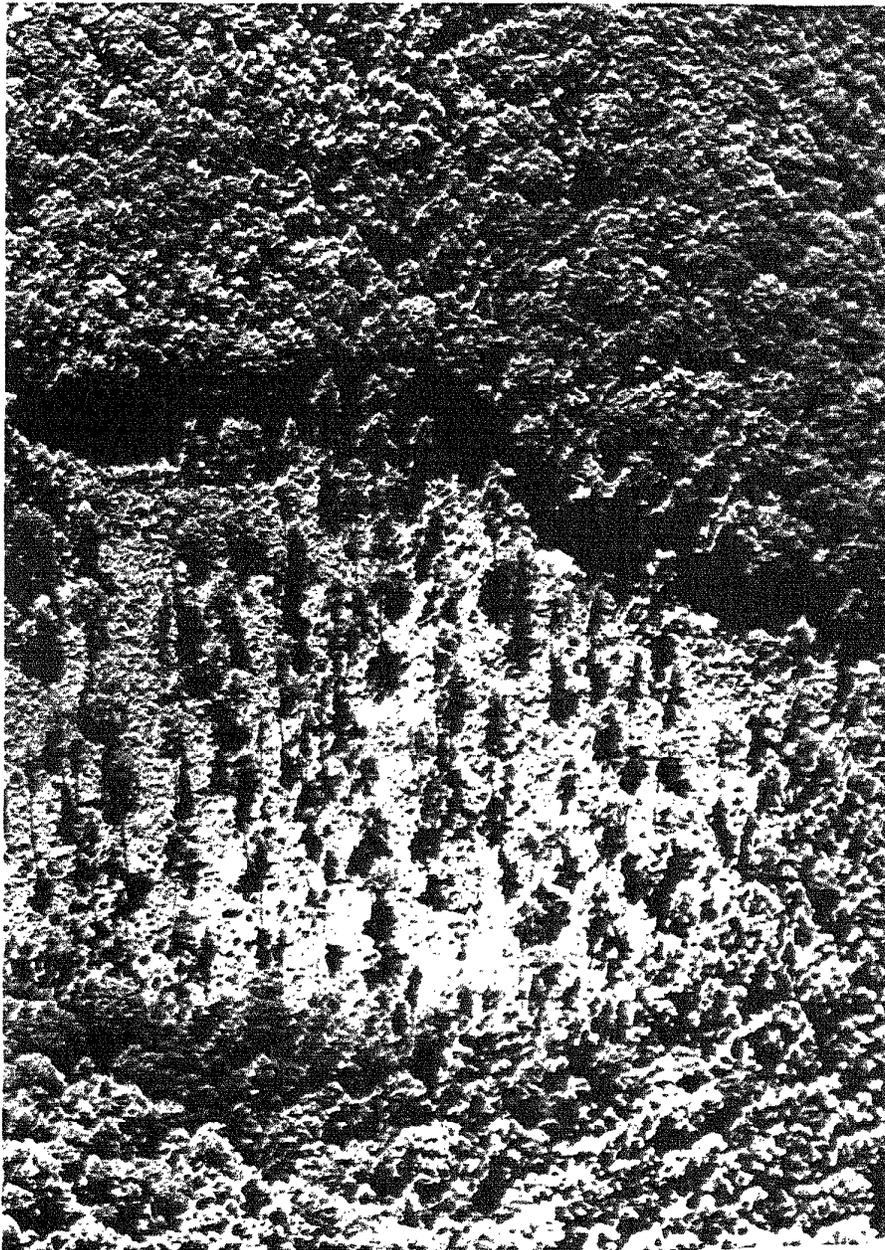
General Technical  
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# Proceedings

## 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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## ACKNOWLEDGMENTS

The editors would like to acknowledge and thank all of the people who served as manuscript reviewers for the Proceedings. The quality of the Proceedings has been improved due to your efforts. We would like to thank Becky Rosenberger for her assistance in typing the program, preparation of the table of contents, typing abstracts, proofreading, and in managing the manuscripts, reviews, and letters associated with the Proceedings. We thank Gary Miller for providing the cover photograph.

**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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**March 1995**

# 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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## WALKING THE TALK

R. C. Kellison<sup>1</sup>

The preception exists that the forest industry in the United States is the antithesis of the green revolution. For instance, I recently saw the results of a poll that listed three forest products companies among the 10 worst polluters in the United States. That's all there was; their names splashed across the TV screen on the early morning news. That very appearance undoubted resulted in lost sales because some viewer would have immediately determined that those organizations, and thus the industry, were irresponsible members of society.

One wonders on what basis the poll was taken and how the results were interpreted. Did someone ride by a pulp mill on a cool morning and see plumes of water vapor emitting from pipes and stacks and mistake the innocuous condensate for "greenhouse gasses"? Or did they find the smell of hydrogen peroxide, an odiferous gas used in the chemical process of pulping, so disagreeable that the "polling team" gave a red mark to the company? Or perhaps it was the harvesting of a stand of timber that the pollster had long held in reverence as his own veiwshed even though the timber was on someone else's property.

I contend that forest industry is the leader in natural resource management and, for that matter, in industrial cleanup of the environment. What other industry has gone from about 25% to 67% in self sufficiency in energy production since the oil embargo of 1974, and what other industry has spent over a billion dollars annually during the last decade in meeting regulatory requirements? But even with that enviable record, the Environmental Protection Agency has determined that more is needed. It is proposing the "Cluster Rule" which purports to integrate EPA's various authorities over air, water and land pollution sources. The philosophy is to combine regulations, as opposed to the piecc-meal approach used heretofore. The proposed rules are to be completed by 1996, and be implemented by 1999.

The American Forest & Paper Association estimates the cost of compliance of the "Cluster Rule", over three years, at \$12 billion, with an additional \$600 million annual operating cost. The conclusion by AF & PA and EPA is that some mills will be closed because they can't meet the standards. Even though the forest industry supports the effort to protect the environment and enhance other forest resource values, they are working to identify other, less costly ways to achieve the same results.

As a natural resource manager, forest industry sets the pace. They have surplanted the USDA Forest Service during the last decade because that agency has been beseiged by greiviances, court orders and appeals that have greatly hampered their operation. Morale among its employeecs has suffered, and so has the management, research and extension for which the agency had worldwide recognition. Only now are they charting their path to the future.

Forest industry is also leading the way for the nonindustrial private land owner. Landowner assistance programs which have been continuously supported by organizations such as Westvaco for the last 40 years, are finding a new lease on life. Organizations without a land base, such as Stone Container and Alabama River, have become very aggressive in contracting with farmers and other nonindustrial owners in managing their forest land. This aggressiveness has caused others of the wood products industry to renew their landowner assistance programs. The reason is simple: a large part of the wood for future manufacturing needs will come from non-industry lands.

In the midst of increased production on their own lands and expanded landowner assistance programs, the forest products industry is implementing a set of principles to assure that the land they manage and, to the extend possible, the land from which they buy timber, is managed in a responsible way. The guidelines, developed by AF&PA, are

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entitled "Sustainable Forestry Principles and Implementation Guidelines". They contain principles on reforestation practices, water quality, wildlife, aesthetics, and, among other items, protecting special places. A checks-and-balance system in which the public is involved, will be used to gauge the effectiveness of the program.

In keeping with the theme of this conference, forest industry is beginning to manage the native hardwood resource much more intensively than in the past. Because of the degraded condition of many of the hardwood stands in the Eastern Deciduous Forest, the best regeneration alternative is nearly always to clearcut when timber production is the objective. However, clearcutting can scar the landscape. Being sensitive to the concerns of the public, the industry has decreed that clearcutting will not be the option of choice in environmentally sensitive areas. Such areas include vistas associated with the Southern Appalachians and buffer zones of major bodies of water and recreational areas. The alternatives, even though more costly to apply and being less efficient for timber production, are to use partial-harvest systems such as shelterwood, group selection, patch clearcuts, and leave-tree cuts. Within our Hardwood Research Cooperative at North Carolina State University, the 13 industrial members and 2 state forest services have committed to the installation of 10 such studies, stretching from Virginia to Mississippi, inclusive of West Virginia. The purpose is to compare the regeneration success of a two-stage shelterwood and a leave-tree cut to a clearcut. Some of those same organizations are already applying these alternative regeneration systems to their timber stands that lie in environmental sensitive areas. This commitment to timber production in combination with environmental ethics is here to stay.

The hoped-for result from all of these actions is a list in which none of the forest products companies are among the 10 or even the 100 worst polluters. AF & PA members propose to do this by "walking the talk".

## FOREST HEALTH ASSESSMENT FOR EASTERN HARDWOOD FORESTS

Daniel B. Twardus<sup>1</sup>

Information presented here, was obtained generally from 3 sources: the Cooperative Forest Health Protection Program, the Forest Inventory Analysis Program, and the National Forest Health Monitoring Program. The Cooperative Forest Health Protection Program is a joint State-Federal effort responsible for forest-wide surveys of forest damage. From these surveys, we gather information about the nature and extent of insect, disease, and weather caused damage to trees and forests. These surveys are conducted by State and Federal pest specialists. Forest Inventory and Analysis Surveys are conducted by the U.S. Forest Service within each State on generally a ten-year basis and provide periodic updates on such forest statistics as growth rates, volume changes, and rates of mortality and cutting. The National Forest Health Monitoring Program uses a network of permanent plots, visited annually, to monitor tree conditions such as crown vigor, signs of insect and disease damage, ozone damage, and foliar and soil chemistry. To date, plots have been established throughout New England, New Jersey, Delaware, Maryland, and the Lake States. Crown vigor is an aspect of tree condition that has become of particular interest in monitoring forest health. The Forest Health Monitoring Program has divided crown vigor into three components: foliage transparency, crown density, and crown dieback. Foliage transparency is a measure of the "fullness" of a tree's crown. That is, the greater the transparency the more light passes through, indicating that foliage may be missing. Changes in foliage transparency occur as a result of insect feeding, deformed foliage, or reduced amounts of foliage. Crown density, estimates a tree's crown in relation to a normal or expected shape and size. It is the amount of crown branches and foliage that block light coming through the canopy. Crown dieback, is defined as branchlet or twig mortality in the upper portions of the crown. Crown dieback is often thought of as the first sign of tree stress. Taken together, these three crown rating factors can be used to assess crown vigor.

### FOREST CONDITIONS

#### Beech (*Fagus grandifolia*)

The forest type known as maple/beech/birch encompasses nearly 5 million acres in the east. The largest concentrations of beech are found in New York, Pennsylvania, and West Virginia. In New England and the mid-Atlantic States, the volume of beech has generally increased with the exception of Maine where a 6% decrease in growing stock volumes has occurred (Tables 1 and 2). New York and Vermont have higher than average annual beech mortality rates, as a percent of growing stock volume.

A very important factor in the health of beech, is the beech bark disease. This disease, first introduced into Maine in the 1930's from Canada has spread throughout New England into Pennsylvania and West Virginia. By the mid-1970's, it was estimated that over 30 percent of the beech in New Hampshire and Vermont and 50 percent of the beech in Maine over 8 inches in diameter were killed by this disease. It is worth noting that in New England, the percent of growing stock volumes in trees less than 15 inches in diameter is quite high. In Maine, where beech is decreasing, 86% of the growing stock volume is in smaller trees. Mortality has also occurred on over 500,000 acres of forest containing beech in West Virginia, and on over 250,000 acres in New York. What we are seeing in the New England and mid-Atlantic States is that older, larger beech are being killed by the disease and then replaced by new, smaller beech. In many instances, these young trees are sprouts and are just as susceptible to the disease. Most become infected by beech bark disease, but because they are able to outgrow infection, they are not always killed. However, this so-called "aftermath" forest consists of many highly deformed, defective trees.

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Results of Forest Health Monitoring, illustrate that for American beech, nearly 47% of the trees have poor crown density and slightly more than 27% have severe crown dieback. Though only small percentages of the trees are being monitored, the results are significant in that they are higher percentages than for other hardwood species.

Table 1. Change in volumes and annual mortality for American Beech - Mid-Atlantic States (data from FIA survey reports).

State	% change in growing stock volume between inventory periods ('72-'92)	% of growing stock volume in trees less than 15 inches	annual mortality as % of growing stock volume
DE	-47	47	
NJ	85	56	.1
MD	30	49	0
PA	24	63	.5
WV	19	52	.2
OH	64	38	.6
Average	34	52	.3

Table 2. Change in volumes and annual mortality for American Beech - North Central States (data from FIA survey reports).

State	% change in growing stock volume between inventory periods	% of growing stock volume in trees less than 15 inches	annual mortality as % of growing stock volume
MI	-18	63	.7
MO		32	.6
IL	-16	20	.4
WI	13	51	2
IA			
Average	-7	42	.9

### Maples (*Acer* spp.)

Of the hardwood species growing in the East, oaks are the most common accounting for one-third of the hardwood volume (Powell et al. 1993). The maples (*Acer* spp.) are next in abundance, and are one of the fastest growing components of our hardwood forest. Sugar (*A. saccharinum*) and red maples (*A. rubrum*) together account for 17% of all hardwood volumes in the East (Powell et al. 1993). Table 3 illustrates changes in growing stock volumes for both sugar and red maples. The largest gains in sugar maple volumes occurred in Ohio with a whopping 98% increase in growing stock volumes between 1979 and 1991, and a 138% increase in red maple volumes for the same time period.

Why the increases? Both sugar and red maple are very tolerant of shade and both are prolific seeders. Maples will increasingly occupy sites as openings are created or other species are cut and removed. Large increases in one species mean others loose ground. In Ohio, red maple has replaced hickory as the most abundant tree species in the forest.

In recent years there has been concern expressed over the health of sugar maple. Sugar maples, used for the production of maple syrup and as a roadside and yard tree, are a valuable component of our forests in the east. In many cases, various stressing agents have been associated with dieback and decline of individual sugar maples, especially insect defoliators and physical damage. In northern New York the forest tent caterpillar defoliated over 120,000 acres of sugar maple in 1993. Pear thrips defoliation continues in Vermont, Pennsylvania, and New York, however, the area affected is down from the 1980's when the most extensive damage occurred. In northern Pennsylvania, an area of 260,000 acres has been defoliated for several years by the elm spanworm. Most heavily impacted within this area has been red maple and American beech.

The North American Maple project has been collecting information at permanent sample sites throughout eastern Canada and the northeastern US. Results of this effort have shown that more than 90 percent of all sugar maples within the survey were considered to have healthy crowns. Of those with more than 50% dieback, nearly all had major root or trunk damage. Within the survey area, sugar maple mortality is estimated to be only 1 percent of trees per year. This isn't to say the local problems won't develop. In Pennsylvania, for example, red and sugar maple volumes are up, statewide. However, several northwestern counties in an area known as the Allegheny Plateau are experiencing decreases in sugar maple growing stocking relative to other species. Some of this may be due to the affects of Pear thrips defoliation, or just to an overabundance of sugar maple resulting in increased competition for soil and water resources. Experts have been gathering information related to this localized problem, but answers are not yet available.

### Oaks (*Quercus* spp.)

Our present oak-hickory forests rose out of the natural catastrophe known as the chestnut blight. Forests once referred to as oak-chestnut covered huge areas of the eastern US from southern New England to northern Georgia. Chestnut blight, caused by a fungus, was introduced to this country in 1904, and by the 1930's virtually all chestnut trees were infected and dying. Natural replacement of the chestnut followed resulting in forests in which oaks, yellow poplar, and hickory became dominant. Today, we refer to these replacement forests as oak-hickory forests, but as the noted ecologist Lucy Braun wrote in 1950, "it is impossible as yet to predict the final outcome of the partial secondary successions everywhere in progress."

Within the present day oak-hickory forests, a new forest health factor looms--the gypsy moth. This defoliating insect was introduced into the US in 1890 in Massachusetts. It has gradually spread throughout the East, now occupying a place in the forests from Maine to Virginia and west to Wisconsin. The larvae of the gypsy moth feed on a variety of hardwood species but favor oaks (*Quercus* spp), sweetgum (*Liquidambar styraciflura*), basswood (*Tilia americana*), and willow (*Salix* spp). Repeated gypsy moth defoliation can result in growth loss, tree mortality, changes in forest composition, and loss of habitat for various animal species. In some areas, oak mortality due to gypsy moth defoliation has been quite significant. Areas of south-central Pennsylvania have experienced extensive oak mortality during outbreaks in the late 1980's. Gypsy moth will not disappear from these forests, and a new balance must be struck between forest and insect. Overall, in Pennsylvania a state with a 20 year history of gypsy moth defoliation, oaks still account for 43 percent of the total forest volume (Gansner et al. 1993 ).

Table 3. Change in growing stock volumes for hard and soft maples (data from Forest Inventory Analysis Reports (1972-1992)).

	sugar	red	years
	-----percent change-----		
<b>Mid-Atlantic States</b>			
NJ	-	-	
PA	20	37	1978-1989
WV	56	74	1975-1989
OH	98	138	1979-1991
MD	47	56	1976-1986
DE	-	-	
Average mid-Atlantic	55	76	
<b>Northcentral States</b>			
WI	48	79	1967-1982
MI	21	78	1965-1979
IL	63	32	1962-1985
IN	65	102	1967-1986
MN	40	94	1977-1989
IA	4	44	1974-1990
Average Northcentral	40	55	

#### Hickories (*Carya* spp.)

Of the total amount of hardwood volume in the East, oaks comprise nearly a third while hickories account for only about 4%. Recently, some concern has been raised over declining hickories in various parts of its range—notably Wisconsin, West Virginia, and Ohio. Table 4 shows that though hickory growing stock has increased in most states during the past 20 years, much of this increase has occurred in trees of smaller size. Larger trees (over 15 inches in diameter) appear to be succumbing to mortality or cutting in Minnesota, Delaware, Rhode Island, New York, Massachusetts, and Connecticut. States with higher than average rates of hickory mortality are Massachusetts, Rhode Island, Missouri, and Illinois. At present, the causes of hickory decline in these areas is unknown though several wood-boring insects are suspected of playing a role.

#### White Pine (*Pinus strobus*)

White pine extends from Maine to the Lake States and south throughout the Appalachian Mountains. It grows in a variety of conditions from pure stands to stands in which it is only a minor component. I mention it here, because in the East, it is found associated with many different hardwood species including aspen, birch, oaks, and hickory, and because it is coming back. White pines' moderate shade tolerance, its long life, and its resistance to fire, make it a very adaptable species. The lumber industry of the east was based upon white pine for much of the 1800's and early 1900's. Today, however, (and due, in part, to exploitive logging) white pine sawtimber is only regionally important. In total, white and red pines account for only about 3 percent of the volume of softwood growing stock in the US. In most areas of the East, white pine is coming back. Growing stock volumes are up 105% in West Virginia, 52% in Connecticut, and 43% in Pennsylvania, all in the last 20 years. Within the Northeastern area, today, Michigan has the largest concentration of white and red pines totaling an estimated 2,017 million cubic feet of growing stock, followed by Maine with 1,916, and New York with 1,809.

Table 4. Change in volumes and mortality rates for hickory (data from Forest Inventory Analysis Reports, 1972-1993).

State	% change in growing stock volume between inventory periods	% of growing stock in trees less than 15 inches in diameter	annual mortality as a % of growing stock volume
CT	19	85	0.5
NY	23	82	.4
MA	-22	92	2.1
RI	73	95	.7
NJ	---	78	.3
MD	12	67	.6
PA	12	79	.8
WV	32	77	.4
OH	35	68	.6
DE	- 70	71	NA
IN	19	67	.5
MO	45	85	.8
IL	52	70	1.0
MN	54	87	.3
MI	3.0	79	.1
WI	82	90	.2
IA	74	82	.4

Ash (*Fraxinus* spp)

White ash and black ash are components of the elm-ash-cottonwood forest type which encompasses over 10 million acres in the northeastern and northcentral states from Maine to Minnesota. White ash is the most common native ash species, while black ash is found more often along streams and rivers.

In the central Appalachians, ash growing stock increased 36 percent since the last inventories. However, some problems have been occurring. A disease, ash yellows, caused by a mycoplasma-like organism, has been confirmed occurring in almost every state within the Northeastern Area. Not all ash problems can be attributed to this disease, since damage from drought, insects, and rust diseases are also found in association with declining ash trees.

Decline of black ash was reported in 1993 in Maine on 120,000 acres. Numerous trees with severe crown dieback have been observed along streams in Maine. In New York, ash anthracnose, a foliage disease was reported in 1993 on 105,000 acres.

Results of FHM assessments of white ash crown conditions in 1993 show that white ash is second only to American beech in percent of trees with severe dieback and poor crown density.

#### Butternut (*Juglans cinerea*)

Butternut, or white walnut, is associated with many other hardwood species and occurs sporadically throughout the east. The tree is most valued for its nut production for wildlife and for furniture wood. In the past the majority of butternut timber production has been in West Virginia, Wisconsin, and Indiana. However, it is hard to find healthy butternut in forest stands today, as the species is being threatened by a devastating disease known as butternut canker caused by *Sirococcus clavigignenti-juglandacearum*, a fungus of unknown origin.

The disease was first reported occurring in Wisconsin in the mid-1960s, but has probably been in the United States prior to that time. It is now present throughout the range of butternut. The cankers girdle the branches and tree stems, causing mortality. There is no known control for butternut canker disease. Efforts now center on finding resistant individual trees within infected stands.

In 1993, a ground survey confirmed the presence of the disease in central coastal Maine. Surveys for the disease were also conducted in New York, where most of the counties surveyed were found infected, and Vermont, where the presence of the disease was confirmed throughout the state. In Wisconsin, where over 1000 trees were sampled in 32 counties, 91 percent of the live trees were found to be infected and 27 percent of the surveyed trees were dead. In the last decade the number of live butternut decreased 58 percent in Wisconsin and 84 percent in Michigan. Several evaluation surveys indicate that the disease has spread rapidly within infected stands.

Two other factors affecting the eastern deciduous forest that are worth mentioning are **weather** and **air quality**.

#### Floods

In the summer of 1993, in the mid-west, thousands of acres of bottomland hardwood areas were flooded for 4 to 12 weeks. The flood waters also backed up into upland areas, affecting urban areas forested with trees not well adapted to flooding. The states along the Missouri and Mississippi Rivers and their tributaries were severely affected. Flood stressed trees exhibited a range of symptoms including leaf yellowing, early leaf drop, and dieback. It is possible that these affected trees will show symptoms for several years. They may also be affected by various insects and diseases.

#### Air quality

There are 3 aspects of air quality that are presently of concern with respect to the health of eastern deciduous forest: ozone, and emissions of sulfates, and nitrates.

**Ozone.** Ozone is an air pollutant in the lower atmosphere, formed from the reaction of compounds produced by automobile emissions and industrial processes, in combination with sunlight. There is increasing concern as to how ozone may be influencing the health of the forest resource. Atmospheric concentrations are monitored through a network of ozone monitoring stations throughout the area. And, damage to sensitive plant species, called bioindicators, has been assessed on National Forest Lands and on State and Private Lands as part of the National Forest Health Monitoring program. The results for 1993 indicate that there was little ozone injury encountered. This is mainly because of the low incidence of damaging ozone in the atmosphere during the summer of 1993. The incidence of damage was higher in 1990, which was a year when ozone concentration were high due to dry and hot summer conditions.

Using bioindicator plants allows for a general assessment of the air quality. Research is currently being conducted to determine the link between visible symptoms and foliar injury. At this time, the bioindicator information cannot be used to make a statement about the effects on the productivity of or damage to the forest. We know that across a broad range of ozone concentrations dose-responses of net photosynthesis and growth of trees are dependent upon ozone concentrations. We know that significant differences exist among species in sensitivity to ozone. And, we know that ambient ozone concentrations are probably sufficient to cause reductions in photosynthesis and growth in most vegetation of the east. However, we do need long-term ecological studies of the interactions between ozone and natural factors before we can quantify the response of forest ecosystems to ambient ozone pollution (Reich 1987).

Sulfates and nitrates. We know that the eastern US receives the highest depositions of sulfates and nitrates in the country, and that, at least for sulfates, 90% of this deposition is due to man-made sources (Galloway and Whelpdale 1980). The effects of these air borne pollutants upon forest ecosystems was described by Smith (1974) as ranging anywhere from subtle changes in species composition and forest structure to obvious structural simplification and major changes in ecosystem function. Presently, however, adverse effects of the deposition of sulfates and nitrates (acid rain) are limited to high-elevation spruce forests. The National Acid Precitation Program (NAPAP) was unable to provide evidence of widespread forest damage in the US. (Barnard et al. 1989). Although no direct adverse effects on terrestrial vegetation has been documented, indirect effects may result from long-term changes in soil chemistry. In fact, NAPAP, concluded that changes in soil chemistry may progress for 50 to 60 years before effects on forests are observed. These concerns must be taken seriously and links between possible changes in soil chemistry and the incidence of disease and insect attacks investigated. For example, it is plausible that changes in soil chemistry may alter tree physiology to the extent that resistance to disease or insect attack is lessened.

### CONCLUSIONS

Overall, if we look at all hardwoods in the East using data compiled by the USDA Forest Service for the Resource Planning Act Assessments, we find increasing volumes and mortality generally stable, except for the last few years (Fig. 1).

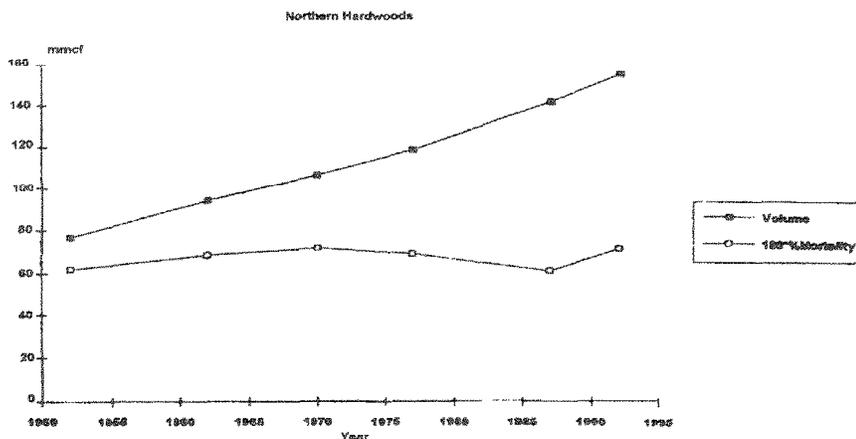


Figure 1. Data from Resource Planning Act Assessments. Personal communication, Eric Smith, USDA Forest Service, Ft. Collins, Co.

Evaluating forest health requires analysis of several conditions. In this paper, I have examined incidence of insects and disease, growth, rates of mortality, and species composition changes. Growth or measures of productivity, by themselves, do not reflect forest health. For the eastern hardwood forest, it is important to evaluate not only growth, but factors such as mortality rates, diversity, changes in species composition, the effects of management and fragmentation, and the exogenous effects of changes in air quality. Health, as a concept in forestry is only beginning to be understood. On the surface, our tendency is to view the health of the forest from an organismic viewpoint. But forests exist as complex communities, constantly changing, and constantly being affected by what happens within the environment within which they too exist.

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## CHARACTERISTICS AND DYNAMICS OF AN UPLAND MISSOURI OLD-GROWTH FOREST

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**Abstract:** We describe the structure, composition, and dynamics of Schnabel Woods, an 80-acre mixed mesophytic old-growth stand located in the loess-covered River Hills adjoining the Missouri River floodplain in central Missouri. In 1982 all trees on a 1.5-ac northwest-facing plot and a 1.5-ac southeast-facing plot were mapped and measured. In 1992 we remeasured those plots to observe current conditions and changes in species composition and stand structure over time. In 1992 density was 381 trees/acre, basal area was 124 ft<sup>2</sup>/ac, and the mean dbh was 5.2 in (for trees  $\geq$  0.8 in dbh). The stand was fully stocked at 101%. Between 1982 and 1992 tree density decreased by 11% while total basal area remained constant. However, basal area did shift among species groups; basal area for northern red oak and white oak increased by 10% while basal area for other species groups remained the same or decreased. The volume of down wood with a minimum diameter  $\geq$  4 in averaged 338 ft<sup>3</sup>/ac over both plots. Litter dry weight averaged 4.9 tons/ac and was significantly greater on the southeast than the northwest aspect. Northern red oak dominated the overstory, but maple dominated the understory and comprised 67% of the ingrowth. Current dynamics are driven by fine-scale treefall gaps, where maples are replacing oaks.

### INTRODUCTION

Schnabel Woods is one of the few remaining remnant old-growth tracts in the loess-covered River Hills of Boone County, within Missouri's Ozark Border Natural Division (Thom and Wilson 1980). Less than 0.07% of the original old-growth forest in the central hardwoods region remains (Parker 1989), and in Missouri only 0.05% of the existing forest is classified as old-growth (Shifley 1994). Remnant old-growth tracts such as Schnabel Woods are of interest because they are rare, but more importantly they provide the best available information about probable long-term patterns of development and succession in the surrounding second-growth forests. To the extent that silvicultural practices resemble gap dynamics, old-growth can also reveal successional tendencies in managed stands (Abrams and Scott 1989). Moreover, old-growth forests are at one end of the spectrum of forest development. As such they provide an ecological frame of reference from which to quantitatively evaluate the current structure, composition, diversity, and dynamics of second-growth forests.

Schnabel Woods was first studied by Kucera and McDermott (1955) who reported that dominant white oaks<sup>5</sup> averaged 165 years old with dbhs (diameter at breast height) between 27 and 31 in. The species with the highest importance values were sugar maple, northern red oak, and basswood. At that time they noted that the tract was "representative of the original forest" and Kucera (personal communication, Nov. 94) found no evidence of significant anthropogenic disturbance at the time of his study.

Since Boone County was first surveyed in 1816-17, the species composition of Schnabel Woods appears to have gradually shifted from predominantly oak to predominantly maple. Wuenschel and Valiunas's (1967) study of

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<sup>5</sup>Scientific names of all species are given in Table 4.

surveyor records for the River Hills of Boone County indicates that in the first quarter of the 19th century, the importance value of white oak exceeded that of sugar maple. Similarly, Howell and Kucera's (1956) study of surveyor records for Boone County, Missouri, showed that 58% of the witness trees in the original land surveys were *Quercus* spp., primarily white oak and bur oak (39% and 16%, respectively). By 1955, Kucera and McDermott (1955) reported that the importance value of sugar maple was almost twice that of red oak. Species with lower shade tolerance followed in importance ranking: *Tilia americana*, *Ulmus* spp., *Fraxinus* spp., and *Quercus* spp. The transition from an oak-dominated forest to one with more shade tolerant species, particularly sugar maple, is consistent with findings for numerous other mesic mature and old-growth remnants in the central hardwood region (e.g., Nigh and others 1985, Schlesinger 1989, Shotola and others 1992, Wuenscher 1967, Lindsey 1962, Parker and Leopold 1983, McGee 1984, Barton and Schmelz 1987).

In this paper we describe the current structure, composition, growth, and mortality at Schnabel Woods. We compare the structure and composition of a northwest-facing and southeast-facing aspect in Schnabel Woods and we examine the dynamics over a ten-year interval. In addition, we compare our findings with Kucera and McDermott's (1955) compositional study.

## METHODS

### Study Area

Schnabel Woods is located approximately 2.5 miles southeast of McBaine in Boone County, Missouri (Figure 1). The 80-acre tract sits in the River Hills immediately east of and above the Missouri River floodplain. The deep Menfro loess soils are capable of supporting rich mesic upland forest and diverse ephemeral ground flora (Kucera and McDermott 1955). With the exception of this tract, the surrounding area has been extensively cut over, grazed, and/or farmed. During the 1940s light selective logging of some high quality timber took place in or around Schnabel Woods (Tom Douglas<sup>6</sup>, personal communication, 1994). In 1954 the tract was deeded to the University of Missouri as an arboretum

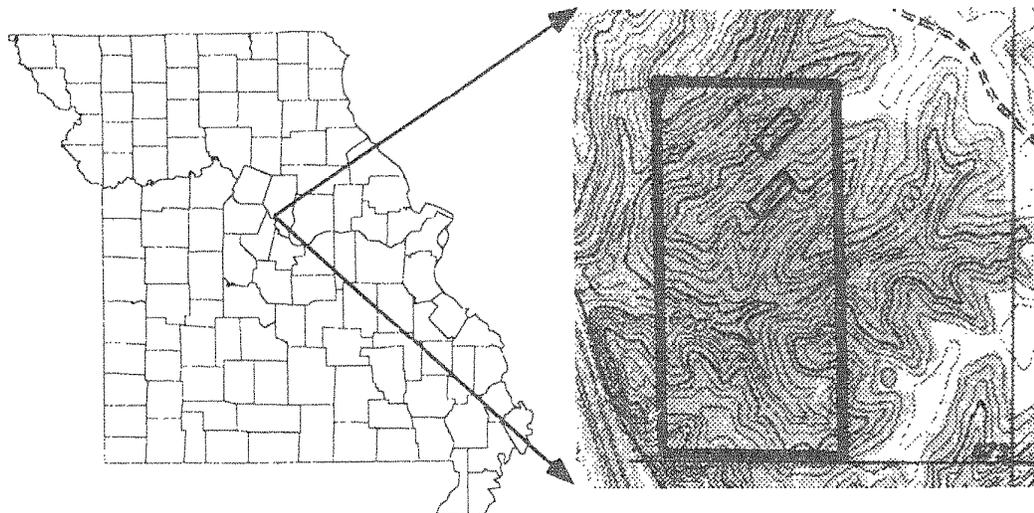


Figure 1. Boundary of Schnabel Woods showing approximate plot locations, Boone County, Missouri. Schnabel Woods legal description is W ½, SE ¼, Sect. 7, T48N, R13W.

<sup>6</sup>Tom Douglas owns the farm adjacent to Schnabel Woods and is a long-term resident of the area.

and demonstration woods. Since acquisition by the University of Missouri, no active vegetative management has occurred. In 1978 the tract was designated a state natural area. Three small fires have been documented as well as a few brief incidents of grazing by stray cattle from the surrounding pastures.

#### Field Procedure

In 1982 Chaplin and students mapped all live trees  $\geq 0.8$ -in (2.0-cm)<sup>7</sup> dbh in two 1.5-ac (0.6-ha) plots. To compare the current composition and structure of two separate aspects, one plot was located on the major northwest-facing slope in the tract; the other plot was placed on the opposite southeast-facing slope on the same ridge (Figure 1). The plots have a vertical relief of approximately 100 ft and a slope of approximately 35%. Although placement of plots was not random, we believe these plots are representative of Schnabel Woods.

Species and dbh were recorded for each live tree  $\geq 0.8$ -in dbh. Stem maps for each plot were created by subdividing each plot into sixty 0.025-ac (100-m<sup>2</sup>) square subplots and recording the Cartesian coordinates of each tree within its respective subplot. In 1992 we relocated the plots and measured dbh, crown class (dominant, codominant, intermediate, overtopped), crown ratio percent, and status (live, dead, ingrowth) for each tree  $\geq 0.8$  in dbh. On every second subplot (half the total sample area) the number of cavities in each individual tree was recorded by minimum opening size (1-2, 2-4, or 4+ in; 2-5, 5-10, or 10+-cm). Ingrowth during the ten-year period was defined as any live tree ( $\geq 0.8$  in) present in 1992 that was not recorded in 1982. In 1992 down woody material  $\geq 4$ -in (10 cm) in diameter was recorded by length and midpoint diameter on the main plots. Volume of each piece of down wood was computed as the volume of a cylinder, and each piece was classified into one of five decay stages following the classification system of Maser and others (1979). Within each main plot, forest floor litter was collected from four systematically established locations. Each litter sample totaled 10.8 ft<sup>2</sup> (1.0-m<sup>2</sup>) in area, and was collected as the composite of eight 1.4-ft<sup>2</sup> (0.125-m<sup>2</sup>) subplots. At four of the litter subplots, soil was collected to a depth of 20 cm and sent to an independent lab for organic matter determination. In 1982 soil samples were also collected and analyzed for percent organic matter by the weight loss on combustion method.

#### Analysis

Density (i.e. number of trees per unit area), basal area, and stocking were calculated for each tree and summed to obtain plot means or class summaries. Stocking was computed using the tree area ratio equations of Gingrich (1967) and Stout and others (1987). Trees were grouped into 2-in (5-cm) dbh classes to observe and compare dbh frequency distributions. Species groups (Table 1) were created to clarify trends for those species which were relatively rare. Contingency table analysis (chi-square test) was used to test for differences in the diameter distributions and species groups distributions between aspects. Student's t-test was used to test for differences in dry litter weight between aspects. Spatial patterns were tested using Ripley's K(t) or K12(t) (Diggle 1981, Ripley 1977). The K(t) function uses distances between mapped objects (e.g. trees) to measure the degree of clumping (attraction), regularity (repulsion), or randomness (independence) among individuals.

## RESULTS

#### Structure

In 1992 the average density of live tree and shrub stems  $\geq 0.8$  in dbh across both plots was 381 trees/ac (942/ha). At 452 trees/ac (1116 /ha), density on the southeast aspect was 50% greater than that observed on the northwest aspect. However, the basal area on the southeast aspect was 10 ft<sup>2</sup>/ac (2 m<sup>2</sup>/ha) less than on the northwest aspect (Table 2).

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<sup>7</sup>A full set of metric equivalents is given following Literature Cited.

Table 1. Species groups used to classify trees at Schnabel Woods.

Species Group	Included species
Ash	<i>Fraxinus americana</i> , <i>F. quadrangulata</i> , <i>F. pennsylvanica</i>
Maple	<i>Acer saccharum</i> , <i>A. nigrum</i>
Red oak	<i>Quercus rubra</i> , <i>Q. shumardii</i>
White oak	<i>Q. alba</i> , <i>Q. muehlenbergii</i>
Hickory	<i>Carya laciniata</i> , <i>C. texana</i> , <i>C. cordiformis</i>
Elm	<i>Ulmus rubra</i> , <i>U. americana</i>
Basswood	<i>Tilia americana</i>
Understory	<i>Cornus florida</i> , <i>Ostrya virginiana</i> , <i>Asimina triloba</i> , <i>Cercis canadensis</i>
Mesic	<i>Juglans nigra</i> , <i>Celtis</i> spp., <i>Gymnocladus dioica</i>

Table 2. Summary of mean stand characteristics observed at Schnabel Woods, 1982-1992.

Characteristic	Live trees (trees/ac)	Live basal area (ft <sup>2</sup> /ac)	Mean dbh (in)	Stocking %	Standing dead basal area (ft <sup>2</sup> /ac)
1982 Total					
Combined	452	124	4.6	102	--
NW	367	124	5.3	103	--
SE	539	123	4.2	101	--
1992 Total					
Combined	381	124	5.2	101	9.37
NW	310	129	6.0	104	6.32
SE	452	119	4.6	97	12.4
Net change 1982-1992					
Combined	-71	0	0.6	-1	
NW	-57	5	0.7	1	--
SE	-87	-4	0.4	-4	--
Relative change 1982-1992					
Combined	-16%	0%	13%	-1%	--
NW	-15%	4%	13%	1%	--
SE	-16%	-3%	10%	-4%	--

The combined diameter distribution for both aspects has a reverse J-shape (Figure 2) and 86% of the trees are < 10 in (25 cm) dbh. Interestingly, the shapes of the diameter distributions for live and dead trees are very similar, but there is a 10-fold difference in densities. This is consistent with observations for other old-growth sites in Missouri (Shifley and others 1995).

Diameter distributions were significantly different on the two aspects (chi-square,  $p = 0.004$ , 15 d.f.). (Figure 3). The southeast aspect had almost twice as many stems < 10-in dbh than the northwest aspect.

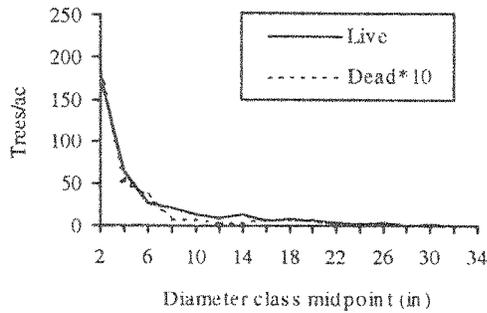


Figure 2. Number of live and dead (scaled by a factor of 10) trees/ac in 2-in dbh classes at Schnabel Woods, 1992.

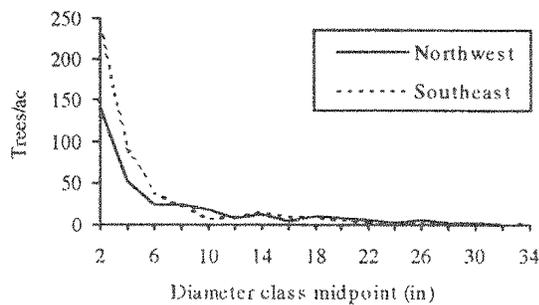


Figure 3. Number of live trees/ac by aspect in 2-in dbh classes at Schnabel Woods, 1992.

Five percent of the standing trees (live or dead) had natural or excavated cavities. The probability of a tree of a given dbh having one or more cavities increased linearly from 8% for a 4-in (10-cm) dbh tree to 30% for a 30-in dbh tree.

Down wood  $\geq 4$  in dbh on the two plots averaged 563 ft<sup>3</sup>/ac. Most of this volume was in the intermediate decomposition class (Table 3). The number of pieces decreased exponentially with increasing volume per piece (Figure 4). The largest piece of down wood we observed had a volume of 88 ft<sup>3</sup>. There were relatively few pieces shorter than 3 ft.

Table 3. Volume of down wood  $\geq 4$  in diameter at Schnabel Woods, 1992. Decomposition classes follow Maser and others (1979).

Decomposition class	Defining characteristics	Volume (ft <sup>3</sup> /ac)
Class 1	Round log, bark intact, small twigs present, log elevated on support points	0
Class 2	Round log, bark intact, twigs absent, log elevated on support points	130
Class 3	Round log, traces of bark, twigs absent, log sagging near ground	286
Class 4	Round to oval log, bark absent, twigs absent, log entirely on ground	101
Class 5	Oval log, bark absent, twigs absent, log entirely on ground	46
Total		563

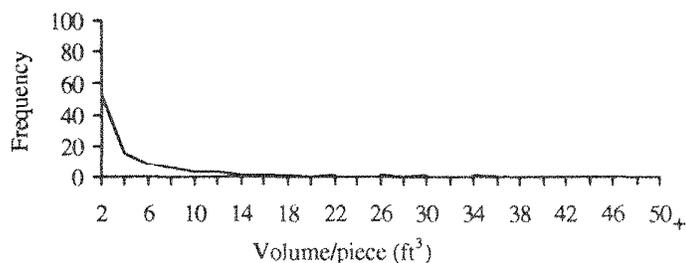


Figure 4. Frequency of down dead wood by volume (ft<sup>3</sup>) class midpoint for Schnabel Woods, 1992. Note that graph stops at 50 ft<sup>3</sup> but the largest piece was 89 ft<sup>3</sup>.

Soil organic matter averaged 8.6% in 1982 and 8.5% in 1992. No difference was observed between measurement intervals (t-test,  $p=.47$ , 20 d.f.), between aspects in 1982 (t-test,  $p=.47$ , 4 d.f.), or between aspects in 1992 (t-test,  $p=.25$ , 14 d.f.).

Dry weight of litter on the forest floor averaged 4.9 tons/ac (1.1 metric tons/ha). The mean mass of litter was significantly greater on the southeast (5.6 tons/ac) than the northwest plot (4.2 tons/ac) (t-test,  $p = 0.002$ , 6 d.f.).

#### Species Composition

Twenty-two tree species were observed at Schnabel Woods in 1992: 19 on the northwest aspect and 17 on the southeast aspect (Table 4). Eight species on the northwest aspect and ten on the southeast aspect had fewer than five stems. In addition, three vine species were observed on both aspects.

Sugar maple was by far the most common species on both aspects at Schnabel Woods, comprising 74% of the trees and 35% of the basal area (Table 4). In terms of importance value, northern red oak was the second most dominant species. The magnitude of the difference between a species' relative basal area and relative density (Table 4) gives some indication of that species' relative size structure. For example, the relative basal area for northern red oak is approximately 10 times its relative density, while sugar maple has a relative basal area that is half of its relative density. This indicates that northern red oaks are, on average, substantially larger in diameter than sugar maples. Dominance of northern red oak in the overstory and sugar maple in the understory is clearly illustrated by Figure 5, which shows the relative basal area by crown class. Maples comprise over 80% of the basal area at lower crown positions but < 20% in the dominant crown class. Northern red oak accounts for 64% of the basal area in the dominant crown class but is absent in the overtopped crown class. Differences among species by aspect were most notable in the smaller size classes. Maple comprised 93% of trees  $\leq 10$  in dbh on the southeast aspect, but only 67% of the trees on the northwest aspect (Table 5). The understory species group (*Cornus florida*, *Ostrya virginiana*, *Asimina triloba*, and *Cercis canadensis*) comprised an additional 19% of the stems  $\leq 10$  in dbh on the northwest aspect.

Compared to importance values reported for Schnabel Woods nearly 30 years earlier by Kucera and McDermott (1955), the importance of sugar maple increased by 20%, primarily at the expense of basswood (Table 4). However, given that the field sample by Kucera and McDermott did not necessarily coincide with our sample site, there is some ambiguity associated with interpreting such differences.

Table 4. Importance percentages for Schnabel Woods, northwest and southeast aspects combined.

Species	Aspect where spp. occurs	1992		1955	
		Relative density	Relative basal area	Importance value	Importance value <sup>a</sup>
Sugar maple ( <i>Acer saccharum</i> )	NW, SE	74.2	35.1	54.7	35
Northern red oak ( <i>Quercus rubra</i> )	NW, SE	2.9	27.3	15.1	19
Chinquapin oak ( <i>Quercus muehlenbergii</i> )	NW, SE	3.3	11.4	7.3	6
American basswood ( <i>Tilia americana</i> )	NW, SE	1.9	5.9	3.9	18
White oak ( <i>Quercus alba</i> )	NW, SE	0.9	5.2	3.0	0
Slippery or red elm ( <i>Ulmus rubra</i> )	NW, SE	2.8	2.1	2.5	0
White ash ( <i>Fraxinus americana</i> )	NW, SE	1.8	3.1	2.4	0
Black maple ( <i>Acer nigrum</i> )	NW	1.5	2.3	1.9	0
Flowering dogwood ( <i>Cornus florida</i> )	NW	3.5	0.3	1.9	4
Shagbark hickory ( <i>Carya texana</i> )	NW, SE	1.1	1.7	1.4	0
Eastern hophornbeam ( <i>Ostrya virginiana</i> )	NW, SE	2.6	0.2	1.4	4
Green ash ( <i>Fraxinus pennsylvanica</i> )	NW, SE	0.5	1.9	1.2	4
American elm ( <i>Ulmus americana</i> )	NW, SE	0.8	1.0	0.9	6
Kentucky coffeetree ( <i>Gymnocladus dioica</i> )	NW, SE	0.4	0.7	0.6	0
Shellbark hickory ( <i>Carya laciniosa</i> )	SE	0.2	0.6	0.4	0
Pawpaw ( <i>Asimina triloba</i> )	NW	0.7	0.0	0.4	0
Shumard oak ( <i>Quercus shumardii</i> )	SE	0.1	0.6	0.3	0
Hackberry ( <i>Celtis</i> spp.)	NW, SE	0.4	0.3	0.3	0
Black walnut ( <i>Juglans nigra</i> )	NW	0.2	0.3	0.3	0
Blue ash ( <i>Fraxinus quadrangulata</i> )	NW, SE	0.2	<0.1	0.1	0
Eastern redbud ( <i>Cercis canadensis</i> )	SE	0.1	<0.1	0.1	0
Bitternut hickory ( <i>Carya cordiformis</i> )	NW	0.1	<0.1	<0.1	4

Importance value are computed as {(relative density + relative basal area)/2}.

<sup>a</sup>Adapted from Kucera and McDermott (1955)

Table 5. Relative density of live trees < 10 in dbh in each species group by aspect.

Group	Northwest	Southeast
Maple	67.4	93.2
Understory	19.0	0.7
Elm	7.9	1.0
Ash	2.6	1.0
Mesic	1.3	0.5
White oak	0.8	1.7
Hickory	0.5	1.2
Basswood	0.5	0.7

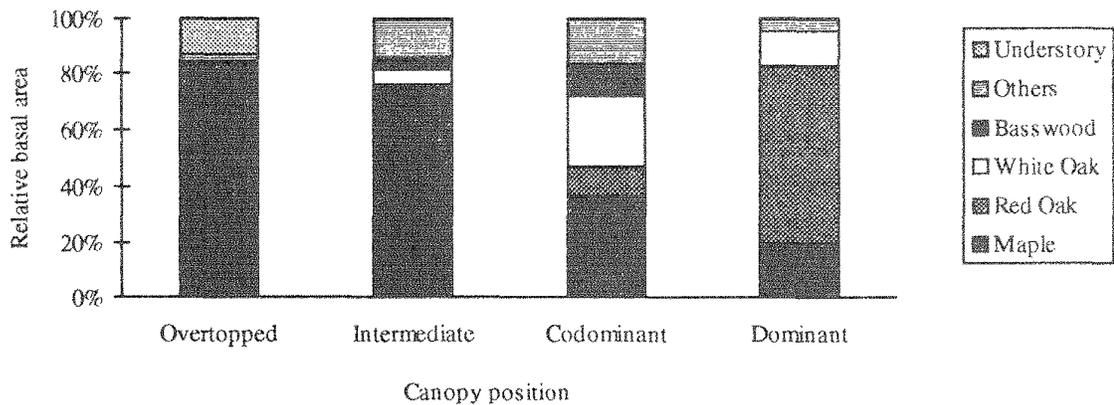


Figure 5. Relative basal area by canopy position at Schnabel in 1992. Note that "others" includes the hickory, ash, elm, and mesic species groups.

The number of trees by species group was significantly different between the two aspects (chi-square test,  $p \leq 0.001$ , 8 d.f.). Overall, more trees in the ash, elm, red oak, and understory species groups were found on the northwest aspect while maple and white oak species groups were more prevalent on the southeast aspect. Basswood had approximately the same number of stems on both aspects. Interestingly, only 4 stems (0.7 trees/ac) consisting of two species (eastern hophornbeam (3) and redbud (1)) were observed in the understory group on the southeast aspect while 73 stems (49 trees/ac) consisting of three species (flowering dogwood (39), eastern hophornbeam (26) and pawpaw (8)) were on the northwest side.

#### Forest Dynamics (1982-1992)

Basal area and stocking remained virtually unchanged over the ten-year period at 124 ft<sup>2</sup>/ac and 101%, respectively (Table 2). However, the density of live trees decreased by 16%, from 452 to 381 trees/ac. There were shifts in the relative importance of species. Although basal area remained constant, the basal area of the oak species groups increased by 10% while the remaining species groups either decreased or did not change (Figure 6).

Individual-tree diameter growth rates varied considerably among species and by crown class for a given species (Table 6). Dominant and codominant trees grew at least twice as fast as intermediate and overtopped trees for all species. The majority of northern red oaks were dominants or codominants; whereas, the majority of sugar maples were overtopped or intermediate.

Mortality rates were lowest for the oaks and maples and highest for the understory species (Table 7). The low mortality rate for maple is consistent with its high shade tolerance and ability to persist for long periods in a suppressed state. The relatively low mortality rate for oaks can be partially attributed to their exclusive position in dominant or codominant canopy classes. However, we have observed numerous northern red oak treefalls outside the plots, suggesting that overall mortality rates for northern red oaks across the entire tract may be higher than observed in our study area. We performed a brief "pilot study" and censused 56 gaps in a 20-ac 8-ha block encompassing the plots, and maples dominated the midstory in 82% (46) of these gaps. Due to few observations, meaningful mortality rates could not be calculated for individual crown classes. The high annual mortality rate for the understory species group reflects its characteristic high turnover rate as these trees struggle to maintain a foothold in the lower canopy strata. Spatial analysis showed that dead trees were randomly distributed throughout all distance classes (Ripley's  $K(t)$ ,  $p > 0.05$ ) on both aspects.

Table 6. Tree diameter growth (inches per decade) by species and crown class at Schnabel Woods, 1982 to 1992.

Species group	Crown class				Average of all crown classes
	Overtopped	Intermediate	Codominant	Dominant	
Northern red oak	--	--	1.3	1.9	1.7
Basswood	0.0	0.5	1.2	--	1.0
Mesic	--	0.6	1.5	0.7	1.0
White oak	0.1	0.4	1.1	1.3	1.0
Elm	0.8	0.6	1.5	--	0.9
Ash	0.2	0.6	1.1	1.7	0.9
Maple	0.2	0.4	0.8	0.9	0.4
Hickory	0.0	0.2	0.8	0.0	0.4
Understory	0.2	0.7	0.0	0.0	0.2
Average	0.2	0.4	1.1	1.5	0.5

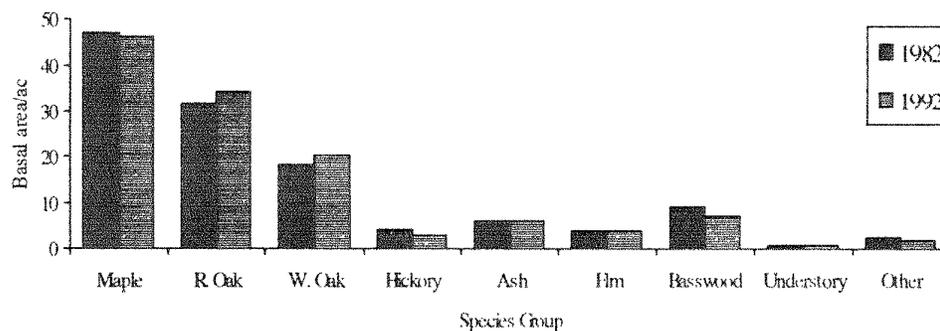


Figure 6. Basal area by species group in 1982 and 1992.

Table 7. Annual mortality rate by species group at Schnabel Woods during the 1982-1992 interval.

Species group	Annual mortality rate (%)
Understory	6.3
Basswood	6.0
Hickory	5.7
Ash	5.4
Elm	5.1
Mesic	5.0
Maple	2.3
Northern red oak	1.4
White oak	1.0
Average	2.8

Ingrowth (trees crossing the 0.8-inch dbh threshold) over the remeasurement interval consisted of 83 trees/ac and 1 ft<sup>2</sup>/ac of basal area. Ingrowth trees were primarily sugar maple (67%), dogwood (8%), slippery elm (7%), hophornbeam (6%), and pawpaw (5%). Of these species, only maple and elm are capable of becoming part of the overstory, and elm usually succumbs to Dutch elm disease before becoming established as a dominant tree. A single chinquapin oak was the only oak ingrowth observed for the 10-year period.

Small maples, including ingrowth, were highly clumped on both aspects (Ripley's  $K(t)$ ,  $p < 0.05$ ), but there was no strong spatial association (Ripley's  $K12(t)$ ,  $p > 0.05$ ) with overstory trees of any species. There was a tendency for small maples (< 2.0 in dbh) to be clumped under large oaks (> 10 in dbh); however, it was only statistically significant on the northwest aspect. In contrast, small maples tended to be negatively associated with large maples (> 10 in dbh), but again, this was not significant.

## DISCUSSION

The differences observed between aspects at Schnabel Woods were substantial, and greater than we would have expected prior to conducting the inventory. Although northeast- and southwest-facing slopes present large differences in environmental conditions, northwest- and southeast-facing slopes are generally expected to present more moderate or neutral environmental conditions (Hartung and Lloyd 1969). The southeast slope at Schnabel Woods had 170 more trees/ac than the northwest slope, but the basal area was 10 ft<sup>2</sup>/ac less and the mean dbh was 1.4 in less on the southeast slope than on the northwest slope. This pattern is generally indicative of lower site quality and corresponding slower development. A further indication of site quality differences is the mass of forest floor litter which was 38% higher on the southeast slope. The lower value on the northwest slope is indicative of more mesic conditions and a higher rate of litter decomposition.

Large volumes of standing dead and down wood are often associated with old-growth forests (e.g. Parker 1989, Martin 1992). The 10-to-1 ratio of live to dead trees at Schnabel Woods is a phenomenon that has been observed in other old-growth and mature second-growth forests (Shifley and others 1995). At 563 ft<sup>3</sup>/ac, total volume of down wood was 90 ft<sup>3</sup>/ac greater than observed at two xeric old-growth sites in southern Missouri (Shifley and others 1995), but well below the 683 ft<sup>3</sup>/ac (for logs > 7.9 in in diameter) observed by Mueller and Liu (1991) for a mixed mesophytic old-growth forest in Kentucky. The volume of down wood at Schnabel Woods was more than twice that observed for a second-growth oak-hickory forest in southern Missouri (Shifley and others 1995).

While the total basal area and stocking at Schnabel Woods have remained constant over the last decade, this old-growth forest is changing in many ways. The dominant trees, red oaks in particular, continue to increase in size at the expense of trees in the lower canopy strata. Approximately 3% of the total number of trees die each year, but this mortality is offset by growth on surviving trees and by annual ingrowth which amounts to approximately 2% of the number of live stems. The conspicuous absence of oaks in the ingrowth portends a substantial change in the future species composition at Schnabel Woods. This future change in composition is further indicated by the size structure of the species that are present. Red, white, and chinkapin oaks, which currently make up 44% of the basal area, are virtually nonexistent in the lower crown classes. As seen most clearly in Figure 5, red oak is the most abundant species in the dominant crown class, and white oak and sugar maple share the remainder of the class. The codominant crown class is comprised predominantly of trees in the white oak and maple species groups. Over time, we expect the red oaks, which are faster growing and shorter-lived than the white oaks, to die and be replaced by the white oaks and maples currently in the codominant crown class. The white oaks will likely be a significant component of the overstory for a century or more, but in the absence of some dramatically altered disturbance regime, the sugar maples in the intermediate and overtopped crown classes will relentlessly move their way into dominance as individual oaks die. This suggested gradual pattern of increasing maple dominance is consistent with apparent patterns of forest change inferred from early surveyor records and with patterns of change in Schnabel Woods since the earlier inventory of Kucera and McDermott (1955). The oak domination of the Schnabel Woods overstory probably reflects past disturbance regimes (e.g. burning) more than present dynamics, which are driven by fine-scale treefall gaps.

Historically, fires in mixed mesophytic forests were found primarily on ridgetops or other restricted topographic positions (Runkle 1990). A prudent management plan for Schnabel Woods might include a careful reintroduction of fire on ridges to maintain shade intolerant species.

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#### METRIC CONVERSIONS

1 inch = 2.54 cm	1 ft <sup>2</sup> = 0.092903 m <sup>2</sup>	1 ft <sup>3</sup> = 0.028317 m <sup>3</sup>	1 U.S. ton = 0.90718 metric tons
1 foot = 0.3048 m	1 ft <sup>2</sup> /ac = 0.2296 m <sup>2</sup> /ha	1 ft <sup>3</sup> /ac = 0.06997 m <sup>3</sup> /ha	1 U.S. ton/ac = 2.241 metric tons/ha
1 mile = 1.6093 km			

STRUCTURAL AND COMPOSITIONAL DIFFERENCES BETWEEN  
OLD-GROWTH AND MATURE SECOND-GROWTH FORESTS IN THE MISSOURI OZARKS

Stephen R. Shifley<sup>1</sup>, Lynn M. Roovers<sup>2</sup>, and Brian L. Brookshire<sup>3</sup>

Abstract: There are currently only about 7,900 acres (3,200 ha) of remnant old-growth forest in Missouri, but public land management plans call for old-growth acreage to increase to more than 200,000 acres (81,000 ha). To develop a better quantitative understanding of the transitions that are likely as current forests mature to an old-growth state, we compared a number of characteristics measured for two old-growth sites with values for two mature second-growth sites. The stocking and the basal area of both live and dead trees were similar for the old-growth and second-growth forests. The diameter distribution (number of trees by dbh class) for all species combined had a negative exponential (reverse-J) shape that varied little from old-growth to second-growth. However, the old-growth sites consistently had more trees  $\geq 17$  inches (43 cm) dbh than did the second-growth sites. The absolute number of these larger trees was small; 14 per acre (35 per ha) for the old-growth sites compared to 7 per acre (17 per ha) for the mature second-growth sites. The white and red oak species groups dominated the overstories at all sites. Mean volume of down woody debris  $\geq 4$  inches in diameter was  $476 \text{ ft}^3 \cdot \text{ac}^{-1}$  ( $33.3 \text{ m}^3 \cdot \text{ha}^{-1}$ ) on the old-growth sites vs.  $240 \text{ ft}^3 \cdot \text{ac}^{-1}$  ( $16.8 \text{ m}^3 \cdot \text{ha}^{-1}$ ) on the second-growth comparison site.

INTRODUCTION

Old-growth forests currently occupy approximately 7,900 acres (3200 ha) in Missouri, roughly 0.05 percent of the existing forest land in the state (Shifley 1994). Most of these tracts are less than 100 acres (40 ha) and held in some form of protective status. Public land management plans in Missouri call for at least 10 percent of the publicly-owned forested acreage to be managed as old-growth. This will eventually increase the amount of old-growth forest in the state to over 200,000 acres (81,000 ha). These acreages are necessarily rough estimates because there is no precise definition of what conditions constitute an old-growth forest.

Table 1 summarizes characteristics that are typically associated with old-growth forests. While this list is comprehensive, it lacks the quantitative detail to provide a rigorous definition of the old-growth condition. Hence, the acreage of what is called old-growth forest can change when definitions are modified or when different individuals interpret the existing definitions.

Virtually every old-growth tract in Missouri has been subjected to some degree of past anthropogenic disturbance. Fire (pre- and post-European settlement) and limited livestock grazing have affected every old forest in the state. Most Missouri old-growth remnants also have had a few trees selectively harvested during the past century. Despite these disturbances, existing remnant old-growth forests provide the best available information about the likely future development of forests managed for old-growth characteristics.

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Table 1. Characteristics reported in literature to be associated with Midwestern old-growth forests<sup>a</sup>.

Defining characteristics from Meyer (1986)	Defining characteristics from Parker (1989)	Defining characteristics from Martin (1991)
Diverse species distribution for dominant trees. Relatively high percentage of shade tolerant trees.	Tree species richness 20 to 40. Herbaceous species richness 17 to 53. Breeding bird species richness 18 to 33.	High species richness/diversity. Species richness $\geq 20$ canopy trees.
Multi-layered canopy. Wide range in tree height and age.		Uneven-aged with canopy species in several size classes.
Live trees $\geq 14$ inches dbh are $\geq 25\%$ of stocking.		Several large canopy trees.
		Large, high-quality commercially important trees. (indicative of no past harvest)
Dominant trees $\geq 100$ years.	Mean age of overstory 135 to 210 years. Maximum age of overstory 190 to 375 years.	Oldest trees $\geq 200$ years.
	Overstory density approximately 65 to 173 trees $\cdot \text{ac}^{-1}$ ( $\geq 4$ in dbh).	Overstory density approximately 100 trees $\cdot \text{ac}^{-1}$ ( $\geq 4$ in dbh).
	Overstory basal area in the range of 110 - 150 $\text{ft}^2 \cdot \text{ac}^{-1}$ .	Overstory basal area $\geq 90 \text{ft}^2 \cdot \text{ac}^{-1}$ .
Evidence of large tree decadence: broken and dead tops, rot, cavities. Large dead snags and large down logs. Large logs in streams and drainages.	From 8 to 18 snags $\cdot \text{ac}^{-1}$ ( $\geq 4$ in dbh).  Down wood 7 to 11 tons $\cdot \text{ac}^{-1}$ .	Logs and snags present in various sizes and stages of decay.
Variable understory density --from open to dense. Variable degree of herbaceous ground cover.	Gaps are 7-8% of forest, randomly distributed, range 0.012 - 0.09 ac in size.  Annual mortality 0.6-0.9 %.	Treefall gaps formed by windthrow.
		Plant and animals that prefer old-growth.
		Undisturbed soils and soil macropores.
		Little or no evidence of human disturbance.
	Volume 16,000 to 25,000 $\text{bd.ft} \cdot \text{ac}^{-1}$ .	

<sup>a</sup> cm = 2.54(inches), trees  $\cdot \text{ha}^{-1}$  = 2.471(trees  $\cdot \text{ac}^{-1}$ ), basal area  $\text{m}^2 \cdot \text{ha}^{-1}$  = 0.2296(basal area  $\text{ft}^2 \cdot \text{ac}^{-1}$ ),  $\text{Mg} \cdot \text{ha}^{-1}$  = 2.241(tons  $\cdot \text{ac}^{-1}$ )

In this paper we compare and contrast a range of structural and compositional characteristics measured in two remnant old-growth forests with the same characteristics measured in two mature second-growth forests. This work provides new information about similarities between second-growth and old-growth forests. It also identifies some characteristics that differ sufficiently to be useful in judging where a given forest lies along the gradient from second-growth to old-growth.

## STUDY SITES

The two old-growth and two second-growth sites evaluated in this study are shown in Figure 1 and described below.

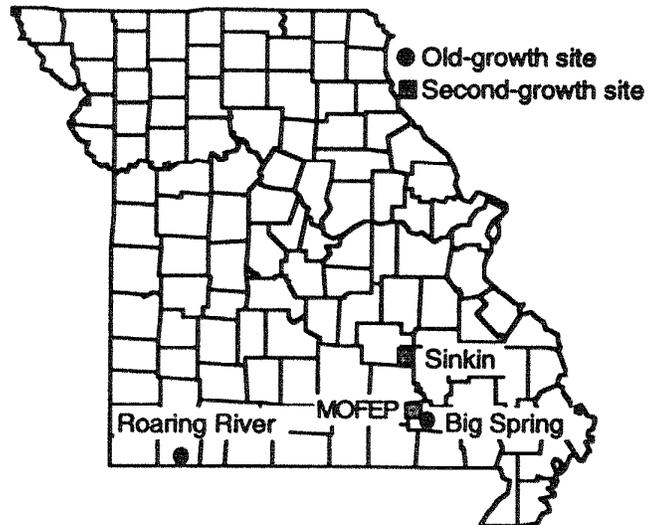


Figure 1. Location of old-growth and second-growth study sites in Missouri.

### Big Spring (old-growth)

The Big Spring site is a 330-acre tract in the Ozark National Scenic Riverway in Carter County. Prior documentation for the site classified the tract as a mixture of old-growth and old second-growth oak and oak-shortleaf pine forest (Nigh and others 1992). Forest associations are xero-mesic to xeric oak-hickory and oak-pine. Our increment cores from 13 dominant and codominant trees showed ages ranging 63 to 141 years. Some trees on the tract exceed 200 years (Nigh and others 1992). There is evidence of past selective logging at a few sites along the ridges and in the bottoms. Elevation at the site ranges from 480 to 820 feet (150 to 250 m) with most slopes ranging from 20 to 40 percent. Soils are very cherty loams and silt loams that are well- to excessively-drained.

### Roaring River (old-growth)

The Roaring River site is a 120-acre old-growth tract in Roaring River State Park in Barry County. A prior dendrochronological study at the site reported white oaks in the 200 to 250 year age class (Stahle and others 1985). Forest associations are principally xeric oak-hickory. With the exception of some past selective logging along the tops of the ridges that border the site, anthropogenic disturbance appears to have been limited to periodic fires that were historically common throughout the Ozarks (Ladd 1991). Elevation ranges from 1260 to 1440 feet (380 to 440 m) with slopes typically ranging from 20 to 70 percent. Most soils are cherty and moderately- to excessively-drained. Some ridgetop soils have a fragipan at approximately 14 inches (35 cm). Available water capacity and fertility are low, and rock outcrops occur at several locations on the site.

### Sinkin Experimental Forest (second-growth)

The 4,100 acre (1660 ha) Sinkin Experimental Forest, located in Dent and Reynolds Counties, was used as a second-growth comparison site. Prior to establishment as an experimental forest in 1950, the tract was treated much like other forests in the area. It was extensively logged for shortleaf pine<sup>4</sup> between 1900 and 1920; grazing and burning were common in the following years. Since 1950 grazing and wildfire have been excluded from the Sinkin. Numerous silvicultural studies have been established on the experimental forest, but the majority of the acreage is well-stocked, second-growth, oak-hickory and oak-pine forest in the 70- to 90-year age class. Elevation ranges from 1000 to 1350 feet (300 to 410 m) with slopes typically from 10 to 35 percent. Soils are cherty loams and cherty silt-loams. For this study, we excluded areas that had been harvested since 1950.

### MOFEP (second-growth)

MOFEP, the Missouri Forest Ecosystem Project is a large-scale study of the impacts of silvicultural treatments on an array of ecosystem attributes (Brookshire and Hauser 1993). The MOFEP study includes 9 large, contiguous experimental tracts or compartments. We used the 3 compartments in the Peck Ranch Wildlife Area (MOFEP compartments 7, 8, and 9 in Carter County) as second-growth comparison sites. These three compartments range in size from 825 to 1240 acres (334 to 502 ha), lie in a single township, are the closest ones to the Big Spring old-growth site, and generally have been excluded from harvest for longer than the other MOFEP sites (approximately 40 years). All utilized data were collected prior to implementation of experimental treatments planned for the sites. With the exception of the exclusion of harvesting, these mature second-growth oak-hickory forests are fairly typical of Ozark forest sites. More than ninety percent of the MOFEP comparison plots were on ecological land types (ELTs) that support dry to xeric chert or limestone forest similar to the old-growth sites. Soils on the MOFEP sites are generally well- to excessively-drained and cherty. Site conditions for MOFEP compartments 7, 8, 9 are described in great detail by Brookshire and Hauser (1993).

## METHODS

In 1992, thirty 0.25 ac (0.1 ha) circular inventory plots per tract were systematically established at the Big Spring and Roaring River sites. On each main plot all trees  $\geq 4$  inches (10 cm) dbh were inventoried. Trees  $\geq 1$  inch (2.5 cm) and  $< 4$  inches (10 cm) dbh were inventoried on a concentric 0.025 ac (0.01 ha) circular subplot. Species and dbh were recorded for each tree. The number of cavities with smallest dimension  $\geq 0.8$  inch (2 cm) was also recorded for each tree at the Big Spring site and for trees on every second plot at the Roaring River site. The length and mid-point diameter of each piece of down wood with minimum diameter  $\geq 4$  inches (10 cm) was measured on the 0.25 ac (0.1 ha) main plot. Each piece of down wood was classified by decay stage using a system described by Maser and others (1979) for western conifers (Table 2). Volume of each down log was computed as the volume of a cylinder of known length and midpoint diameter. The ground area covered by each down log was computed as the product of its length and diameter.

In 1992-93, nearly identical protocols were used to sample 96 plots systematically distributed across the Sinkin Experimental Forest. The only deviation was that cavities were not measured. Of the 96 plots on the Sinkin, 73 were utilized in this comparison. The remaining 23 were excluded because they fell in areas that had been subjected to harvest or other disturbance since the experimental forest was established in 1950.

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<sup>4</sup>Scientific names for all species are given in Table 4.

Table 2. Decomposition classes used to classify down logs. From Maser and others (1979).

Decomposition Class	Defining characteristics
Class 1	Round log, bark intact, small twigs present, log elevated on support points
Class 2	Round log, bark intact, twigs absent, log elevated on support points
Class 3	Round log, traces of bark, twigs absent, log sagging near ground
Class 4	Round to oval log, bark absent, twigs absent, log entirely on ground
Class 5	Oval log, bark absent, twigs absent, log entirely on ground

The MOFEP sites were sampled with a total of 210 plots during 1990-91. Plot location was random subject to the constraint that at least one plot had to fall in each identified forest stand. The 0.5 ac (0.2 ha) circular main plots were used to sample trees  $\geq 4.5$  inches (11.4 cm) dbh. Trees  $\geq 1.5$  inches (3.8 cm) and  $< 4.5$  inches (11.4 cm) dbh were sampled on four circular 0.05 ac (0.02 ha) subplots. The MOFEP samples included species and dbh for each tree. Percent of the ground covered by down wood  $\geq 2$  inches (5 cm) in diameter on the MOFEP sites was sampled along four 56.5-foot (17.3 m) transects originating at plot center and oriented along the cardinal directions. Percent cover was computed as the percent of the transect length actually covered by down logs larger than the 2-inch (5 cm) size threshold.

Per acre values for each characteristic were computed by plot and summarized to obtain means and variances for each tract. Stocking percent was computed from the tree area ratio equations of Gingrich (1967), Rogers (1983), and Stout and others (1987). Importance values for each tract (all plots combined) were computed as  $[0.5(\text{relative number of trees} + \text{relative basal area})]$ . Two types of statistical comparisons were made among characteristics observed at the study sites. The first test was a one-way analysis of variance by site for the 4 sites with all plots per site used in the comparison ( $n = 343$ ). The null hypothesis is that the characteristic of interest (e.g. basal area, number of trees, etc.) is equal on all sites. Although this is an appropriate test for differences among the specific sites, the procedure introduces the problem of pseudoreplication (Hurlbert 1984) if multiple observations per tract are used to make inferences concerning the more general comparison of old-growth vs. second-growth sites. A more appropriate and more conservative comparison of old-growth and second-growth forest characteristics can be made by using a t-test to evaluate the null hypothesis that the means observed for the two old-growth sites were equal to those for the two second-growth sites ( $n=4$ ). Whenever possible, this second statistical test was also performed and reported.

## RESULTS

### Structural Characteristics

The most notable trend that emerges from a comparison of composite stand characteristics for the old-growth and mature second-growth forests is the similarity across all sites. (Table 3). Although the MOFEP site had substantially fewer trees per acre than the other sites, the MOFEP sampling scheme excluded live trees between 1 and 1.5 inches (2.5 and 3.8 cm) dbh. Observations on the Sinkin indicate that live trees between 1 and 1.5 inches (2.5 and 3.8 cm) dbh would add approximately  $150 \text{ trees} \cdot \text{ac}^{-1}$  ( $350 \text{ trees} \cdot \text{ha}^{-1}$ ) and  $1.3 \text{ ft}^2 \cdot \text{ac}^{-1}$  ( $0.3 \text{ m}^2 \cdot \text{ha}^{-1}$ ) of basal area to the MOFEP means. This addition would bring the mean number of trees  $\cdot \text{ac}^{-1}$  on the MOFEP sites in line with the observed values for the other sites, although the mean basal area would still be somewhat lower.

Table 3. Comparison of composite stand characteristics for old-growth (Big Spring and Roaring River) and second-growth (Sinkin and MOFEP) study areas. Values in parentheses are standard deviations for values by plot at that site. Values are for trees  $\geq 1$  inch (2.5 cm) dbh except as noted<sup>a</sup>.

Site	Sample size	Live trees number*ac <sup>-1</sup>	Live basal area ft <sup>2</sup> *ac <sup>-1</sup>	Stocking percent	Dead trees number*ac <sup>-1</sup>	Dead basal area ft <sup>2</sup> *ac <sup>-1</sup>
Big Spring	30	582 (209)	104 (12)	88 (12)	68 (44)	8.3 (6.3)
Roaring River	30	623 (191)	108 (23)	96 (18)	77 (57)	12.5 (8.4)
Sinkin	73	675 (297)	102 (21)	91 (17)	90 (86)	9.1 (6.9)
MOFEP <sup>b</sup>	210	439 (161)	90 (13)	82 ( 9)	15 (11)	7.4 (5.8)

<sup>a</sup> Trees\*ha<sup>-1</sup> = 2.471(trees\*ac<sup>-1</sup>); basal area m<sup>2</sup>\*ha<sup>-1</sup> = 0.2296(basal area ft<sup>2</sup>\*ac<sup>-1</sup>).

<sup>b</sup> MOFEP data includes only live trees  $\geq 1.5$  inches dbh and only standing dead trees  $\geq 4.5$  inches dbh.

One-way ANOVA using all plots to test for differences among the 4 sites showed significant differences in the mean number ( $p < 0.001$ , 339 d.f.), basal area ( $p < 0.001$ , 339 d.f.), and stocking percent ( $p < 0.001$ , 339 d.f.) for live trees per acre. However, the differences did not follow patterns that could be used to readily distinguish the old-growth sites from the second growth sites. MOFEP means were uniformly smaller than the other three sites which were statistically indistinguishable from one another (Tukey-Kramer HSD,  $\alpha = 0.05$ ) for all three dependent variables. Adjusting for trees between 1 and 1.5 inches (2.5 and 3.8 cm) dbh that were excluded from the MOFEP sampling, eliminates the significant difference among sites in the number of live trees per acre.

The number of standing dead trees per acre was also significantly different among sites (one-way ANOVA by site,  $p < 0.001$ , 339 d.f.) with the MOFEP mean smaller than the other three sites (Tukey-Kramer HSD,  $\alpha = 0.05$ ). Again this was at least partially due to sampling procedural differences at the MOFEP site. Basal area of standing dead trees followed a somewhat different pattern. Means were significantly different among sites (one-way ANOVA by site,  $p < 0.001$ , 339 d.f.), but in this case the Big Spring and MOFEP means were significantly larger than the Roaring River and Sinkin sites (Tukey-Kramer HSD,  $\alpha = 0.05$ ).

A comparison of the means of the two old-growth sites with that of the two second-growth sites showed no significant differences in the number, basal area, or stocking of live trees, nor for the number or basal area of standing dead trees (2 d.f. with  $p$ -values of 0.74, 0.25, 0.46, 0.65, and 0.44, respectively). Nor were the mean differences of sufficient magnitude to generally be considered of practical importance, statistical tests notwithstanding.

At first glance, a comparison of the number of live trees by diameter class also shows little difference among the old-growth and second-growth sites (Figure 2A). At all sites the diameter distribution (based on all tree species) had a negative exponential shape commonly associated with uneven-aged forests. The greatest absolute difference in the diameter distributions occurred for trees in the 2-inch (5 cm) dbh class. The MOFEP site had fewer trees of this size than the other three sites, due primarily to the fact that trees  $< 1.5$  inches (3.8 cm) were not included in the MOFEP sample. The greatest *relative* difference in the number of trees per acre, however, occurred for trees larger than 8 inches (20 cm) dbh. That portion of the diameter distribution is redrawn at higher resolution to highlight those differences (Figure 2B).

The second growth sites had 1.5 to 2 times as many trees between 9 and 17 inches (23 and 43 cm) as the old-growth sites, but this relationship shifts for larger diameter classes. On average the old-growth sites had 14 trees per acre (35 trees per ha) larger than 17 inches (43 cm) dbh compared to 7 trees per acre (17 trees per ha) for the second-growth sites. This difference may appear rather minor, but in terms of basal area (rather than the number of trees) these large trees have much greater impact (Figure 2C). A graphic based on tree volume or biomass would further accentuate the influence of the largest diameter trees.

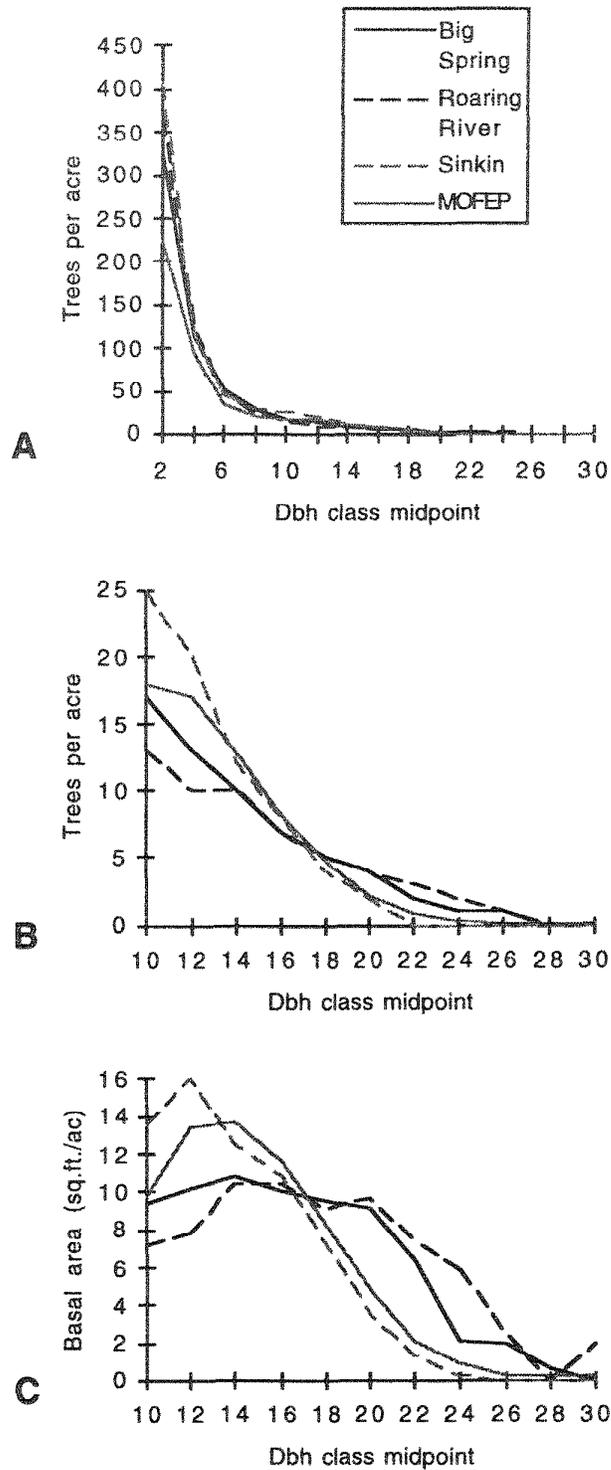


Figure 2. Three views of the diameter distribution (all species) for old-growth and second growth sites showing (A) number of trees  $\geq 1$  inch dbh ( $\geq 1.5$  inches for MOFEP), (B) number of trees  $\geq 9$  inches dbh, and (C) basal area of trees  $\geq 9$  inches dbh.

The functional importance of these relatively few large trees must not be overlooked. One feature that inevitably stands out when walking through an old forest is the large trees, which people tend to notice and recall disproportionate to their low frequency. If humans tend to ascribe high relative importance to large individual trees, other organisms may also do so, either individually or collectively. The largest trees provide the highest and strongest perches. They provide the greatest surface area and volume and the largest cavities. Larger trees are also more likely to have cavities that can be used as nesting sites by wildlife. Observations of cavities by tree size on the Big Spring and Roaring River tracts showed a 15 percent probability of a 10-inch (25 cm) dbh tree having a cavity; that probability increased linearly to over 60 percent for a 25-inch (64-cm) dbh tree.

For all sites the diameter distribution of standing dead trees followed the same general shape as the diameter distribution of live trees, at approximately 10 percent the frequency of live trees. This result was consistent across all sites and might serve as a rule of thumb for the amount and size distribution of dead-standing wood in the maturing oak forests.

### Species Composition

The total number of tree species (tree species richness) was greatest on the Sinkin and MOFEP sites. The number of tree species observed by site was 43, 40, 36, and 33 for Sinkin, MOFEP, Big Spring and Roaring River, respectively. This difference of seven in the tree species richness between the two old-growth and two second-growth sites was near the margin of statistical significance (t-test,  $p = 0.08$ , 2 d.f.) However, the higher species richness values on the second-growth sites were consistent with expectations given the larger sample sizes on those sites. All other factors being equal, the greatest number of species would be expected on these two tracts with the most samples. Because each site had only a single observation for species richness, statistical differences in species richness among all four sites could not be analyzed using one-way ANOVA.

It is informative to compare importance values for species by site. In Table 4, importance values and their ranks are given for all woody species that attained a diameter of at least one inch (2.5 cm) dbh (1.5 inches or 3.8 cm dbh for the MOFEP site). White oak, black oak, scarlet oak and dogwood have high importance values at all sites. Shortleaf pine has a high value at sites other than Roaring River where it did not occur. The high importance value for dogwood is strictly a function of the large number of dogwood stems that are common in the lower canopy strata at these sites. Species importance rank order at a given site does not change if some species or groups of species (e.g. species generally relegated to the understory) are dropped from consideration. Also, the values in Table 4 can be used to compute the importance values for subsets of species.

It is interesting to note that both maple and pawpaw were minor components in these relatively dry old-growth forests. This is in sharp contrast to values reported for more mesic old-growth sites (e.g. Kucera and McDermott 1955, Shotola and others 1992, Wuenscher 1967) where sugar maple is typically more than 20 percent of the total basal area and pawpaw may constitute more than 5 percent of the woody stems in the understory.

Some patterns in forest composition are more easily discerned by examining species groupings by size class. Figure 3 illustrates how the relative importance of various species groups changes with increasing diameter class. Although relatively rare in the smaller diameter classes, the white and red oak groups dominate the overstories at all sites. On the two old-growth sites, the white oaks have greater relative importance in the largest diameter classes than do the red oaks.

Although the composite diameter distribution for all species combined has a negative-exponential shape (as shown in Figure 1), individual species do not necessarily follow that form. For white oak, red oak, and shortleaf pine groups which dominate the overstory at these sites, the composite number of trees by diameter class has a unimodal distribution on all sites (Figure 4). However, on the old-growth sites the peak of the diameter distribution is shifted to the right and the number of trees in the smaller size classes is substantially fewer than observed for the second-growth

Table 4. Importance values and their ranks for woody plants on old-growth (Big Spring and Roaring River) and second-growth (Sinkin and MOFEP) sites. Importance values are computed as  $\{(relative\ number\ of\ trees + relative\ basal\ area)/2\}$  for all live trees sampled. Species are arranged in decreasing rank order for the Big Spring site. Nomenclature follows Little (1953).

Common name	Scientific name	Big Spring		Roaring River		Sinkin		MOFEP	
		IV	Rank	IV	Rank	IV	Rank	IV	Rank
Flowering dogwood	<i>Cornus florida</i>	24.0	1	17.6	2	16.7	2	8.8	4
White oak	<i>Quercus alba</i>	22.5	2	20.8	1	22.7	1	17.9	3
Black oak	<i>Quercus velutina</i>	6.9	3	15.3	3	15.0	3	18.3	2
Scarlet oak	<i>Quercus coccinea</i>	6.5	4	0.4	24	3.9	6	18.8	1
Shortleaf pine	<i>Pinus echinata</i>	5.5	5	<0.1	--	12.9	4	5.9	6
Mockernut hickory	<i>Carya tomentosa</i>	5.3	6	10.8	4	2.3	8	4.5	8
Black hickory	<i>Carya texana</i>	4.4	7	2.2	9	1.5	12	5.1	7
Post oak	<i>Quercus stellata</i>	4.2	8	1.5	11	1.4	14	8.4	5
Blackgum	<i>Nyssa sylvatica</i>	3.8	9	2.3	8	6.4	5	3.0	9
S. red oak	<i>Quercus falcata</i>	2.9	10	<0.1	--	<0.1	--	<0.1	--
N. red oak	<i>Quercus rubra</i>	1.6	11	5.9	6	1.7	10	<0.1	--
Red maple	<i>Acer rubrum</i>	1.6	12	3.0	7	2.1	9	0.8	13
Chinkapin oak	<i>Quercus muehlenbergii</i>	1.2	13	1.1	14	0.8	16	0.4	14
Winged elm	<i>Ulmus alata</i>	0.9	14	0.7	20	0.1	30	0.2	21
Grape	<i>Vitis</i> spp.	0.8	15	1.9	10	<0.1	--	0.2	18
Slippery elm	<i>Ulmus rubra</i>	0.8	16	0.4	23	3.5	7	0.2	19
Serviceberry	<i>Amelanchier</i> spp.	0.7	17	7.4	5	0.1	32	0.1	23
Bitternut hickory	<i>Carya cordiformis</i>	0.7	18	<0.1	35	0.7	17	0.1	26
Pignut hickory	<i>Carya glabra</i>	0.7	19	0.3	26	1.5	11	2.0	11
Sassafras	<i>Sassafras albidum</i>	0.6	20	1.0	15	1.2	15	2.5	10
Buckthorn	<i>Rhamnus</i> spp.	0.6	21	0.7	19	0.1	29	0.3	15
Ironwood	<i>Ostrya virginiana</i>	0.4	22	0.7	18	1.4	13	<0.1	36
Green ash	<i>Fraxinus pennsylvanica</i>	0.4	23	<0.1	--	0.2	24	<0.1	31
Black walnut	<i>Juglans nigra</i>	0.4	24	0.1	34	0.6	20	0.2	22
Blackjack oak	<i>Quercus marilandica</i>	0.4	25	0.1	28	<0.1	34	1.3	12
White ash	<i>Fraxinus americana</i>	0.4	26	1.3	13	0.2	27	0.1	24
Eastern redbud	<i>Cercis canadensis</i>	0.3	27	0.7	17	0.4	22	0.2	17
Blueberry	<i>Vaccinium</i> spp.	0.3	28	<0.1	--	<0.1	--	<0.1	37
Persimmon	<i>Diospyros virginiana</i>	0.3	29	<0.1	--	<0.1	41	0.2	16
Bluebeech	<i>Carpinus caroliniana</i>	0.3	30	<0.1	--	0.7	18	<0.1	--
Paw paw	<i>Asimina triloba</i>	0.2	31	<0.1	--	<0.1	--	<0.1	40
N. pin oak	<i>Quercus palustris</i>	0.1	32	<0.1	--	<0.1	--	<0.1	--
Basswood	<i>Tilia americana</i>	0.1	33	0.2	27	<0.1	37	<0.1	--
Viburnum	<i>Viburnum</i> spp.	0.1	34	<0.1	--	<0.1	--	<0.1	35
Gumbamelia	<i>Bumelia lanuginosa</i>	0.1	35	<0.1	--	<0.1	39	<0.1	32
Black cherry	<i>Prunus serotina</i>	<0.1	36	<0.1	36	0.2	28	0.1	27
Wild plum	<i>Prunus americana</i>	<0.1	37	0.9	16	<0.1	--	0.1	28
American elm	<i>Ulmus americana</i>	<0.1	38	0.1	33	<0.1	--	0.1	30
Sugar maple	<i>Acer saccharum</i>	<0.1	--	1.3	12	<0.1	38	<0.1	42
Spicebush	<i>Lindera benzoin</i>	<0.1	--	0.5	21	<0.1	--	<0.1	--
Shagbark hickory	<i>Carya ovata</i>	<0.1	--	0.5	22	<0.1	--	<0.1	43

Table 4 (continued)

Eastern redcedar	<i>Juniperus virginiana</i>	<0.1	--	0.3	25	0.1	31	0.2	20
Red mulberry	<i>Morus rubra</i>	<0.1	--	0.1	29	0.2	26	0.1	29
Ozark chinkapin	<i>Castanea ozarkensis</i>	<0.1	--	0.1	30	<0.1	--	<0.1	--
Greenbrier	<i>Smilax</i> spp.	<0.1	--	0.1	32	<0.1	--	<0.1	--
Sycamore	<i>Platanus occidentalis</i>	<0.1	--	<0.1	--	0.7	19	<0.1	41
Hackberry	<i>Celtis occidentalis</i>	<0.1	--	<0.1	--	0.4	21	<0.1	33
Butternut	<i>Juglans cinerea</i>	<0.1	--	<0.1	--	0.3	23	<0.1	--
Hawthorn	<i>Crataegus</i> spp.	<0.1	--	<0.1	--	0.2	25	0.1	25
Shellbark hickory	<i>Carya laciniosa</i>	<0.1	--	<0.1	--	0.1	33	<0.1	--
Honeylocust	<i>Gleditsia triacanthos</i>	<0.1	--	<0.1	--	<0.1	35	<0.1	38
Chokecherry	<i>Prunus virginiana</i>	<0.1	--	<0.1	--	<0.1	36	<0.1	--
Blue ash	<i>Fraxinus quadrangulata</i>	<0.1	--	<0.1	--	<0.1	42	<0.1	--
Swamp chest. oak	<i>Quercus michauxii</i>	<0.1	--	<0.1	--	<0.1	43	<0.1	--
Shumard oak	<i>Quercus shumardii</i>	<0.1	--	<0.1	--	<0.1	--	<0.1	34
Sumac	<i>Rhus</i> spp.	<0.1	--	<0.1	--	<0.1	--	<0.1	39
Poison ivy	<i>Rhus radicans</i>	<0.1	--	<0.1	--	<0.1	--	<0.1	44

tracts. The mean diameters of the combined white oak, red oak, and shortleaf pine species groups was 7.7 and 8.8 inches (19.6 and 22.4 cm) for the Big Spring and Roaring River sites, respectively, while those for the Sinkin and MOFEP sites were 6.3 and 6.0 inches (16.0 and 15.2 cm), respectively. The unimodal shape of the diameter distributions in Figure 3 are largely due to the white oak group. When considered separately, the diameter distribution for the red oak group has a unimodal shape on the Big Spring and MOFEP sites. The diameter distribution of shortleaf pine by itself did not have a distinctly unimodal shape at any of the four sites.

#### Down Woody Debris

Mean volume of down woody debris at least 4 inches (10 cm) in diameter on the Big Spring and Roaring River sites was about twice the volume observed at Sinkin (Table 5). There were no distinguishable patterns within decomposition classes, but the classes had been developed for western conifers (Maser and others 1979). Using these class definitions, the majority of the volume consistently fell into classes 3 and 4.

Within each tract the variability in the volume of down wood among plots was high. The coefficient of variation for the total volume of down wood by plot was in the range of 70 to 75 percent. Nevertheless, analysis of variance for the mean volume of down wood per acre for the Big Spring, Roaring River, and Sinkin sites (one-way ANOVA based on all plots per site) showed significant differences among sites ( $p < 0.001$ , 130 d.f.). Pairwise comparison of means for these three sites (Tukey-Kramer HSD,  $\alpha = 0.05$ ) showed no significant difference between Big Spring and Roaring River, but values for those two sites were significantly larger than for the Sinkin. Because of procedural differences in sampling, compatible estimates of down wood volume were not available for the MOFEP site. The mean volume of down wood at least 2 inches (5 cm) in diameter on the MOFEP site is in the approximate range of 200 to 300  $\text{ft}^3 \cdot \text{ac}^{-1}$  (14 to 21  $\text{m}^3 \cdot \text{ha}^{-1}$ ), depending on the set of assumptions used to estimate the volume of down logs. But even at the high end, these estimates are markedly lower than observed at Big Spring and Roaring River. Because a comparable estimate of down wood volume was not available for the MOFEP sites, it was not possible to use a t-test to evaluate differences in down wood volume between the two old-growth and the two second-growth sites.

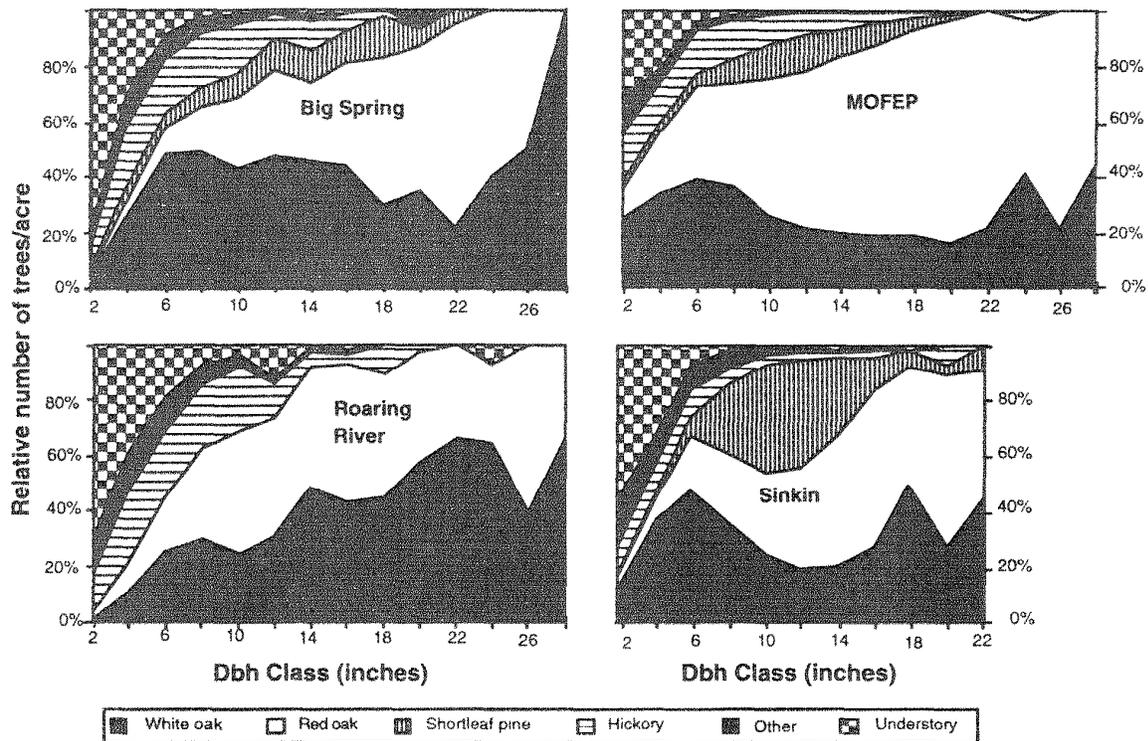


Figure 3. Relative number of trees per acre by 2-inch dbh class midpoint and major species groups. The white oak group includes white, post, chestnut, and chinkapin oak. The red oak group includes northern red, scarlet, black, and blackjack oaks. Hickory includes all *Carya* spp. Understory species include dogwood, blackgum, ironwood, bluebeech, serviceberry, pawpaw, buckthorn, redbud, vines, and shrubs.

The mean percent cover for the two old-growth and two second-growth sites (Table 5) was 1.56 and 1.29 percent, respectively. This difference was not statistically significant ( $p = 0.33$  for t-test with 2 d.f.).

Table 5. Mean volume of down woody debris and percent of ground covered by down wood<sup>a</sup>. Values include pieces  $\geq 4$  inches (10 cm) diameter for Big Spring, Roaring River and Sinkin;  $\geq 2$  inches (5 cm) diameter for MOFEP. Class definitions are from Maser and others (1979) and summarized in Table 2.

Site	(newly fallen)			(decomposed)		Total all classes ft <sup>3</sup> •ac <sup>-1</sup>	Percent of ground covered by down wood
	Class 1 ft <sup>3</sup> •ac <sup>-1</sup>	Class 2 ft <sup>3</sup> •ac <sup>-1</sup>	Class 3 ft <sup>3</sup> •ac <sup>-1</sup>	Class 4 ft <sup>3</sup> •ac <sup>-1</sup>	Class 5 ft <sup>3</sup> •ac <sup>-1</sup>		
Big Spring	15.6	28.1	192.6	180.1	40.7	457.1	1.50
Roaring River	3.1	74.9	265.1	104.1	47.6	494.8	1.61
Sinkin	16.0	45.5	104.9	57.1	16.7	240.2	1.09
MOFEP	--	--	--	--	--	--	1.49

<sup>a</sup>Volume m<sup>3</sup>•ha<sup>-1</sup> = 0.06997(volume ft<sup>3</sup>•ac<sup>-1</sup>)

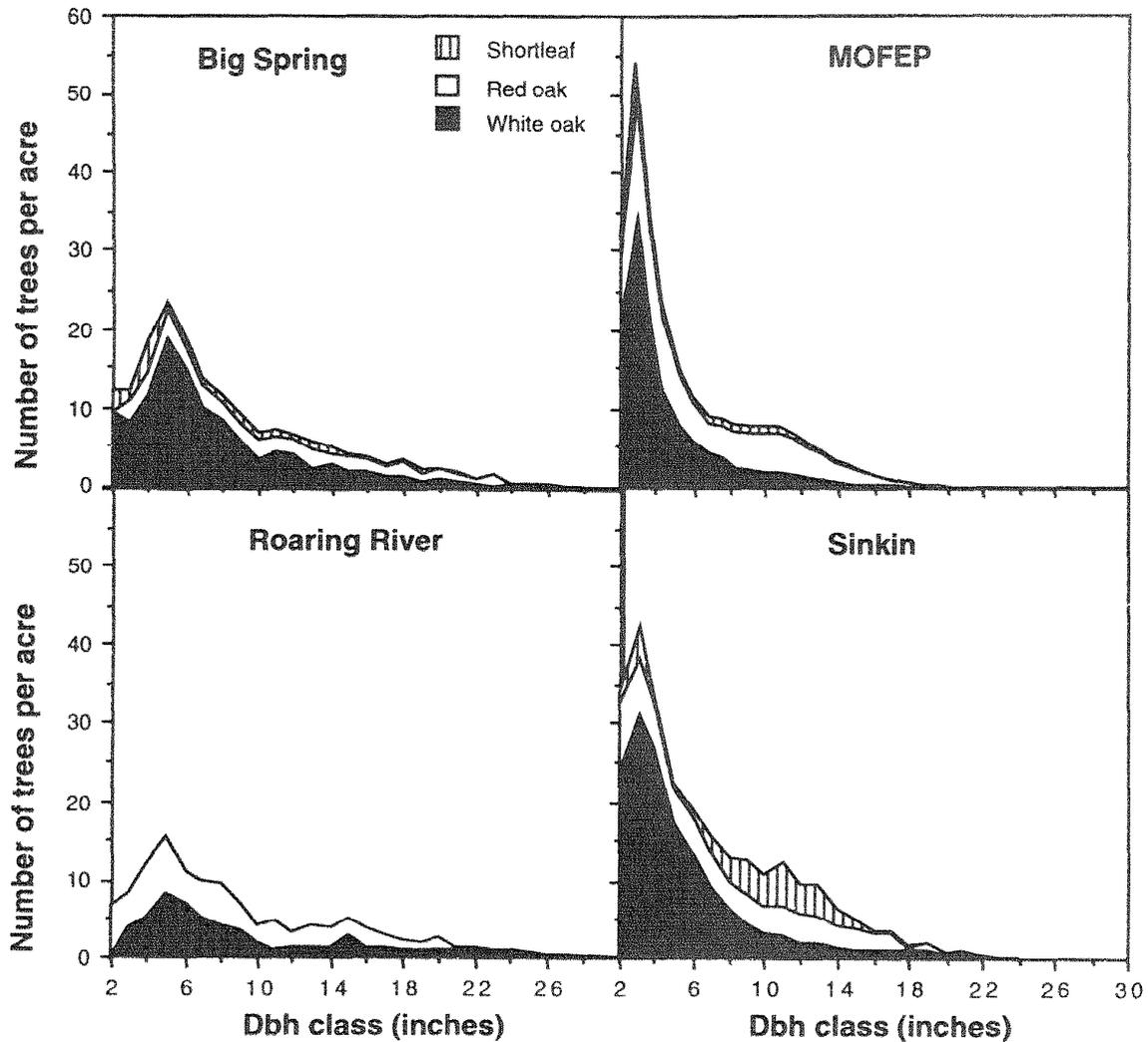


Figure 4. Number of trees per acre by major species groups. The white oak group includes white, post, chestnut, and chinkapin oaks. The red oak group includes northern red, southern red, scarlet, black, blackjack, and pin oaks.

#### CONCLUSIONS

Composite stand characteristics such as basal area and stocking were remarkably similar for the old-growth and second-growth stands compared. Likewise, the diameter distributions for all species combined had a negative exponential shape that was similar for the old-growth and second-growth tracts.

However, the old-growth tracts consistently had more trees per acre  $\geq 17$  inches (43 cm) dbh than did the second-growth sites. The absolute number of these large trees was small at all sites--an average of 14 per acre (35 per ha) for old-growth sites and 7 per acre (17 per ha) for second-growth sites. The overstories at all four sites were dominated by the red and white oak groups, and shortleaf pine was a substantial overstory component for all sites except Roaring

River. Dogwood was the dominant understory species at all sites. When considered jointly, the white oaks, red oaks, and shortleaf pine had unimodal diameter distributions at all sites, although the old-growth sites had fewer and larger trees of these species. Down wood on the old-growth sites was between 450 and 500 ft<sup>3</sup>•ac<sup>-1</sup> (31 and 35 m<sup>3</sup>•ha<sup>-1</sup>), about double that observed for the Sinkin Experimental Forest.

The data we examined indicate that the composite density of second-growth Ozark oak forests may change relatively little as they mature to an old-growth state. Some of the most readily observed changes should be shifts in the number and basal area of trees larger than 17 inches (43 cm) dbh, corresponding changes in the diameter distribution of the dominant overstory species, and large increases in the volume of down wood.

#### ACKNOWLEDGMENTS

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DEVELOPMENT OF A CENTRAL HARDWOOD STAND  
FOLLOWING WHOLE-TREE CLEARCUTTING IN CONNECTICUT

C. Wayne Martin<sup>1</sup>

**Abstract:** Little information is available concerning the initial stages of forest regeneration following intensive harvesting of central hardwood stands in the northeastern part of the range. Establishment of commercial species, density, and rate of biomass accumulation of the regeneration are of major concern to both foresters and landowners contemplating a harvest. To help provide this information, a 6-ha forest stand dominated by the central hardwood forest type of Connecticut was mechanically whole-tree clearcut in 1981. Intensive sampling of the regeneration including herbs, shrubs, tree seedlings, and stump sprouts was conducted the first, third, fifth, and tenth years after cutting. This paper will discuss the development of the stand over the first ten years following clearcutting. Prior to harvesting, the stand contained 1,163 stems ha<sup>-1</sup>  $\geq 2.0$  cm d.b.h.; at year 10 there were 9,500. At year 10, the trees and shrubs  $\geq 2.0$  cm d.b.h. had accumulated 20% of the preharvest levels of biomass, 52% of nitrogen, and 21% of calcium. Based on data from the first 10 years after clearcutting, the future forest should be similar to the preharvest forest with red maples, oaks, and birches being the most numerous trees.

INTRODUCTION

The central hardwood forest type is extensive in southern New England. As of 1985, more than 2.1 million acres of Massachusetts, Rhode Island, and Connecticut were classified as the oak-hickory forest type (Brooks et al. 1993). In Connecticut alone, there were 966,000 acres of the oak-hickory forest in 1985 (Dickson and McAfee 1988). Eighty four percent of the oak-hickory type in Connecticut is in non-industrial private ownership. In 1984, 722,000 cubic meters of hardwood wood products were produced in Connecticut including sawlogs, roundwood, and fuelwood (Dickson and McAfee 1988).

Landowners, foresters, loggers, and the general public are concerned about the future productivity and biodiversity of these forest lands. For long-term planning, landowners and foresters need information on the characteristics of the early stages of regeneration, the development of stands, and the expectations for the future mature stands. Little information is available concerning the regeneration and early successional stages of forest development following logging in the northeastern part of the central hardwood range. The first 5 to 10 years after harvest are critical in the development of the new stand and are not well understood (Hornbeck et al. 1990).

The effects of calcium depletion on the long-term productivity of these forests is another reason for studying the regeneration of these stands. Hornbeck and others (1990) found that 10% of the total calcium pool was removed from a central hardwood stand in Connecticut in wood products removed from the site and in soil water leached to streams following mechanical whole-tree clearcutting. They also predicted that calcium uptake by 3 year-old regeneration would exceed the extractable calcium in the soils of the site. They studied the calcium dynamics of 3 forest types in New England and concluded that calcium is potentially a limiting plant nutrient in the forests of Connecticut. Data on calcium uptake by regeneration through year 10 would add new insight to this hypothesis.

During the energy crisis of the late 1970s and early 1980s, the forests of southern New England were viewed as alternative sources of fuel. Fuelwood cutting on a commercial scale was proposed, much of it on state forest lands. To

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test the potential impacts of fuelwood cutting on state forest lands, the State Forester of Connecticut, requested a study of the effects of mechanical whole-tree clearcutting on site productivity, regeneration, and development of future stands. The purpose of this paper is to report on the development of a southern New England stand over the first 10 years following clearcutting.

## METHODS

### The Study Site

The study site is a 6 ha forested stand located in the Cockaponset State Forest in Chester, CT. Prior to harvesting, the watershed supported an 80- to 110-year old oak-birch-maple forest typical of Connecticut and southern New England. Oaks (*Quercus Prinus* L., *Q. rubra* L., *Q. alba* L., and *Q. velutina* Lam.) accounted for 47% of the basal area; birches (*Betula lenta* L., and *B. alleghaniensis* Britt.) accounted for 27%; and maples (*Acer rubrum* L. and *A. saccharum* Marsh.) accounted for 13% of the basal area. The remainder included miscellaneous hardwoods. The total basal area of all stems larger than 2 cm d.b.h. was 23 m<sup>2</sup> ha<sup>-1</sup>, with a density of 1,163 stems ha<sup>-1</sup> (Tritton et al. 1982).

The soils of the upper slopes of the study site are of the Hollis-Chatfield-Rock association which are loamy, mixed, mesic Lithic Dystrochrepts. These soils consist of shallow, somewhat excessively drained soils with occasional outcrops of exposed bedrock. The bedrock is of the upper Middletown formation, an assemblage of gneisses and schists with inclusions of sillimanite quartz and pegmatite. The soils of the lower slopes are deep, well-drained, coarse, loamy, mixed, mesic, Typic Dystrochrepts of the Chatfield-Canton association. The soils of the valley floor are poorly drained, acidic, coarse-loamy, mixed, mesic Aeric Haplaquepts of the Leicester series (USDA Soil Conserv. Serv. 1981).

In the winter of 1981-82, the entire watershed was whole-tree clearcut. All living and dead trees greater than 5 cm d.b.h. were cut. Trees less than 30 cm stump diameter were cut with a rubber-tired feller buncher. Larger trees were felled with chain saws. Whole trees of all diameters were skidded to the landing outside the watershed by rubber-tired, articulated skidders. Ninety one percent of the aboveground biomass was removed from the site by the harvesting operation (Tritton et al. 1987). Harvesting was completed in March of 1982 and was confined to the dormant season.

### Regeneration Surveys

Prior to harvesting, a 25 X 25 m grid was surveyed on the watershed with the corners permanently marked. From this grid, plots were selected at random for the regeneration surveys. These plots were also permanently marked. Three sizes of plots were selected for vegetation sampling: 1 X 1 m plots for herbs, shrubs, and tree seedlings <130 cm tall; 1 X 25 m plots for saplings 0.1 to 9.9 cm d.b.h.; and 25 x 25 m plots for trees ≥10 cm d.b.h. and for following the fate of stump sprouts. Prior to cutting, all trees ≥10 cm d.b.h. were measured and their location mapped.

The first survey was conducted in August 1982, the first year after harvest. Since all vegetation was <130 cm tall, 50 1 X 1 m plots were sampled. Sprouts from the stumps of the mapped trees were also measured. The second survey was conducted in August 1984, the third year after cutting. The third survey was conducted in August 1986, the fifth year after harvest. On both of these occasions, twenty five of the 1 X 1 m plots were remeasured. In addition, 16 of the 1 X 25 m plots were measured.

The fourth survey was conducted in August 1991, the 10th year after cutting. The twenty five 1 X 1 m plots were remeasured. Twenty five paired plots were harvested for biomass and nutrient analyses. The sixteen 1 x 25 m plots for saplings were remeasured, but because saplings in this size range represented a majority of the vegetation on the area, 20 more plots were added, at random, for a total of 36 plots. Because of the density of the foliage, the stump sprouts on four 25 X 25 m plots were remeasured in November of 1986 and 1991.

## Biomass

Three individuals of each species were clipped, on separate plots, for biomass and nutrient analyses the first year after cutting. These samples were dried at 65°C to constant weight. The average of the 3 samples was multiplied by the number of stems of that species per hectare. Biomass of the vegetation <130 cm tall the 3rd and 5th year after cutting was estimated by clipping twenty one 1 X 1 m plots selected at random using ranked-set sampling techniques (McIntyre 1952). Biomass of the vegetation <130 cm tall in the 10th year was estimated by taking a simple average of the oven-dry weights of twenty five plots paired with the inventory plots. The first year after cutting there were no stems large enough to have a d.b.h. During the 3rd and 5th year inventories, 3 stems of each species in each 1-cm d.b.h. class were clipped in various areas of the watershed. Each stem was weighed in the field, subsampled, and oven dried at 65°C. The average oven-dried weight of each species and size class was then multiplied by the estimated number of stems of that species and size per hectare. The 10th year after cutting, several individuals over a range of d.b.h. were sampled and dried by species. Then allometric equations were developed for each species for predicting oven-dry weight from d.b.h.

## Nutrient Analyses

Vegetation samples collected for biomass estimates were dried to a constant weight at 65°C, and then analyzed chemically. Subsamples were digested in a Technicon BD-20<sup>2</sup> block digester. Total Kjeldahl nitrogen was measured on the digested samples with colorimetric analyses performed on the Technicon Autoanalyzer. Calcium concentrations of the digested samples were determined by flame atomic absorption spectroscopy (Franson 1975).

## RESULTS

### Density

The first year after cutting, there were 49 genera of plants inventoried on the clearcut watershed. These genera included 14 tree species in 11 genera, 12 species of shrubs in 10 genera, and 28 genera of herbs. By the 10th year after cutting, the total number of genera had dropped to 47. However, trees had increased to 22 species in 13 genera. Shrubs had increased to 18 species in 15 genera, and herbs had dropped to 19 genera.

By August of the first year after cutting, there were about 788,000 stems ha<sup>-1</sup> of all types of plants on the watershed with trees, shrubs, and herbs occurring in similar amounts (Fig. 1). By the 5th year after cutting, there were more than 1,000,000 stems ha<sup>-1</sup> on the watershed with about 60% of them herbs and only 10% of them trees. By year 10, the total number of stems had dropped to less than 500,000 stems ha<sup>-1</sup> with herbs still more than 60% and trees down to about 6% of the total number of stems. Of the tree genera, birches, primarily *Betula lenta*, dominated the population through year 5 (Fig. 2). By year 10, birches accounted for 45%, maples 33%, oaks 14%, and all other genera of trees combined only 8%.

A decade after harvest, the density of stump sprouts was low -- only 5% of the total number of stems of trees. Red maple was the most prolific sprouter, but sprouts were only 7% of all red maple stems at year 10. Oak sprouts were only 11% of all oak stems at the 10th year after cutting. At year 10, there were about 23,000 tree saplings tall enough to have a d.b.h. and only 7% of them were sprouts.

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<sup>2</sup>The use of trade, firm, or corporation names 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 might be suitable.

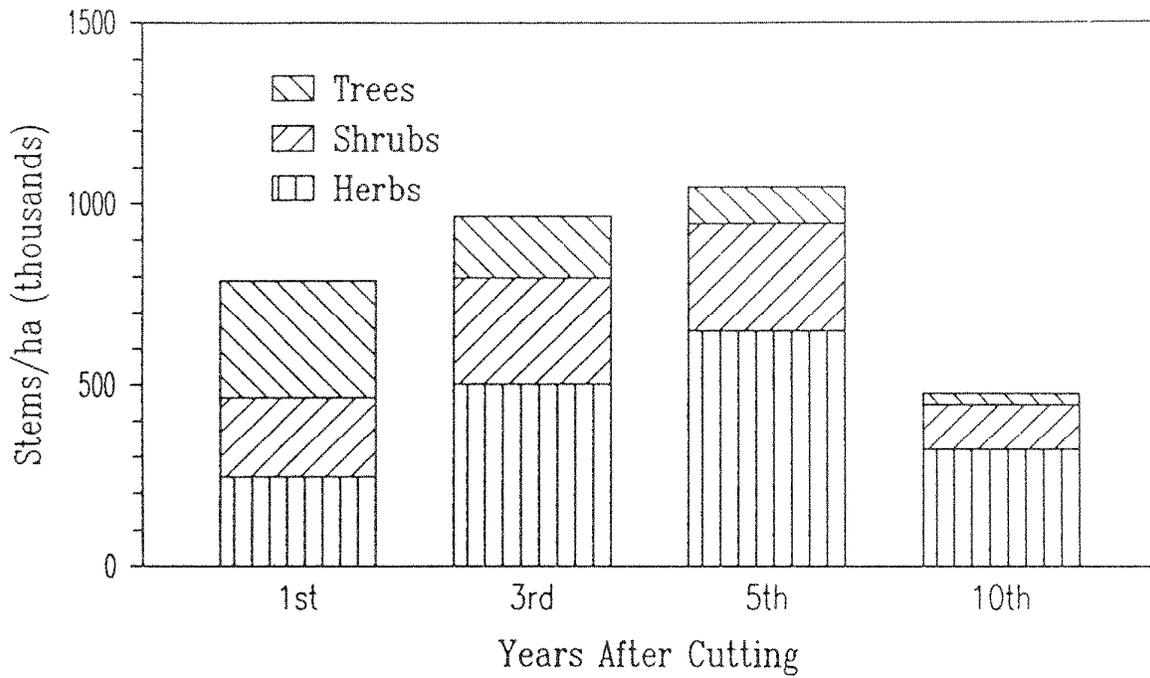


Figure 1. Density of all plants on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

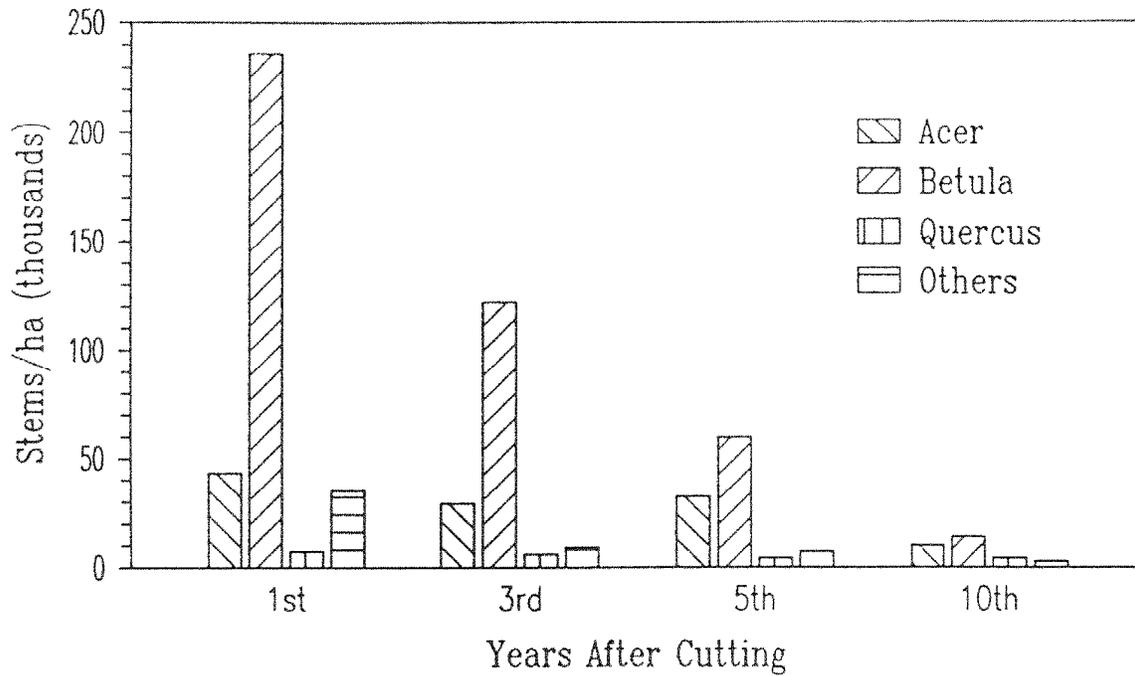


Figure 2. Density of tree genera on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

## Biomass

By August of the 1st year after cutting, there were nearly 2 tonnes ha<sup>-1</sup> of aboveground dry weight of biomass with trees accounting for most of it (Fig. 3). By year 5, biomass had increased to 18 tonnes ha<sup>-1</sup> with trees accounting for two-thirds of it. In the next 5 years the biomass more than doubled to nearly 42 tonnes ha<sup>-1</sup>, with 88% in trees.

Of the tree genera present one growing season after cutting, the maples produced the most biomass, followed by chestnut (*Castanea dentata*), followed by the oaks, followed by the birches. By year 3, the maples still had accumulated the most biomass, followed by the birches, then by chestnut, and then by the oaks. By year 5, the order had changed again with the maples still dominant, in terms of biomass, followed by the birches, with the oaks in 3rd place and chestnut moved to 4th (Fig. 4). At year 10, the maples, birches and oaks accounted for 90% of the tree biomass with the maples at 45%, and chestnut relegated to 0.2% due to mortality from the chestnut blight. Sprouts accounted for more than 20% of the tree biomass. Maple sprouts were 20% of the maple population, but oak sprouts were nearly 50% of the oak population in terms of biomass. Of the total biomass in tree genera, 99% was in trees tall enough to have a d.b.h. at year 10.

## Nutrients

The 1st year after cutting, 9 kg ha<sup>-1</sup> of Ca accumulated in the above ground biomass with three-quarters of it in trees. Nearly 30 kg ha<sup>-1</sup> of N accumulated in plant tissue the first year with about two-thirds in trees (Fig. 5). By year 10, about 150 kg ha<sup>-1</sup> of Ca had accumulated in aboveground living plant tissue with 86% of it in tree genera. Nearly 200 kg ha<sup>-1</sup> of N was sequestered in plant tissue at year 10 with about 86% of it in trees.

At year 10, the maples accounted for nearly 40% of all of the above ground biomass and contained about one-third of the Ca. The oaks contained only 20% of the biomass of the watershed, but they contained 27% of the Ca (Fig. 6). The maples contained 3.1 kg of Ca per 1000 kg of biomass, while the oaks contained 4.8 kg of Ca per 1000 kg of biomass. Of the total Ca in trees, 24% was in sprouts, but 43% of the Ca in oaks was in sprouts.

At year 10, maples had sequestered 35% of the N, and oaks 26% (Fig. 7). The maples contained 4.0 kg of N for each 1000 kg of biomass. The oaks contained 6.0 kg of N for each 1000 kg of biomass. Sprouts of all genera contained 24% of the N in all tree genera.

## DISCUSSION

Prior to harvesting, the central hardwood forest at the Cockaponset State Forest in Chester, CT was a diverse forest with 22 species of trees and shrubs (Tritton et al. 1982). The first year after whole-tree clearcutting with 91% of the above-ground living biomass removed, there were 26 species of trees and shrubs in the regeneration. By the 10th year after cutting, the number of species of trees and shrubs had increased to 40.

The total numbers of stems of all plants increased through the 5th year after cutting and then by year 10 had dropped considerably as the canopy closed (Fig. 1). Trees were the most numerous the 1st year after cutting followed by herbs and then shrubs. Over the 10 year period the numbers of trees declined steadily; shrubs and herbs increased through year 5 and then declined by year 10. Of the tree species, sweet birch (*Betula lenta*) was clearly the most numerous throughout the 10 years of the study followed by red maple (*Acer rubrum*). The oaks were always important and were the 3rd most numerous tree by year 10 (Fig. 2).

The above ground living biomass of all plants on the watershed increased steadily over the 10 years after cutting, more than doubling between years 5 and 10. Tree species have clearly dominated the biomass throughout the post-harvest period increasing from 67% of the biomass the first year after cutting to 88% by year 10 (Fig. 3). Herbs were a major part of the biomass through year 5. Shrub biomass has increased steadily throughout the period.

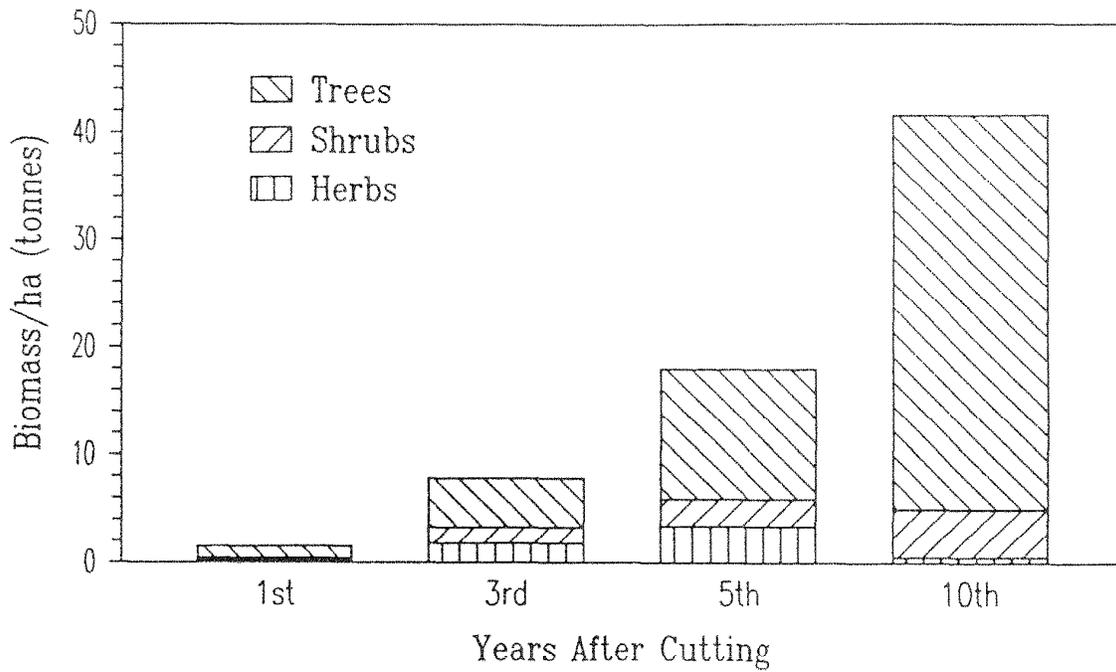


Figure 3. Biomass of all plants on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

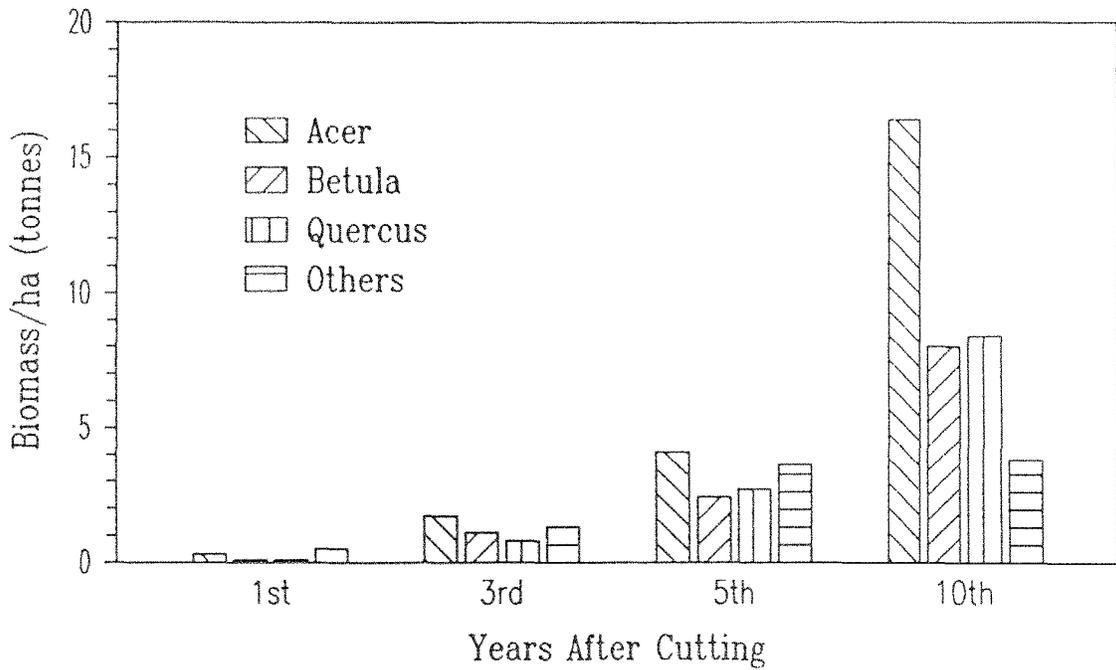


Figure 4. Biomass of tree species on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

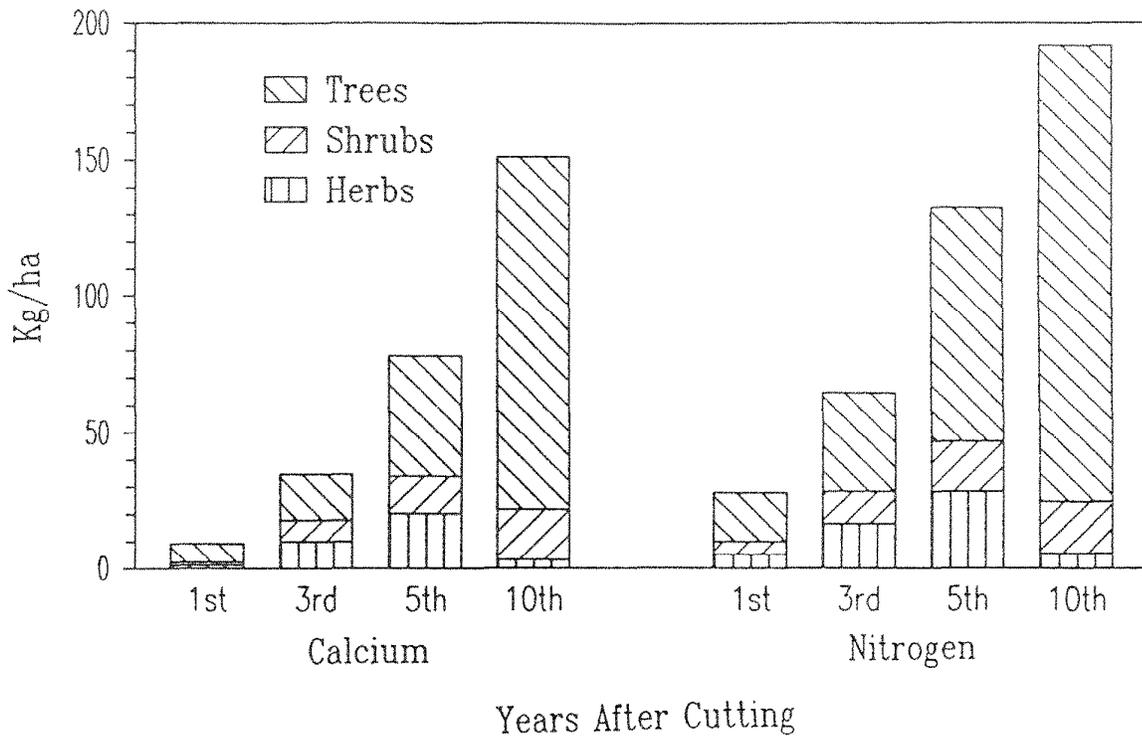


Figure 5. Calcium and nitrogen sequestered in all plants on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

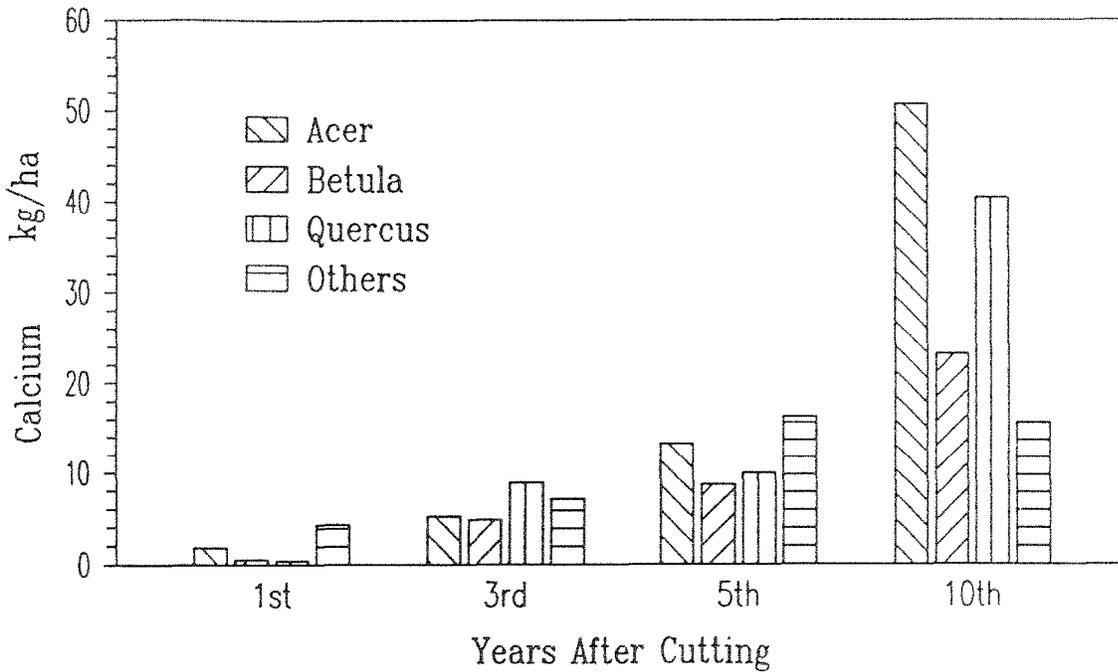


Figure 6. Calcium sequestered in tree genera on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

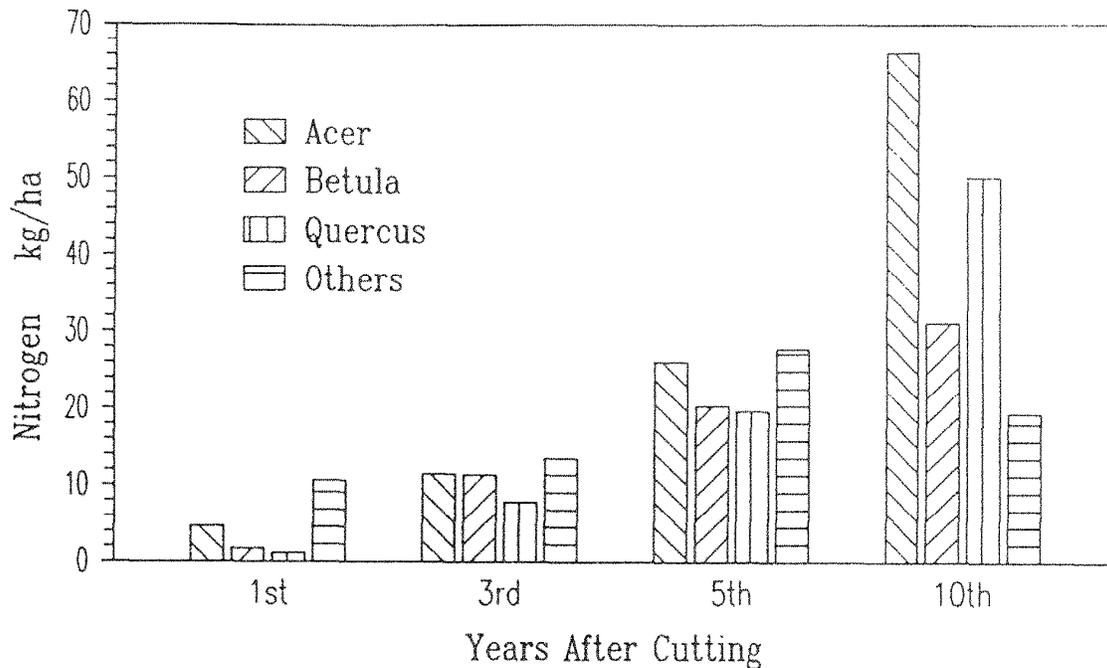


Figure 7. Nitrogen sequestered in tree genera on the whole-tree clearcut at the Cockaponset State Forest, Chester, CT.

Of the trees, red maple accumulated the most biomass of any single species throughout the sampling period followed by sweet birch (Fig. 4). After year 5, biomass of all of the oak species combined exceeded that of the birches.

The accumulation of nutrients in all plants on the site followed the same pattern as the biomass (Fig. 5). Trees sequestered much more Ca and N than did shrubs and herbs from the very first year after cutting. However, no one genus clearly dominated nutrient uptake until year 10, when maple and oaks sequestered the greatest amounts (Figs. 6 and 7).

#### The Future Forest

Comparisons of living trees and shrubs with stems  $\geq 2.0$  cm d.b.h. indicate that prior to cutting, dogwood (*Cornus florida*) was the most numerous tree on the watershed, but was an understory tree with very little biomass (Table 1). Of the major tree species, the maples were most numerous followed by the oaks and then the birches. At 10 years after cutting, the maples were the most numerous trees  $\geq 2.0$  cm d.b.h. followed by the birches and then by the oaks. Prior to cutting, the oaks had accumulated more than 50% of all of the biomass, Ca, and N in stems greater than 2.0 cm d.b.h. At 10 years after cutting, red maple had assumed that role. However, the oaks accounted for 24% of the biomass, 31% of the N, and 32% of the Ca.

Prior to cutting, there were more than 1,100 stems  $\text{ha}^{-1}$ ; at year 10 there were more than 9,500 in trees and shrubs  $\geq 2.0$  cm d.b.h. which are likely to survive. This seems to be adequate stocking. Already by year 10, these trees and shrubs have accumulated 20% of the preharvest biomass; 52% of the preharvest N; and 21% of the preharvest Ca.

Table 1. Living trees and shrubs  $\geq 2.0$  cm d.b.h. on a 6 ha watershed on the Cockaponset State Forest, Chester, CT before and ten years after clearcutting.

Species	Before Cutting				Ten Years After Cutting			
	Density Stems/ha	Biomass Tonnes/ha	N ---kg/ha---	Ca	Density Stems/ha	Biomass Tonnes/ha	N ---kg/ha---	Ca
<i>Quercus</i>	202	93.2	176.0	399.3	1,350	8.1	48.4	38.5
<i>Betula</i>	174	39.6	65.7	89.2	2,058	4.2	18.4	13.4
<i>Acer</i>	305	14.4	29.8	51.0	3,717	15.5	62.5	47.2
<i>Carya</i>	58	4.9	9.1	18.6	400	1.3	7.6	5.0
<i>Cornus</i>	339	0.9	7.3	9.6	293	0.7	3.0	3.7
Other	85	15.4	14.8	20.8	1,720	4.0	16.6	14.0
Total	1,163	168.4	302.7	588.5	9,538	33.8	156.5	121.8

#### CONCLUSIONS

Clearcutting, especially whole-tree clearcutting, is a major disturbance of the forest ecosystem. The rate and success of the regeneration are of concern to forest landowners, foresters, and the general public. The Cockaponset site revegetated rapidly with herbs, shrubs, and tree seedlings during the first growing season after harvesting. Species density increased rapidly for the first 5 years and then declined due to crown closure. Biomass increased exponentially through year 10.

Even though clearcutting disrupts the forest nutrient cycles, regeneration including trees, shrubs, and herbs on the Cockaponset site accumulated nearly 25% of the preharvest levels of biomass, more than 60% of nitrogen, and about 25% of calcium by year 10.

There is always concern about the adequate stocking of commercial species. More than 9,500 stems of trees and shrubs  $\geq 2.0$  cm d.b.h. at year 10 seems to be adequate stocking, especially with the oaks playing a prominent role in both density and biomass.

Based on data from the first 10 years after clearcutting, it would seem that the future forest would be similar to the preharvest forest with red maple, oaks, and birches being the most numerous trees.

#### ACKNOWLEDGMENTS

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IMPACTS OF ELECTRIC DEER EXCLUSION FENCING AND SOILS ON PLANT SPECIES ABUNDANCE,  
RICHNESS, AND DIVERSITY FOLLOWING CLEARCUTTING IN PENNSYLVANIA

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**Abstract:** Electric deer exclusion fencing has become a widely used management tool to promote hardwood regeneration in high deer browsing intensity areas. To assess the impacts of deer browsing on hardwood regeneration and vegetation patterns on clearcuts, six clearcuts with paired electric fenced and unfenced treatments were investigated. Additional data were collected on 10 sites with only fenced clearcut treatments. Overall browse damage on fenced treatments was lower than unfenced treatments, but there were substantial species-specific variability. The vegetation patterns on clearcuts were strongly influenced by pre-harvest ground covers of herbaceous and woody species. Comparisons between fenced and unfenced treatments showed that species richness was not significantly different for any site and that woody species diversity (Shannon Index) was significantly higher on a fenced versus unfenced clearcut on only one site. Observed vegetation patterns may also be influenced by soil nutrient and acidity status. Species richness was significantly related to exchangeable Ca and Al levels in the subsoil and organic horizon pH.

#### INTRODUCTION

There has been much concern surrounding the difficulties in regenerating desirable hardwood species following clearcutting in Pennsylvania and throughout the eastern hardwood region. There is also growing interest in evaluating clearcut plant communities in light of recent efforts to manage forests for biodiversity (Gove and others 1992; Hansen and others 1991; Niese and Strong 1992). Interpreting causal factors responsible for observed vegetation patterns, however, requires detailed analysis of an array of biotic and abiotic factors that may be influencing the structure and composition of vegetation on any given site. In Pennsylvania, excessive browsing by white-tailed deer (*Odocoileus virginianus virginianus* Boddaert) has been widely cited as the primary agent responsible for depleting advance regeneration stocks, reducing hardwood regeneration on clearcuts, and influencing species composition (Jordan 1967; Marquis 1981). However, ground covers of competing species (Drew 1988; Horsley 1977; Horsley and Marquis 1983; Kolb and others 1990), rodent damage and seed predators (Marquis and others 1976), poor seed production (Tryon and Carmean 1958), low levels of soil N and P (Auchmoody 1982), and soil acidity and soil nutrient imbalances (Tomlinson and Tomlinson 1990) may all play a role in determining the success of hardwood regeneration and the overall community that is regenerated after clearcutting.

Deer exclusion fencing has been used for many years as a research and management tool to both ascertain and ameliorate the impacts of deer browse on regeneration and revegetation of clearcuts (Frontz 1930; Grisez 1959; Marquis and Brenneman 1981; Marquis and Grisez 1978; Shafer and others 1961; Tilghman 1987; Trumbull and others 1989). Research results indicating the potential value of wire mesh fences in promoting hardwood regeneration have led to the development and widespread use of less expensive electric deer fencing in high deer density areas. Despite the expanded use of electric exclusion fencing, however, there have been few quantitative studies on the value of these fences in promoting hardwood regeneration (George and others 1991; Kochel and Brenneman 1987) and fewer studies on plant species richness and diversity. The current study was undertaken to obtain additional information on the effectiveness of electric exclusion fencing in reducing deer influence on the composition of plant

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communities, species richness, and woody plant diversity on clearcuts. The study also focused on the assessment of soil chemical factors at each site to determine if and how soil chemistry might be influencing vegetation patterns. Specifically, the study was designed to analyze three components of clearcut revegetation: (1) comparisons of woody and non-woody species density, height, and cover across a range of different sites, (2) comparisons of overall vegetation patterns, species richness, and woody species diversity, and (3) the potential influence of soil acidity factors in influencing hardwood regeneration and vegetation patterns.

## METHODS

### Study Areas

One of the aims of this study was to undertake a field evaluation of the effectiveness of electric fencing on clearcut sites that were representative of typical fencing efforts currently employed in Pennsylvania. The study areas were carefully chosen from a large pool of clearcuts located on Pennsylvania Bureau of Forestry lands. The 16 study sites supported even-aged stands, were approximately the same age when cut, had minimal slopes (0-5%), and were from 2 to 4 years old. Six primary sites had paired fenced and unfenced clearcut treatments, of which four were located on oak forest sites and two on northern hardwood sites. Ten secondary clearcut sites scattered across north-central Pennsylvania with only fenced treatments were used to provide supplemental information. The fencing used on each clearcut was a multi-strand electric fence after the design of Brenneman (1982). Fences were constructed soon after harvest operations and were maintained by Bureau of Forestry personnel. At each site, all vegetation plots were located on the same soil series and soil sample results are based on analysis of the specific soil series. To ascertain any potential influence of soil chemical factors, the sites chosen also represented a range in soil conditions. General characteristics of the study sites are given in Table 1.

### Study Design and Field Measurements

Each of the six primary study sites was divided into three treatments: a fenced clearcut, an unfenced clearcut, and an understory of an adjacent uncut forest stand similar in composition to the original, pre-clearcut stand. A stratified sampling design was used for vegetation analysis. Nine, 1.828 m radius (6-ft radius), sample plots were located within each treatment at each site (3 treatments x 9 plots = 27 plots per site). Bureau of Forestry field data on the composition of the over- and understories at each site prior to clearcutting were used to verify the validity of using vegetation data from understory plots adjacent to clearcuts as a proxy for pre-clearcut vegetation data in this study. The locations of all vegetation plots were restricted to a single soil type within each site. Soil types at each site were identified using SCS soil maps with ground verification using small, hand excavated soil pits. Vegetation plots were laid out on a 25 m x 25 m grid over the specific soil type on each of the 3 treatments with certain restrictions; plots had to be at least 30 m from the exclusion fences and not to be located on areas with major disturbance such as skid trails, uprooted trees or exposed mineral soil.

Vegetation plots were established during the spring of 1992. Full scale quantitative sampling was conducted on each site in August of 1992. On each of the fenced and unfenced clearcut plots, the number, height, and browse status of each species of woody plant were recorded. On the uncut, unfenced forest plots, the number, height, and browse status of each species of woody seedling and sapling were recorded. Cover of both shrubs and herbaceous species was also determined using the Braun-Blanquet system (7 cover categories). Browse damage on hardwood seedlings and saplings was noted if the top or lateral stems showed browse damage. No separation was made between deer browse and other mammal browse due to difficulties in distinguishing browse damage in the field. However, the high population of deer, and widespread evidence of deer activity at each site, suggest that deer were likely to have been responsible for most of the browse damage observed.

Table 1. General characteristics of six primary, and ten secondary study sites.

Site	Location State Forest	Size (ha)	Elev (m)	Stand Age When Cut	Year Cut	Date Fenced	Preharvest Overstory	Soil Series
PRIMARY SITES								
1	Bald Eagle	10.1	510	80	1988	5/89	CO,RO,WO	Laidig
2	Bald Eagle	19.8	520	82	1990	6/90	RO,CO,WO	Hazleton
3	Forbes	6.1	830	65	1989	7/89	RO,RM	Dekalb
4	Moshannon	40.5	695	78	1989	8/89	BC,RO,RM	Cookport
5	Susquehannock	29.9	680	84	1990	7/90	BC,BE,RM	Clymer
6	Tioga	23.8	640	90	1989	4/89	SM,BC,BE	Lordstown
SECONDARY SITES								
7	Moshannon	19.0	695	82	1989	8/89	RO,RM	Hazleton-Clymer
8	Moshannon	12.1	600	78	1989	9/89	RM,RO	Hazleton-Clymer
9	Moshannon	8.1	620	80	1989	9/89	RO,RM	Hazleton-Clymer
10	Moshannon	8.2	525	88	1990	7/90	RO,WO	Berks
11	Moshannon	21.9	680	85	1988	5/89	RO,RM	Cookport
12	Tioga	6.9	720	90	1990	9/90	RO,WO	Clymer
13	Tioga	12.5	730	80	1987	5/88	RO,RM	Oquaga
14	Elk	15.8	520	68	1989	8/89	RM,RO,WO	Wharton
15	Susquehannock	26.3	660	84	1989	5/90	BC,RM,SM	Leetonia
16	Tiadaghton	27.5	680	75	1989	5/90	RM,BE	Wurtsboro

Overstory Species Codes:

RO - Red Oak (*Quercus rubra* L.)

CO - Chestnut Oak (*Quercus prinus* L.)

SM - Sugar Maple (*Acer saccharum* Marsh.)

RM - Red Maple (*Acer rubrum* L.)

WO - White Oak (*Quercus alba* L.)

BC - Black Cherry (*Prunus serotina* Ehrh.)

BE - American Beech (*Fagus grandifolia* Ehrh.)

Soil samples from all horizons to a depth of 30 cm were collected from a random sub-sample of 4 of the 9 vegetation plots. Soils were analyzed by horizon, and soil analysis was performed at The Pennsylvania State University and included pH (glass electrode with 1:1 [w:v] H<sub>2</sub>O), soil texture, CEC and base saturation (North Dakota State University 1988), organic matter, total N, and exchangeable Ca, Mg, K, Mn, and Al using a 0.01M SrCl<sub>2</sub> extraction (Joslin and Wolfe 1989). The latter analysis was performed in order to estimate the "plant available" fraction of these cations. Table 2 provides a summary of the mineral horizon soil conditions (15-30 cm depth) at each of the six primary sites.

Data Analysis

Differences in vegetation and soil parameters across treatments for each site were analyzed by ANOVA and mean separations were performed using Fisher's LSD test. Herbaceous cover was analyzed after the methods of Bannister (1966). Species richness comparisons were based on the mean number of species per plot within each treatment. Total species richness was measured as the sum of all species found within a treatment. Woody plant diversity was measured using the Shannon-Weiner Index (Magurran 1988). Herbaceous species diversity was not assessed because the Braun-Blanquet cover estimates employed in the study were not amenable to diversity measures (Magurran 1988). All significant differences are reported at the alpha  $\leq$  0.05 level. Regression and multiple regression analyses were used to determine relationships between plant composition and the soil parameters being studied.

Table 2. Soil characteristics (15-30 cm depth) of the six study sites.

SITE	pH <sup>1</sup>	C:N	%BS	CEC <sup>2</sup>	----- ppm <sup>3</sup> -----				molar Ca:Al
					Ca	Mg	K	Al	
1 Understory	4.13	44.3	7.2	6.4	2.0	0.3	3.1	9.7	0.14
Clearcut <sup>4</sup>	4.20	36.3	7.5	8.9	2.4	0.4	2.7	9.2	0.18
2 Understory	4.05	30.0	8.1	9.8	4.4	3.2	8.2	8.1	0.37
Clearcut	4.13	31.3	6.1	11.9	5.6	4.4	9.4	7.3	0.52
3 Understory	4.02	26.7	6.5	11.3	3.6	3.7	7.4	21.3	0.11
Clearcut	4.08	30.9	5.2	14.3	3.2	4.1	7.8	19.7	0.11
4 Understory	4.65	32.2	12.3	8.9	5.2	4.9	16.0	11.1	0.32
Clearcut	4.59	27.9	14.6	7.6	6.0	4.6	17.2	10.5	0.38
5 Understory	4.60	22.2	11.1	10.1	8.4	7.1	15.2	15.6	0.36
Clearcut	4.56	28.3	13.0	11.3	11.6	7.3	17.2	11.3	0.69
6 Understory	4.51	21.3	6.9	16.1	14.0	6.8	21.9	13.8	0.67
Clearcut	4.49	24.6	7.5	16.1	12.4	6.1	22.7	12.7	0.66

<sup>1</sup> pH in 1:1 (w:v) H<sub>2</sub>O      <sup>2</sup> CEC in cmol(+) kg<sup>-1</sup>

<sup>3</sup> Using 0.01 M SrCl<sub>2</sub> extraction (Joslin and Wolfe 1989)

<sup>4</sup> Clearcut soil values refer to fenced clearcut sites

## RESULTS

### Pre-Clearcut Vegetation Versus Understory Vegetation

In most cases, the composition of the over- and understory on the pre-clearcut stands paralleled the 1992 sampling plots located adjacent to the existing clearcuts (Table 3). Based on this information, the assumption was made that the pre-harvest clearcut vegetation was similar to the adjacent uncut, unfenced plots before cutting. Nonetheless, caution is warranted in interpreting the results based on this assumption.

### Fencing Impacts on Browse Damage

Based on the single year (1992) browse damage survey, the overall level of browse damage on woody species was significantly lower within fenced clearcut treatments than on either the unfenced or non-clearcut, unfenced treatments. Species-specific browse damage, however, exhibited substantial variation across sites and treatments. Northern red oak (*Quercus rubra* L.) and sweet birch (*Betula lenta* L.) were the only species that consistently had significantly higher percentages of browsed stems in unfenced treatments (61-82% and 45-100% for red oak and sweet birch respectively), compared to fenced treatments (16-43% and 6-38%). Browse on pin cherry (*Prunus pensylvanicum* L.) and black cherry (*Prunus serotina* Ehrh.) was not significantly different on fenced versus unfenced treatments indicating deer penetration through the fence or other mammal browsing inside the fence. Red maple (*Acer rubrum* L.) browse damage was highly variable ranging from 0-100% on both fenced and unfenced treatments across the six study sites. There were no significant correlations between species-specific stem densities and the proportion of those stems browsed.

Table 3. Comparison of pre-clearcut regeneration information<sup>1</sup> versus 1992 understory vegetation survey.

	SITE 1		SITE 2		SITE 3	
Seedlings/ha	pre-cut	1992 survey	pre-cut	1992 survey	pre-cut	1992 survey
Hardwood seedlings	11600	18890	10280	14850	<3000	1810
Oak seedlings	3700	3890	7410	8100	<500	100
<i>Vaccinium</i> cover	67%	82%	37%	49%	sparse	0%
<i>Kalmia</i> cover	40%	46%	53%	44%	<5%	5%
grass cover	3%	1%	sparse	2%	<5%	5%
fern cover	sparse	1%	sparse	0%	70%	95%

	SITE 4		SITE 5		SITE 6	
Seedlings/ha	pre-cut	1992 survey	pre-cut	1992 survey	pre-cut	1992 survey
Hardwood seedlings	25700	18500	29100	23000	140000	195000
Oak seedlings	2500	3200	0	0	0	0
<i>Prunus serotina</i> L.	15000	7500	12000	8530	24000	29100
<i>Vaccinium</i> cover	15%	23%	sparse	0%	sparse	0%
<i>Kalmia</i> cover	0%	0%	sparse	0%	0%	0%
grass cover	10%	12%	>15%	20%	0%	0%
fern cover	65%	81%	>20%	19%	0%	1%

<sup>1</sup> Based on Bureau of Forestry records. All data presented are based on mean densities or mean % cover on vegetation plots except for values with < or > signs which indicate maximum or minimum estimates.

#### Woody Stem Densities and Importance Values

Total woody stem densities varied across sites and treatments (Table 4). Stem densities on fenced treatments differed significantly from unfenced treatments on sites 2 and 6; the former with lower density on the unfenced treatment and the latter with higher density on the unfenced treatment. Woody stem densities on the 10 supplemental sites ranged from  $41 \times 10^3 \text{ ha}^{-1}$  to  $351 \times 10^3 \text{ ha}^{-1}$  in the adjacent forest understory and from  $23 \times 10^3 \text{ ha}^{-1}$  to  $369 \times 10^3 \text{ ha}^{-1}$  on fenced clearcuts. Based on pooled data from the 6 primary and 10 supplemental sites, understory stem densities were a poor, nonsignificant predictor of stem densities on fenced clearcuts ( $r^2 = 38.2\%$ ). Table 4 shows calculated importance values (IV = relative density + relative frequency) for all woody species encountered in the sampling on the six primary sites. Site specific comparisons across treatments show widespread similarity in IV's for most woody species, with some key exceptions. The IV's for red maple (*Acer rubrum* L.) in the adjacent understory were significantly greater than those in the clearcut treatment for sites 3, 4, and 6. The same pattern was observed for American beech (*Fagus grandifolia* Ehrh.) on site 5. IV's for pin cherry were significantly higher on unfenced versus fenced treatments on sites 3, 5, and 6 while sweet birch showed the reverse trend on those same sites. The IV's for laurel (*Kalmia latifolia* L.) and *Vaccinium* spp. varied little; however, on site 2, laurel showed a decrease in IV on the clearcut treatments and on site 4, exhibited an increase in IV on the clearcut treatments.

Table 4. Comparison of importance values<sup>1</sup> (IV) for woody vegetation by treatment.  
N (not cut, unfenced), F (fenced clearcut), U (unfenced clearcut).

SITE	1			2			3			4			5			6		
	N	F	U	N	F	U	N <sup>2</sup>	F	U	N	F	U	N	F	U	N	F	U
<b>TREES</b>																		
<i>Quercus alba</i> L.	2	-	-	5a	2a	5a	-	-	-	3a	4a	3a	-	-	-	-	-	-
<i>Quercus prinus</i> L.	16a	10a	13a	21a	19a	17a	-	-	-	-	-	-	-	-	-	-	-	-
<i>Quercus rubra</i> L.	12a	9a	6a	5a	5a	3a	23	-	-	25a	22a	15a	-	-	-	-	-	-
<i>Quercus velutina</i> Lam.	-	-	-	-	2	-	-	-	-	2	-	-	-	-	-	-	-	-
<i>Acer rubrum</i> L.	22a	19a	17a	35a	24a	39a	115a	14b	16b	99a	57b	77b	44a	32b	19b	55a	30b	13c
<i>Acer saccharum</i> Marsh.	-	-	-	-	-	-	-	-	-	-	-	-	5a	4a	7a	-	-	-
<i>Fagus grandifolia</i> Ehrh.	-	-	-	-	-	-	-	-	-	-	-	-	97a	23b	26b	15a	24a	18a
<i>Sassafras albidum</i> (Nutt.) Nees	-	13a	14a	-	-	-	40a	82a	84a	-	2a	2a	-	-	-	-	-	-
<i>Liriodendron tulipifera</i> L.	-	-	-	-	-	-	-	10a	5a	-	-	-	-	-	-	-	-	-
<i>Acer pensylvanicum</i> L.	-	-	-	-	-	-	-	-	4	-	-	-	-	8a	4a	12a	31a	29a
<i>Prunus serotina</i> Ehrh.	-	-	-	-	-	-	-	-	-	24	32a	29a	-	19a	8a	34a	20a	25a
<i>Prunus pensylvanica</i> L.f.	-	-	-	-	7	-	23a	41a	58b	-	7	-	19a	66b	103c	68a	44b	82a
<i>Betula lenta</i> L.	-	-	-	-	-	-	-	28a	4b	-	-	-	38a	40a	20b	14a	45b	31a
<i>Betula alleghaniensis</i> Britton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
<i>Pinus strobus</i> L.	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tsuga canadensis</i> (L.) Carr.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-
<i>Populus tremuloides</i> Michx.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
<b>SHRUBS</b>																		
<i>Kalmia latifolia</i> L.	21a	24a	23a	30a	14b	11b	-	19a	21a	-	-	-	-	-	-	-	-	-
<i>Vaccinium</i> spp.	107a	107a	107a	91a	111a	102a	-	5	14a	28b	33b	-	-	-	-	-	-	-
<i>Amelanchier</i> spp.	-	-	-	3	-	3	-	6	4	19a	23a	28a	-	3a	4a	-	-	-
<i>Myrica asplenifolia</i> L.	-	-	4	-	-	5	-	-	-	2	-	-	-	-	-	-	-	-
<i>Hamamelis virginiana</i> L.	20a	19a	16a	12a	15a	13a	-	3	-	2a	2a	-	5a	2a	-	-	-	
<i>Viburnum</i> spp.	-	-	-	-	-	-	-	-	-	17a	20a	12a	-	-	-	-	-	-
Hardwood seedling density <sup>3</sup>	19a	14a	6a	22a	23a	32a	1	4a	3a	78a	52a	59a	23a	78b	99b	195a	41b	71b
Total stem density <sup>3</sup>	29a	22a	7b	32a	27a	38a	1	5a	4a	87a	78a	84a	23a	79b	100b	196a	41b	71b

Different letters denote significant differences ( $P \leq 0.05$ ) in means within each site using Fisher's LSD test.

<sup>1</sup> IV = (relative density + relative frequency)

<sup>2</sup> IV values for the uncut forest are of limited value due to the extremely low stem density

<sup>3</sup> (1000 / ha)

#### Fencing Impacts on Seedling Heights

Figure 1 illustrates differences in mean heights of the dominant (tallest), non-stump sprout origin, tree seedling stems of each tree species found on fenced versus unfenced treatments. On sites 1 and 3 the dominant seedling heights were greater in the fenced than in the unfenced treatments. The relatively tall dominant seedling heights on site 4 reflected the dominance of black cherry growth at the site. However, if black cherry was not included in the mean determinations, there were still no significant differences in dominant seedling heights between the fenced and unfenced treatments. Overall growth performance of hardwood seedlings appeared to be poor relative to that of other published height data. On the oak forest sites, northern red oak seedling height was also found to be positively and significantly related to covers of *Vaccinium* spp. ( $r^2 = 32.4\%$ ).

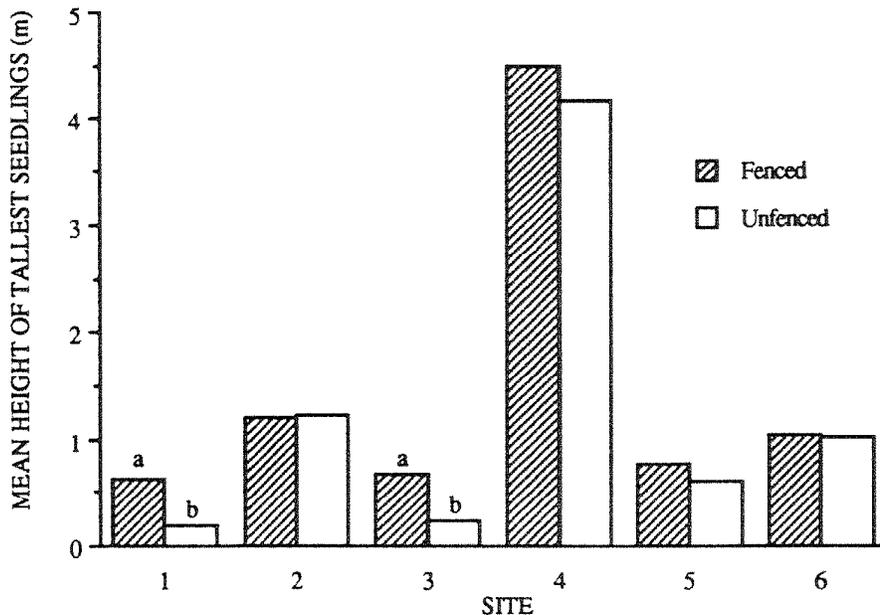


Figure 1. Mean height of the dominant commercial tree seedlings in fenced vs. unfenced clearcuts. Letters denote significant differences ( $P \leq 0.05$ ).

#### Fencing Impacts on Herbaceous Species

Table 5 provides a condensed summary of herbaceous species cover on the six primary study sites. Ground covers of fern, grass and sedge were found across all sites and treatments. Fern cover was generally higher on unfenced versus fenced treatments, although significant differences were found only on sites 3 and 6. Site 6 also had significantly greater fern cover on the clearcut treatments compared to the adjacent understory. Grass and sedge covers on clearcut treatments were generally higher than in the understory. The only significant difference in grass and sedge cover on clearcut treatments was observed on site 5. Cover of *Rubus* on unfenced treatments was significantly lower than the fenced treatment on sites 3 and 5. The remaining covers of herbaceous species were highly variable across sites and treatments, yet the herbaceous cover at each site was generally dominated by a single herbaceous species.

#### Fencing Impacts on Species Richness and Diversity

Total and woody species richness comparisons are summarized in Table 6. Total species richness ranged from 9 to 26 species across sites and treatments. Total species richness on the 10 supplemental sites ranged from 9 to 29 species. Comparisons of the mean number of species per plot between fenced and unfenced clearcut treatments showed no significant differences in either total or woody species richness. Sites 4 and 5 did have significantly lower total species richness in the understory compared to the clearcut treatments. Regression analysis was performed to predict species richness using herbaceous covers on fenced clearcuts (pooled from the six primary and 10 supplemental study sites). Significant negative relationships were found between total species richness and grass and sedge cover ( $r^2 = 31.6\%$ ) and fern cover ( $r^2 = 34.4\%$ ), although the variation explained by these variables is modest.

Table 5. Percent cover<sup>1</sup> of dominant herbaceous species.  
 N (not cut, unfenced), F (fenced clearcut), U (unfenced clearcut).

SITE	1			2			3			4			5			6		
	N	F	U	N	F	U	N	F	U	N	F	U	N	F	U	N	F	U
Ferns <sup>2</sup>	0.5	4.0	1.0	0.0	1.7	0.0	95.1	74.2	91.5	81.0	47.7	73.0	18.9	18.7	28.1	5.0	5.8	29.0
Grass/Sedge	0.7	1.6	0.0	1.7	3.3	1.0	5.1	16.3	14.5	12.1	48.6	53.3	20.0	27.6	14.1	2.5	8.1	14.1
<i>Rubus</i>	1.0	0.0	0.0	0.0	7.0	0.4	0.0	31.4	16.3	3.1	12.3	12.1	2.0	27.6	14.5	4.0	19.7	17.2
Other Herbs	12.0	64.9	18.6	16.3	19.9	53.6	51.7	16.3	57.3	27.5	44.3	51.7	4.2	9.1	5.3	3.7	9.6	9.7

<sup>1</sup> % covers listed have been back transformed from Domin values (Bannister 1966).

<sup>2</sup> predominantly hay-scented fern (*Dennstaedtia punctilobula* [Michx.] Moore)

Table 6. Species richness<sup>1</sup> comparisons for three treatments at each site.

SITE	1	2	3	4	5	6
<i>total species richness</i>						
Not cut (adjacent forest understory)	9	14	16	19	9	12
Fenced Clearcut	13	16	19	26	14	15
Unfenced Clearcut	11	13	18	26	18	17
<i>woody species richness</i>						
Not Cut (adjacent forest understory)	7	8	4	7	4	7
Fenced Clearcut	7	9	8	12	8	6
Unfenced Clearcut	8	10	9	9	10	7

<sup>1</sup> Species numbers represent total number of species tallied at each site

Computed Shannon-Weiner diversity index values (H') are listed in Table 7. Comparison of diversity indices showed no significant difference in diversity between fenced and unfenced treatments on five of the six primary sites. Only site 5 had a significantly lower H' value on the unfenced treatment. This low H' value can largely be attributed to the influence of a high proportion of pin cherry seedlings on the unfenced site.

Table 7. Shannon diversity values ( $H'$ ) for treatments on all sites.

SITE	1	2	3	4	5	6
Not Cut (adjacent forest understory)	0.52a <sup>1</sup>	0.96a	0.95a	0.89a	0.98a	1.15a
Fenced Clearcut	0.55a	0.47b	1.20a	1.67b	1.54b	1.40a
Unfenced Clearcut	0.41a	0.68b	1.18a	1.26b	0.68a	1.24a

<sup>1</sup>Letters denote significant differences ( $P \leq 0.05$ ) in means within each site.

#### Potential Impacts of Soil Parameters

To test the potential direct and/or indirect influence of soil parameters on species richness, soil and species richness data from the 10 supplemental sites were added to the six primary study site data. Only data on fenced clearcuts were used in this analysis due to the lack of unfenced treatments on the supplemental sites. Regression and multiple regression analysis indicate that species richness on fenced clearcuts covaried with some of the soil parameters investigated. As shown in Figure 2, a significant positive relationship was found between species richness and exchangeable Ca levels in the subsoil ( $r^2 = 61.0\%$ ). A significant positive relationship was also found between species richness and organic horizon pH. ( $r^2 = 22.4\%$ ). Significant negative relationships between species richness and exchangeable Al ( $r^2 = 33.4\%$ ) and the molar Ca:Al ratio in the mineral soil horizons ( $r^2 = 35.1\%$ )

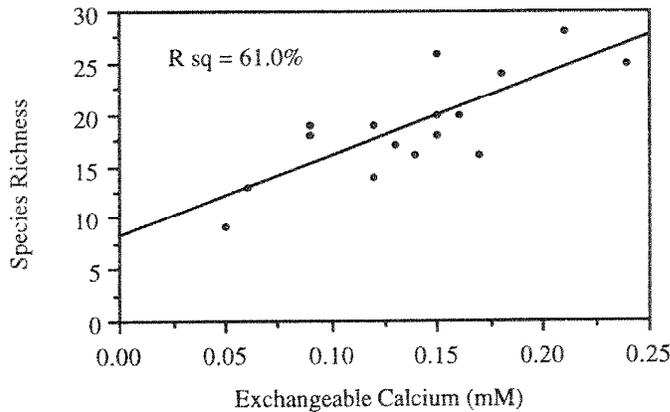


Figure 2. Regression between species richness on fenced clearcuts and exchangeable Ca in the mineral subsoil (15-30 cm depth).

## DISCUSSION

No accurate data were available as to deer densities at the different study sites during the study period. Thus, comparisons with previous deer exclusion and enclosure studies must take into account potential differences in deer browsing pressure as well as differences in foraging patterns. Historically, most exclusion studies have employed woven wire mesh fencing. It is likely that the five- and six-strand electric exclusion fencing present on the study sites discussed here provided less protection than woven mesh fencing. George and others (1991) reported increased deer penetrations through electric fencing after two years of service. The results of the present study also are based on a single sampling period (1992); and the results must be interpreted within that limited framework. These caveats notwithstanding, comparisons of the results of the present study with woven mesh studies can provide useful information in ascertaining the effectiveness of the electric fencing.

Overall, electric exclusion fencing treatments provided limited improvement in promoting increased stocking of desirable hardwood species, enhancement of total species richness or woody species diversity compared to non-fenced treatments. Based on the assumption that the vegetation data collected on adjacent, uncut stands in the current study is representative of the pre-clearcut vegetation on the site, the composition of clearcut vegetation was strongly influenced by the composition of species prior to clearcutting. This result implies that the influence of fencing must be assessed within the framework of vegetation cover prior to harvest. Similar patterns in post-clearcut vegetation composition were noted by Hughes and Fahey (1991). In addition, the results of the current study showed few differences in shrub densities and IV's between understory, fenced and unfenced treatments at each site similar to results presented by Martin and Hornbeck (1989). Few significant differences in absolute woody stem densities were found between fenced and unfenced treatments in this study and by other investigators (Jordan 1967; Marquis 1981). The present study also found significant browse damage and IV declines for sweet birch on unfenced versus fenced treatments as reported by Marquis (1981) and Shafer and others (1961). Other tree species densities and IV's showed variable patterns across treatments and sites. Lack of consistent increases in fern cover in unfenced versus fenced treatments in the current study was also reported by Trumbull and others (1989). Also, paralleling their results, we found a general increase in grass cover following clearcutting on half the study sites.

Contrary to previous studies that found pin cherry nearly eliminated by browse in unfenced clearcut treatments (Marquis 1981), the current study found no differences in mean seedling height or dominant seedling height for pin cherry between fenced and unfenced treatments. In addition, the IV of pin cherry significantly increased in unfenced clearcut treatments on 3 of the 5 sites where it was present. We also found no significant increases in beech or striped maple density, height or IV on unfenced plots as reported by Marquis (1981). These results indicate first, that browse impacts can be highly site specific and second, that vegetation within electric exclusion fencing did not differ as dramatically from unfenced treatments as reported in previous woven mesh fencing studies. The latter point is further reinforced by comparing our results with the deer enclosure study of Tilghman (1989). Tilghman reported that the mean heights of the tallest woody stems on clearcuts were significantly shorter under higher deer densities. While we do not have accurate deer density estimates in the current study, our results show significantly lower heights for dominant woody stems on only 2 of 6 unfenced plots. Thus, despite increased browse pressure on unfenced seedlings, on 4 of the 6 study sites we investigated, some stems were able to reach heights comparable to those within the exclusion fencing.

The present study sites were from 2 to 4 years old and the low woody species richness and diversities observed could be considered an artifact of clearcut age (Gove and others 1992). The improbable recruitment of new seedlings into the clearcuts, however, suggests that woody species richness will show few gains in the short-term. It is difficult to make meaningful comparisons in species richness and diversity across geographical regions which support very different assemblages of species and where different sampling designs have been employed. Nonetheless, the range in woody species richness (4-12 species) and the range in Shannon diversity values reported here (0.41-1.67), although low, fall in the range of values reported by other authors (Locasio and others 1991; Niese and Strong 1992; Tilghman 1989). In terms of herbaceous species richness, the current study showed few differences on fenced versus unfenced clearcuts and only modest gains in numbers of herbaceous species on 2 to 4 year old clearcuts when compared with the understory. This is in contrast to Stransky and others (1986) who reported a greater than doubling

of herbaceous species following the first year after clearcutting of a loblolly pine-hardwood forest and a peak in species richness after 3 years.

Regression analysis of soil variables and species richness on clearcuts in this study provides some preliminary evidence that soil acidity factors may be directly or indirectly influencing plant species growth and composition. Similar to the present study, studies on the North Carolina Piedmont have noted a strong correlation between calcium and magnesium levels in soil and species richness (Palmer 1990; Pect and Christensen 1980). Sharpe and others (1991) also reported increased diversity following liming in a forest understory in western Pennsylvania. In the current study, the low pH's and the low base saturations observed point to potential increased solubility of Al which might play a role in inhibiting cation availability and uptake and ultimately reducing root and shoot growth. In fact, we found significant negative relationships between species richness and both exchangeable Al in the subsoil and the molar Ca:Al ratio in the subsoil. The potential negative impacts of high Al and low Ca levels in subsoils on root uptake, root growth, and overall vigor have been addressed by Tomlinson and Tomlinson (1990). The combined impact of the predisposing stress of extremely acidic soils and the contributing stress of herbivory by deer may be too severe for regenerative success on some sites and indicate that soil evaluation should be considered as an integral component when formulating forest management strategies on extremely acidic forest soils.

#### SUMMARY

The influence of electric deer exclusion fencing on vegetation patterns, species richness, and woody species diversity were investigated on 16 clearcut sites across Pennsylvania. Many site specific and interacting factors are likely to have influenced hardwood regeneration success and the growth and development of plant communities on these sites. The results of this study indicated that hardwood seedling density, species richness, and woody species diversity were not enhanced by the use of electric deer fencing on the hardwood clearcuts studied. Some additional conclusions can be drawn from the current study.

1. Pre-harvest (understory) ground covers of both woody and herbaceous species appeared to have had an impact on species composition in clearcuts regardless of the presence of electric exclusion fencing as evidenced by a high degree of overlap between pre- and post-harvest plant communities. In addition, comparisons of the importance values of woody species (especially shrubs) across fenced versus unfenced treatments on all sites showed few significant differences.
2. Electric deer fencing did reduce browse damage but did not promote increased species richness on clearcuts. No significant differences in total or woody species richness were observed across treatments. Computed Shannon diversity values for woody species on fenced, versus unfenced, clearcuts were significantly higher on only 1 of 6 fenced clearcut treatments.
3. On sites with extremely acidic soils, soil acidity/nutrient factors may be influencing both hardwood regeneration success and the overall composition of plant communities. Because of the variable effectiveness of electric exclusion fencing, it was difficult in this study to separate the effects of deer browse pressure from acidity/nutrient problems. It was clear that use of electric exclusion fencing did not guarantee acceptable hardwood regeneration in terms of relative density and frequency of seedlings or diversity of woody stems. Furthermore, significant positive relationships were found between species richness and soil Ca levels, organic horizon pH, and Ca:Al ratios in the mineral subsoil. A significant negative relationship was found between species richness and exchangeable Al levels in the subsoil.
4. The combined impact of the predisposing stress of extremely acidic soil and the contributing stress of herbivory by mammals (primarily deer), may be too severe for regeneration success on some sites. This indicates that soil chemical evaluation, and possibly remediation through liming and fertilization, should be added to the management equation when formulating forest management strategies on sites with extremely acidic soils, even when deer exclusion fencing is to be utilized.

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## VARIABILITY IN OAK FOREST HERB LAYER COMMUNITIES

J. R. McClenahan and R. P. Long<sup>1</sup>

**Abstract:** This study evaluates forest herb-layer sensitivity to annual-scale environmental fluctuation. Specific objectives were to determine the between-year variation in herb-layer community biomass, and to contrast and evaluate the temporal stability of spatial relationships in herb-layer community structure and composition between successive years. Aboveground dry weights of herbs and of woody species <2.5 cm dbh were estimated in June of 1988 and 1989 in 13 ecologically analogous, oak-dominated stands along a 170-km east-west transect in north-central Pennsylvania. An approximately 50% reduction in total herb-layer biomass was measured from 1988 to 1989, presumably due to a residual or lagged effect of the early summer drought in 1988. Herb biomass reductions were inferred to largely result from reduced plant size rather than decreased spatial distribution. Smaller and (or) less-consistent biomass reductions for woody species may have resulted from high first-year seedling mortality in the case of *Acer rubrum* L., and possibly from intensified deer browsing of shrubs and saplings as a consequence of reduced herb forage resulting from the drought. Classification and ordination also indicated a 1989 reduction in importance of mesic-type species and an increase in similarity of herb-layer communities among stands. Conversely, greater spatial differences in species diversity measures were evident in 1989. Comparisons among herb layer communities based on single or infrequent measurements may be misleading due to large temporal variability and the spatially differential responses that broad-scale environmental factors such as climate may superimpose. Monitoring herb layer biomass in this oak forest ecosystem offers a sensitive means for detecting short-term environmental fluctuations such as annual climate variation, and additional data may enable identification of vegetation trends with statistical confidence.

### INTRODUCTION

Eastern North American deciduous forests receive a multitude of natural and anthropogenic stresses, including climatic extremes, air pollution, and disease and insect outbreaks. These stresses can eventually alter ecosystem composition, structure and function (Graham et al., 1990; Hinrichsen, 1987). A national research priority is to identify and monitor sensitive forest ecosystem indicators that portend such changes.

The forest herb-layer can be a sensitive indicator of microsite (Pregitzer and Barnes, 1982), and is useful for classifying forest ecosystem types (Host and Pregitzer, 1991; Hix, 1988). An altered understory community is theorized to be an early response of forested landscapes to global change (Davis, 1989). However, most long-term studies involve measurement intervals of several years to decades (Rodenkirchen, 1992; Mueggler, 1992), thus masking any effects of climate or other high-frequency environmental fluctuation.

Few annual-scale studies of forest understory have been published. A six-year study of vegetation cover and frequency in a Pinyon-Juniper community demonstrated the high variability to be expected among both perennial and annual herbs, with little fluctuation among shrubs and trees (Treshow and Allan, 1979). It thus appears that spatial and temporal monitoring of herb-layer community dynamics may yield sensitive bioindication of both environmental fluctuations and trends. Further, with appropriate measurements of forest overstory, site, climate, atmospheric pollution and other intervening factors, the influence of these environmental variables can also be assessed.

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This paper focuses on evaluating the spatial and temporal variability of herb-layer biomass in mixed oak forests. Specific objectives were: (1) to determine the between-year variation in herb-layer community biomass and, (2) to contrast and evaluate the temporal stability of spatial relationships in herb-layer community biomass between successive years.

## Background

Ecological monitoring can be a useful approach for investigating long-term processes such as effects of climate change and atmospheric pollution (Likens, 1989). Substitution of space for time is one technique employed to investigate long-term processes on shorter time scales (Pickett, 1989). We used a spatial gradient of wet sulfate and nitrate deposition across north central Pennsylvania to capitalize on an existing range of atmospheric inputs as a substitute of space for time (Likens, 1989). Data reported here were collected as part of the broader study of oak forest condition and response along this gradient (Nash et al., 1992).

Ecologically similar sites are often used to reduce experimental variation, but in studies such as ours where space is substituted for time, different site conditions or histories can lead to erroneous conclusions (Pickett, 1989). Therefore, initial emphasis was placed on selecting ecologically analogous sites. The selection process included ordination and classification analyses of candidate sites using preliminary data on soil physical properties, physiography, canopy stratum species abundances, and evaluation of disturbance history as determined from insect defoliation surveys, forest management records, and on-site evidence of fire and cutting (Long et al., 1991). Our rationale was to confine selection criteria to factors unlikely to have been influenced by chemical deposition. Subsequent intensive sampling of herb-layer biomass on the selected sites in 1988 and 1989 form the basis for this report.

## METHODS

### Study Area

The study region lies within the Appalachian Plateaus Physiographic Province (Ciolkosz et al., 1983). Soils of the study sites are derived from residual sandstone and are mostly Typic Dystrachrepts with small areas of Ultisols and Alfisols. Thirteen ecologically analogous sites (6-50 ha) were selected within four approximately equally-spaced core areas (clustered sites) across the 170-km gradient (Long et al., 1991). The core areas, from west to east and corresponding to the state forests in which they are located, are referred to as Clear Creek (C), Moshannon (M), Sproul (S) and Tiadaghton (T). The 13 sites occupied gently sloping, mostly broad uplands at a mean elevation of 576 m (range: 490-661).

Forest canopy trees on the sites were 70-80 yr old, even-aged, and dominated by *Quercus rubra* L. Common associated canopy species were *Acer rubrum* L., *Quercus alba* L., *Quercus prinus* L., and *Betula lenta* L.

Basal areas for canopy trees on the 13 sites averaged 25.1 (19.7-28.9) m<sup>2</sup>/ha, with a mean overstory density of 291 (243-334) stems/ha. *Sassafras albidum* (Nutt.) Nees, *Hamamelis virginiana* L., *Amelanchier* spp, *Cornus florida* L., and in the Tiadaghton core area, *Acer pensylvanicum* L., were common understory trees.

### Sampling

Herb-layer above-ground biomass was destructively sampled on the 13 sites in 1988 and 1989. Pairs of 3.1 m<sup>2</sup> (1-m-radius) plots were located 14 m north and south (1988) or east and west (1989) of permanent, randomly-established reference stakes. Depending on area of the site, 10 or 20 plots per site were sampled, for a total of 160 plots each year.

Sampling was conducted after the initial growth flush by clipping at the ground surface all herbaceous plants and all woody stems <2.5 cm dbh. In 1988 sampling was completed between June 6 and June 23, and in 1989 between June

5 and June 16. Clipped material was placed in paper bags by species. In the laboratory, samples were temporarily refrigerated, dried at 70° C to constant weight, and weighed to 0.01 g. A voucher collection was prepared. Species identification of *Carex*, *Viola* and other difficult genera was verified by consultation with personnel at The Ohio State University Herbarium.

#### Data Analysis

A split-plot ANOVA fixed effects model was one method used to evaluate spatial and temporal differences in herb layer biomass. Stands were tested as spatial (main) effects, and years and the years by species groups interaction terms were subunits used to test for temporal differences and possible interactions between species and years (Neter et al., 1985). Means of factors with significant F-values ( $P \leq 0.05$ ) were separated by Student-Newman-Keuls' test. Species were combined into groups to avoid non-normality problems resulting from high frequencies of zero's for individual species. The groupings were based mostly on species abundances and taxonomic relationship. One analysis tested two groups consisting of total woody biomass and total herbaceous biomass. A second analysis used the following nine species groups: (1) *Dennstaedtia punctilobula*, (2) other fern species, (3) *Viola* spp., (4) *Gramineae* and *Carex* spp., (5) other herbaceous species, (6) *Vaccinium* spp. and *Gaylussacia* spp., (7) other *Ericaceae*, (8) other shrubs and, (9) tree seedlings. *Kalmia latifolia* was omitted from the second analysis due to its extreme variability in biomass, a result of the wide range in plant size and clumped spatial distribution.

The herb-layer communities were compared on the basis of species biomass by classification and ordination techniques to examine geographical and temporal trends. Plots were classified using Hill's (1979a) TWINSPAN algorithm, and ordinated by detrended correspondence analysis (DCA) using computer program DECORANA (Hill, 1979b).

Species diversity was compared geographically (among core areas) on the basis of Hill's (1973) diversity numbers:  $N_0$ ,  $N_1$ , and  $N_2$  (Ludwig and Reynolds, 1988).  $N_0$  is the number of species.  $N_1$  is calculated as  $e^{H'}$ , where  $e$  is the base of natural logarithms and  $H'$  is Shannon's diversity index, yielding the biomass-weighted or *effective* number of relatively well-represented species.  $N_2$  is  $1/\lambda$ , where  $\lambda$  is Simpson's diversity index, which provides a biomass-weighted *effective* number of relatively dominant species. The modified Hill's ratio (Alatalo, 1981), a measure of evenness ( $E$ ), was calculated for core areas as  $(N_2 - 1)/(N_1 - 1)$ . Thus,  $E$  achieves a maximum of 1.0 when all species are equally abundant, whereas values of  $E$  approaching the minimum of 0 indicate increasing dominance by a single species.

Biomass distribution among species was also compared between years and among core areas on the basis of dominance-diversity curves (Bonham, 1989).

## RESULTS

Biomass for each species sampled on plots is presented in Table 1. Analysis of variance detected no significant differences in biomass among the 13 sites ( $P \leq 0.05$ ) on the basis of the nine species groups; nor were site differences found when total woody and total herbaceous biomass groupings were used.

However, there was a significant difference in biomass between years when the nine species groups were used in ANOVA, with mean biomass decreasing nearly 50% from 1988 (283.5 kg/ha) to 1989 (151.1 kg/ha). Between-year biomass reductions were consistent for the nine species groups. The relative decreases were close to 50% (40.4% - 56.6%) for all four herbaceous groups and the miscellaneous shrubs, while the smallest decrease (12.1%) occurred within the tree seedling group. A significant species group by year interaction resulted from the comparatively large biomass reduction of *Dennstaedtia punctilobula*. For other individual species, primarily those with low plot frequencies (e.g., *Dryopteris spinulosa*, *Podophyllum peltatum*, *Vaccinium vacillans*; Fig. 1) between-year biomass differences were less consistent (Table 1).

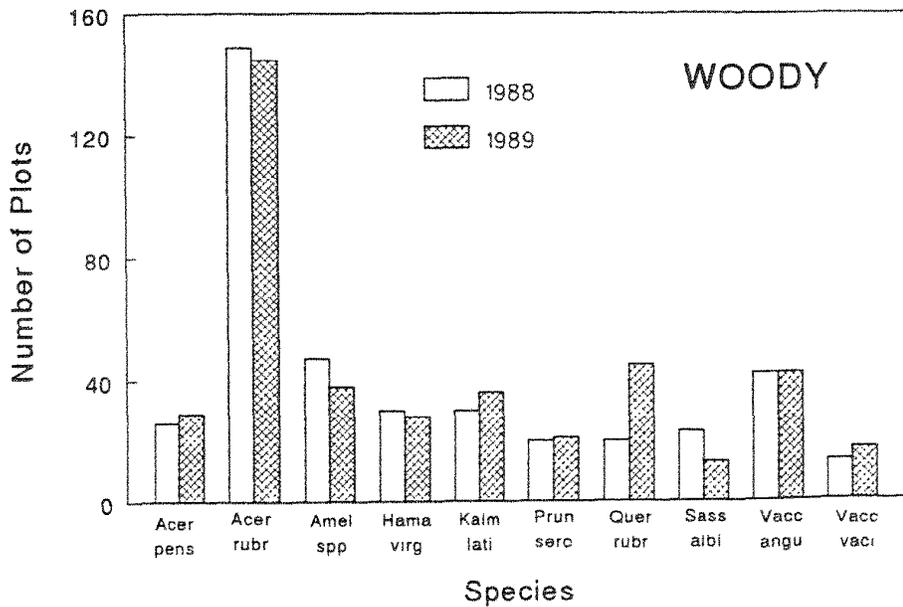
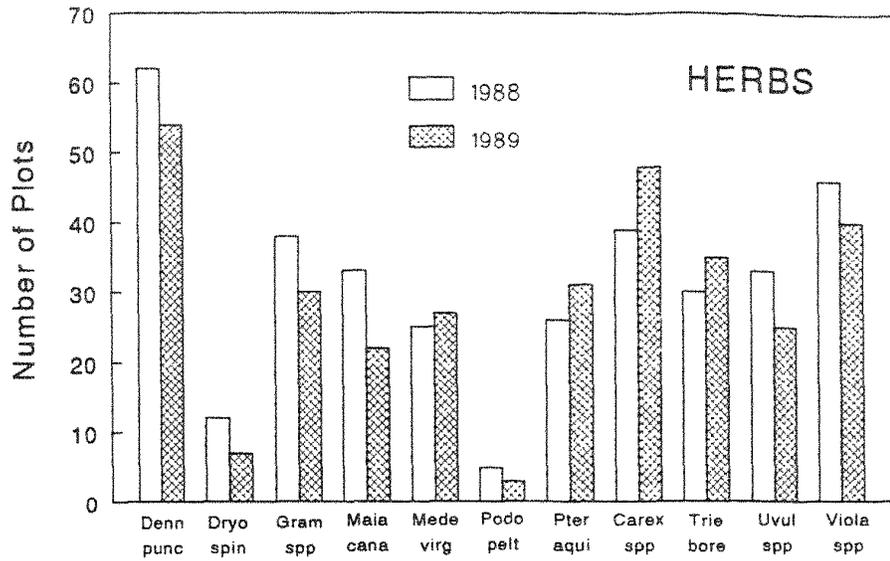


Figure 1. Plot frequencies of selected herbaceous and woody species. Complete species names are found in Table 1.



Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
<i>Cornus florida</i> L.	1988	-	0.41	-	-
	1989	-	-	-	-
<i>Craetegus</i> spp.	1988	1.46	-	0.35	-
<i>Danthonia compressa</i> Aust.	1988	-	41.0	55.1	-
	1989	-	3.44	3.08	-
<i>Dennstaedtia punctilobula</i> (Michx.) Moore	1988	112.2	200.6	239.0	504.8
	1989	58.3	67.3	89.1	398.2
<i>Dryopteris spinulosa</i> (O.F. Muell.) Watt	1988	5.15	6.22	0.16	28.1
	1989	1.61	12.5	0.13	7.64
<i>Euonymus</i> spp.	1988	-	-	-	0.16
	1989	-	-	-	-
<i>Eupatorium rugosum</i> Houtt.	1988	-	-	-	1.56
	1989	-	-	-	-
<i>Fagus grandifolia</i> Ehrh.	1988	0.22	26.7	-	8.50
	1989	-	104.4	-	4.96
<i>Fraxinus americana</i> L.	1988	-	-	-	0.84
	1989	0.03	0.08	-	0.30
<i>Galium</i> spp.	1988	0.52	-	-	-
	1989	0.03	0.32	-	-
<i>Gaultheria procumbens</i> L.	1988	2.83	29.7	1.31	2.70
	1989	3.86	6.22	1.28	2.26
<i>Gaylussacia</i> spp.	1988	50.2	-	-	-
	1989	244.	-	-	-
<i>Hamamelis virginiana</i> L.	1988	10.9	1.68	0.13	83.1
	1989	6.70	1.38	0.32	9.32
<i>Hepatica acutiloba</i> DC.	1988	-	-	-	-
	1989	-	0.06	-	-
<i>Hypericum</i> spp.	1988	-	0.03	-	-
	1989	-	-	-	-
<i>Ilex verticillata</i> (L.) Gray	1988	2.29	0.13	-	-
	1989	-	1.02	0.32	-

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
<i>Kalmia latifolia</i> L.	1988	0.89	3690	2120	2394
	1989	110.6	65.0	1091	2993
<i>Liriodendron tulipifera</i> L.	1988	0.03	-	-	-
	1989	-	-	-	-
<i>Lycopodium obscurum</i> Var. <i>dendroideum</i> (Michx.) D.C. Eat.	1988	-	-	-	-
	1989	0.35	-	-	-
<i>Lysimachia quadrifolia</i> L.	1988	2.96	0.11	0.06	0.60
	1989	0.89	0.48	-	0.70
<i>Magnolia acuminata</i> L.	1988	-	-	-	-
	1989	-	2.16	-	-
<i>Maianthemum canadense</i> Desf.	1988	0.90	1.00	0.06	0.29
	1989	0.70	0.20	-	0.48
<i>Medeola virginiana</i> L.	1988	2.38	3.21	0.21	0.23
	1989	0.78	2.96	0.34	1.05
<i>Mitchella repens</i> L.	1988	2.59	4.68	-	-
	1989	0.40	3.50	0.67	1.75
<i>Monotropa uniflora</i> L.	1988	-	1.92	1.95	-
	1989	-	-	-	-
<i>Nyssa sylvatica</i> marsh.	1988	0.83	-	1.53	-
	1989	0.53	5.57	0.10	-
<i>Onoclea sensibilis</i> L.	1988	1.59	-	-	-
	1989	-	-	-	-
<i>Oryzopsis asperifolia</i> Michx.	1988	3.41	15.2	17.7	-
	1989	-	5.51	2.51	-
<i>Panax trifolius</i> L.	1988	-	-	0.32	-
	1989	-	-	-	-
<i>Panicum</i> spp.	1988	0.64	0.16	-	-
	1989	0.06	8.54	-	-
<i>Phlox</i> spp.	1988	-	-	-	-
	1989	-	-	0.03	0.37

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
<i>Pinus strobus</i> L.	1988	0.16	-	0.03	-
	1989	-	-	-	-
<i>Poa</i> spp.	1988	-	-	-	1.37
	1989	-	-	-	-
<i>Podophyllum peltatum</i> L.	1988	6.12	-	-	-
	1989	24.4	-	-	-
<i>Polygala paucifolia</i> Willd.	1988	-	-	-	-
	1989	-	0.13	0.16	-
<i>Populus grandidentata</i> Michx.	1988	2.20	-	-	-
	1989	-	-	-	-
<i>Potentilla</i> spp.	1988	1.81	-	-	-
	1989	-	-	-	-
<i>Prenanthes</i> sp.	1988	0.60	0.09	-	0.42
	1989	0.03	0.14	0.17	0.95
<i>Prunus serotina</i> Ehrh.	1988	0.67	0.40	-	0.40
	1989	0.30	0.21	-	4.22
<i>Pteridium aquilinum</i> (L.) Kuhn	1988	8.59	111.7	-	-
	1989	1.02	66.5	-	-
<i>Quercus alba</i> L.	1988	-	0.58	-	-
	1989	0.29	0.53	0.10	0.80
<i>Q. coccinea</i> Muenchh.	1988	1.81	-	-	-
	1989	-	-	-	-
<i>Q. prinus</i> L.	1988	1.29	1.20	-	1.69
	1989	-	-	-	13.8
<i>Q. rubra</i> L.	1988	0.54	0.54	1.02	1.09
	1989	0.80	1.74	0.93	0.55
<i>Q. velutina</i> Lam.	1988	0.83	0.40	0.22	0.68
	1989	-	-	-	-
<i>Rubus</i> spp.	1988	0.38	0.57	-	-
	1989	-	0.10	-	0.06
<i>Sassafras albidum</i> (Nutt.) Nees	1988	0.44	4.51	2.65	-
	1989	-	0.66	0.37	-

Table 1 (continued)

Species	Year	C	M	S	T
		-kg/ha-			
<i>Smilacina racemosa</i> (L.) Desf.	1988	-	-	-	-
	1989	-	-	0.89	-
<i>Smilax herbacea</i> L.	1988	-	-	-	-
	1989	2.43	-	-	-
<i>S. rotundifolia</i> L.	1988	0.60	0.92	3.47	-
	1989	0.38	0.29	0.13	-
<i>Solidago</i> spp.	1988	-	-	-	-
	1989	0.32	0.04	-	-
<i>Streptopus</i> spp.	1988	-	0.06	-	0.10
	1989	0.21	0.43	-	0.76
<i>Thelypteris noveboracensis</i> (L.) Nicuwl.	1988	-	41.2	2.58	-
	1989	-	7.25	-	-
<i>T. palustris</i> Schott	1988	-	62.3	-	-
	1989	0.13	-	-	-
<i>Trientalis borealis</i> Raf.	1988	2.05	0.75	-	1.27
	1989	1.15	1.49	-	1.40
<i>Trillium undulatum</i> Willd.	1988	-	0.65	-	0.51
	1989	0.37	0.41	0.03	0.60
<i>Uvularia perfoliata</i> L.	1988	0.22	1.05	-	-
	1989	0.70	-	0.06	1.46
<i>U. sessilifolia</i> L.	1988	1.25	0.80	0.14	0.11
	1989	0.70	0.97	-	1.72
<i>Vaccinium angustifolium</i> Ait.	1988	127.1	133.4	28.3	24.1
	1989	103.9	100.2	14.2	10.3
<i>V. vacillans</i> Torr.	1988	62.3	48.2	-	6.68
	1989	23.8	73.5	2.39	-
<i>Viburnum acerifolium</i> L.	1988	5.49	-	-	2.10
	1989	-	-	-	20.2
<i>Viola hastata</i> Michx.	1988	0.46	0.13	-	-
	1989	0.32	1.24	-	1.24
<i>V. pallens</i> (Banks) Brainerd	1988	19.2	0.03	-	-
	1989	-	-	-	-

Table 1 (continued)

Species	Year	C	M	S	T
			-kg/ha-		
<i>V. rotundifolia</i> Michx.	1988	4.06	-	-	0.28
	1989	-	-	-	-
<i>V. spp.</i>	1988	1.29	0.48	0.06	0.76
	1989	1.74	-	-	-
<i>Vitis</i> spp.	1988	0.04	0.08	0.06	8.12
	1989	0.05	0.20	-	0.12
Total Woody	1988	279.2	3924.	2164.	2875.
	1989	496.0	372.0	1111.	3257.
Total Herbaceous	1988	266.3	576.7	351.9	569.5
	1989	112.4	200.7	117.2	429.2
TOTAL	1988	545.5	4500.	2516.	3445.
	1989	608.4	572.7	1228.	3686.

#### Spatial Relationships

**Classification.** TWINSpan analysis revealed considerable overlap in species composition among core areas (Fig. 2). With the notable exception of Tiadaghton, plots were not strongly segregated by core areas in either year. The most important indicator species in both years were *K. latifolia*, *D. punctilobula* and *A. rubrum*, with high relative abundances of *K. latifolia* and *A. pensylvanicum* distinguishing most Tiadaghton plots from those of other core areas. *A. rubrum* and *Vaccinium angustifolium* were additional consistent indicator species between years.

Other indicators in 1988 were mostly representative of mesic sites, including *Viola pallens*, *Amelanchier* spp., *Trientalis borealis*, *Maianthemum canadense*, *D. spinulosa* and *Brachyelytrum erectum*. In contrast, additional indicators in 1989, *Carex pensylvanica* and *Gaultheria procumbens*, were typical of dry or acidic sites, except for the unique occurrence of *Podophyllum peltatum* as an indicator on two plots (Fig. 2).

The shift between years from mesic to xeric indicator types and associated species (preferentials) was also evident at more refined divisions (not shown). Mesic herbs (e.g., *Viola* spp.) in the 1988 analysis tended to be replaced by xeric shrubs and herbs (e.g., *Vaccinium pallens*, *V. angustifolium*, *Pteridium aquilinum*, *G. procumbens*) in 1989. Moreover, compared to 1989, the 1988 analysis identified more indicator species, and revealed more detailed vegetational trends.

**Ordination.** The 1988 DCA ordination generally confirmed the considerable overlap of plots from Clear Creek, Moshannon, and Sproul, and the distinction of most Tiadaghton plots as indicated by TWINSpan (Fig. 3). The 1989 ordination reflected a more homogeneous vegetation structure than did that for 1988, especially regarding the Tiadaghton samples (Fig. 3). The three outlying Moshannon plots seen in the 1988 and 1989 ordinations and classifications are due to the presence of *Fagus grandifolia* Ehrh.

The 1988 species ordinations (Fig. 4) suggest a weak moisture gradient on the first axis. The gradient extends from species mostly associated with well-drained soils (*A. pensylvanicum*, *F. grandifolia*, *Fraxinus americana* L., *Carex swanii* (Fern.) MacKen. and *K. latifolia*) to those associated with more mesic sites (*Viola* spp., *P. peltatum*) and finally to species typical of very moist sites (*Thelypteris noveboracensis* (L.) Nieuwl. and *Thelypteris palustris* Schott).

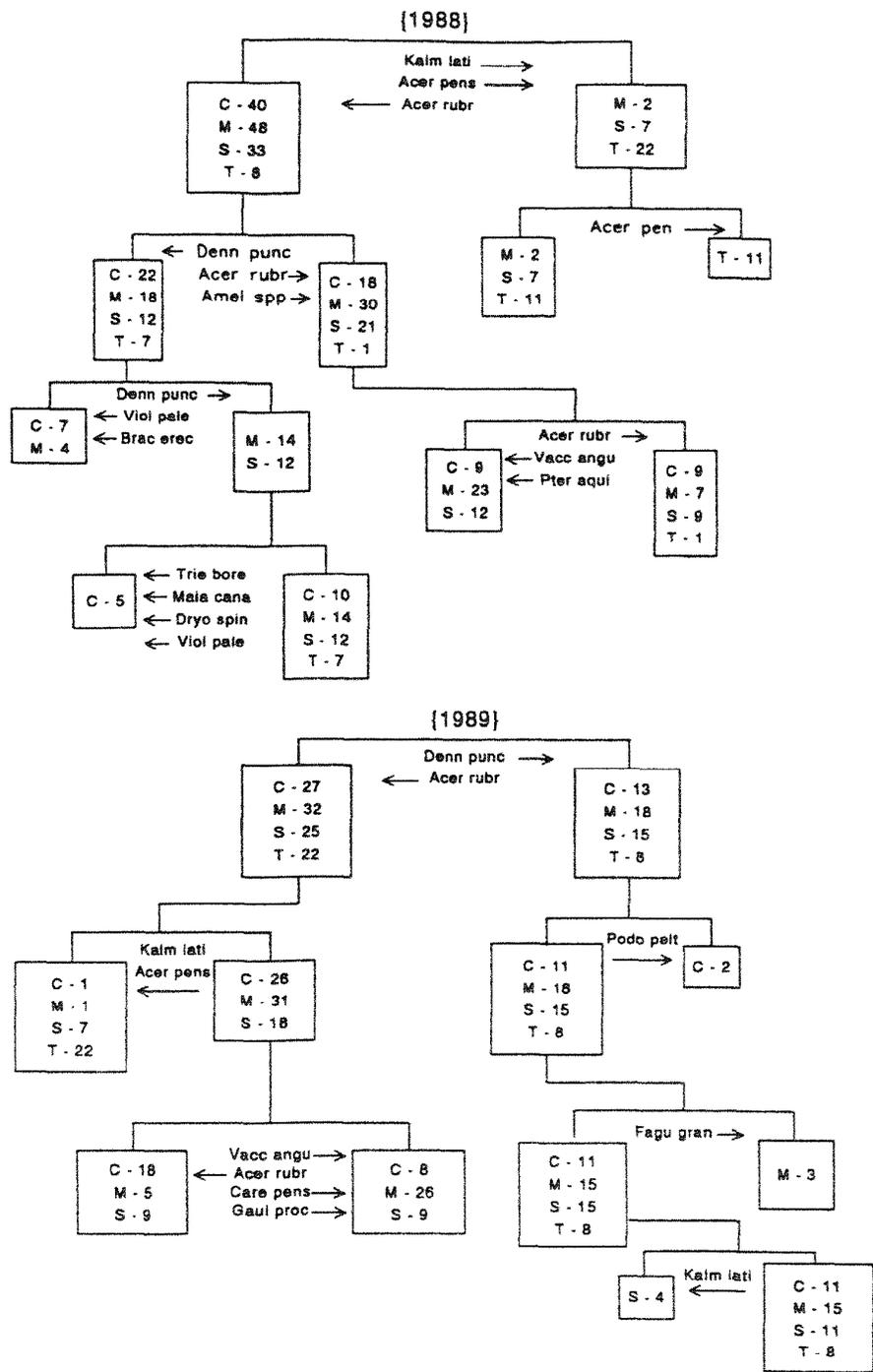


Figure 2. Hierarchical (TWINSPAN) classification of plots according to core areas in 1988 and 1989. Major indicator species and their directional indication are shown by arrows.

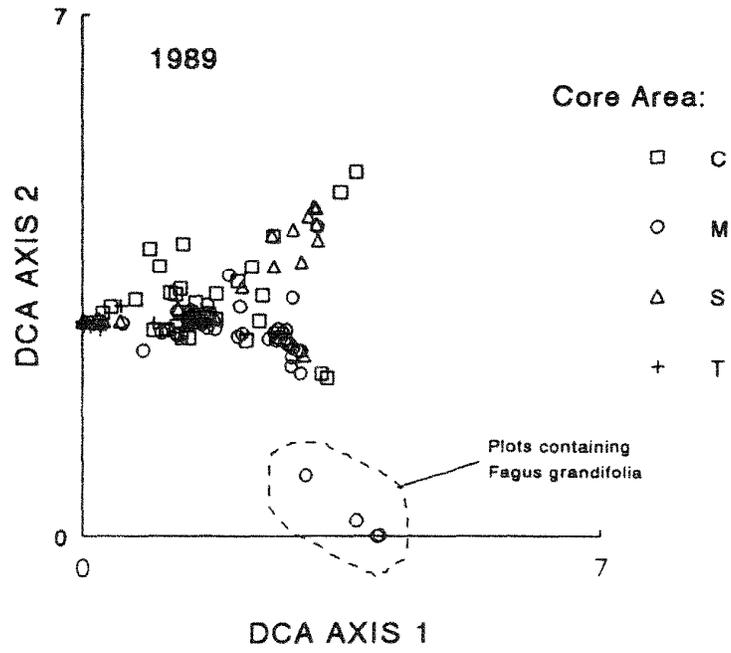
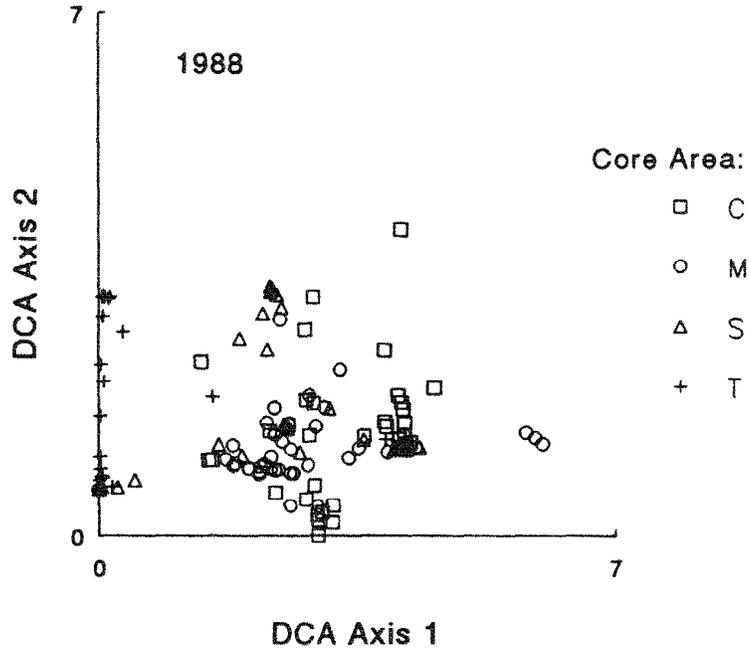


Figure 3. Detrended correspondence analysis (DCA) ordinations of plots in 1988 and 1989 in relation to core areas.

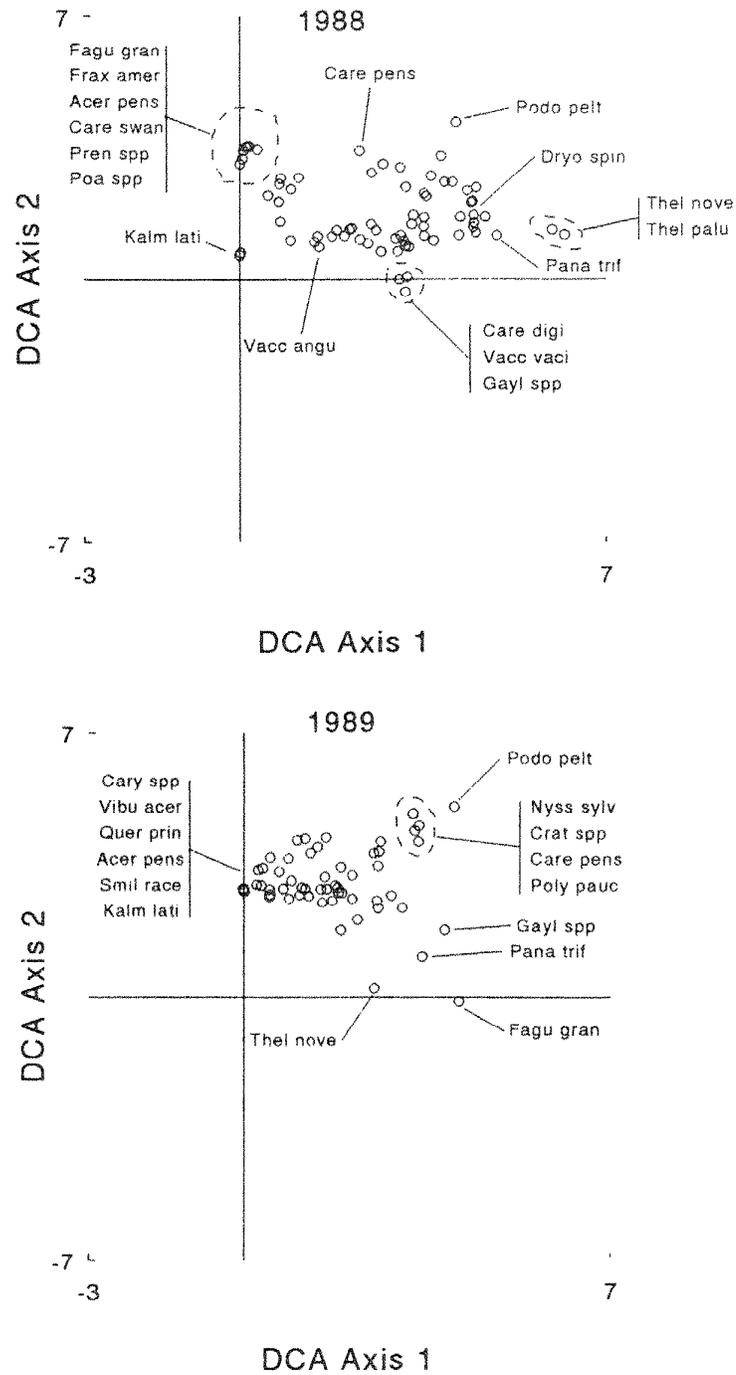


Figure 4. Detrended correspondence analysis (DCA) ordinations of species in 1988 and 1989 in relation to core areas. Species names are found in Table 1.

The second DCA axis revealed a slight trend from mostly ericaceous shrubs typical of infertile, acidic soils (e.g., *K. latifolia*, *Gaylussacia* spp., *Vaccinium* spp.) to more fertile, mesic site species such as *P. peltatum*, *C. swanii*, *Poa* spp., *A. pensylvanicum*, *F. grandifolia*, and *F. americana*. In 1989, these relationships were not evident and, as was the case for the plot ordinations, there was little differentiation except for a few outliers (Fig. 4).

Differences in herb-layer composition on the Tiadaghton core area suggested by classification and ordination are evident in the comparative species abundances (Table 1). Seven species were sampled almost exclusively at Tiadaghton in 1988, while four species sampled on most or all other core areas were absent at Tiadaghton. Particularly notable were the comparative abundances of *A. pensylvanicum* and *C. swanii* at Tiadaghton, and the absence of three species well-represented on other core areas: *S. albidum*, *Smilax rotundifolia* L., and *Oryzopsis asperifolia* Michx.

**Species Diversity.** On the basis of Hill's diversity numbers, the western pair of core areas (Clear Creek and Moshannon) had greater species richness (N0) and more abundant (N1) and very abundant (N2) species than the two eastern core areas in both years (Table 2). Conversely, evenness was similar among all four core areas in 1988; however, between 1988 and 1989 it increased at Clear Creek and Moshannon, but decreased at Sprout and Tiadaghton. This same temporally diverging pattern is evident for N1 and N2 between the western and eastern pairs of core areas. However, within the western and eastern pairs of core areas these diversity measures were consistently similar.

The dominance-diversity curves indicate a lognormal distribution typical of relatively complex, species-rich communities (Fig. 5). They clearly illustrate the distributional differences in species abundances between the western and eastern pairs of core areas noted above. A shift toward greater similarity in species distributions is also revealed between Clear Creek and Moshannon from 1988 to 1989, making each half of the gradient appear even more distinct in 1989. These spatial patterns reveal distinctly lower species diversity in the eastern half of the gradient.

## DISCUSSION AND CONCLUSIONS

Lacking site-specific environmental monitoring data, reasons for the large between-year differences in herb-layer biomass cannot be definitely determined. However, a severe drought developed over the 1988 growing season. Palmer Drought Severity indices revealed mild drought conditions across the study area by the end of April (Figure 6). Drought conditions were rated moderate (-2.3 to -2.5) by mid-June, becoming severe (-3.3 to -3.5) in July. Despite increased rainfall in mid-July, drought conditions prevailed through August (Figure 6). There was little difference in drought severity across the study transect. In contrast, growing season precipitation in 1987 and 1989 was at or above normal.

We suggest that the 1988 drought could have produced a lagged decrease in herb layer production as measured in 1989. Such a lag might occur among perennial herbs with large belowground storage organs if initial growth flush is largely determined by stored reserves. For herbaceous plants, this decrease would likely have occurred primarily through a reduction in the size of individual plants and, for rhizomatous species, perhaps the numbers of stems as well. Both of these factors could have been operative in the case of *D. punctilobula*, the most abundant and widely distributed herbaceous species (Table 1, Fig. 1). The nearly 50% reduction in total biomass between years cannot be attributed entirely to the small reduction in distribution (Fig. 1). Mortality or decreased reproductivity probably contributed relatively little to the herbaceous biomass decrease, as suggested by the comparatively small reductions or even increases in plot frequencies. For example, there was a large between-year decrease in *Carex* spp. biomass (Table 1), yet plot frequency increased (Fig. 1). Thus, herb-layer biomass reductions between years are inferred to result more from reduced plant size rather than decreased spatial distribution.

The above hypothesis cannot, however, be directly invoked to explain the apparent 1989 woody biomass reduction. The large but non-significant decrease in *K. latifolia* biomass is evidently an artifact of extreme variability in plant size and patchy distribution. Seedlings of many tree species such as *Q. rubra*, *Amelanchier* spp., *H. virginiana*, and *Prunus serotina* Ehrh. also did not change perceptibly in frequency (Fig. 1), but were relatively uncommon and highly variable in individual plant size, all of which contributed to inconsistent between-year differences.

Table 2. Species diversity measures summarized for core areas and years.

Core Area	Year	n <sup>1</sup>	NO <sup>2</sup>	N1 <sup>2</sup>	N2 <sup>2</sup>	Evenness <sup>3</sup>
Clear Creek	1988	40	58	6.53	3.74	0.50
	1989	40	51	7.43	5.44	0.69
Moshannon	1988	50	55	4.95	3.24	0.57
	1989	50	49	7.65	5.28	0.63
Sproul	1988	40	31	1.83	1.41	0.49
	1989	40	33	1.66	1.31	0.47
Tiadaghton	1988	30	41	2.31	1.78	0.59
	1989	30	38	1.75	1.36	0.48

<sup>1</sup>Number of 3.1 m<sup>2</sup> plots

<sup>2</sup>Hill's diversity numbers (Hill, 1973); includes unidentified species.

<sup>3</sup>Modified Hill's ratio (Alatalo, 1981).

In contrast, *A. rubrum* seedling density can fluctuate markedly even within a growing season (McClenahen and Hutnik, 1979). This species was widely distributed (Fig. 1), but newly germinated seedlings predominated. Prolific seed production often results in large *A. rubrum* populations in late spring when the current seed crop is dispersed and germinates. Many of these seedlings disappear by autumn (McClenahen and Hutnik, 1979).

*A. pensylvanicum* was well-represented at Tiadaghton, but not elsewhere (Table 1), and significantly decreased by almost 50% in biomass between years. The most abundant and well-distributed shrub, *V. angustifolium*, also declined in biomass (by 27%) between years (Table 1). Plot frequency did not change (Fig. 1), but it is unclear from the data how this biomass reduction occurred. An interesting conjecture, however, is that deer browsing and drought may have interacted. Deer browsing has had a major, long-term impact on forest understory vegetation in northern Pennsylvania (Hough, 1965; Marquis, 1974). In order to compare deer browsing intensities on the study sites, we used the pellet group count method to estimate deer population densities for each site in 1992 (Eberhardt and Van Etten, 1956). Sampling was confined within the site boundaries, so deer densities reflect comparative deer use of the sites during the dormant season (October - April); they cannot be interpreted as actual population estimates. Densities averaged 9.4 deer per km<sup>2</sup> (range: 1.8 - 28.3). Except for one Sproul site, all density estimates were above levels believed to reduce understory richness and cover (D. deCalesta, personal communication).

Thus, intensive deer browsing has probably altered the herb-layer over the long term at virtually all sites and may have exacerbated the impact of other stresses on existing vegetation. As a result of drought-reduced herbage by early summer of 1988, deer may have more intensively browsed woody vegetation. Woody species most clearly reduced in biomass were *V. angustifolium* and, at Tiadaghton, *A. pensylvanicum*. These two species are utilized by deer (Marquis, 1974; Bramble and Goddard, 1953), and may have been more heavily browsed if herbaceous forage was less available. The potential for interactions between deer browsing and other environmental stresses to impact forest understory community dynamics is poorly understood and deserves further investigation.

Classification and ordination revealed no clear geographical separation of herb layer communities in either year. Although these analyses indicated that Tiadaghton communities were less like those in other core areas, this was only evident in 1988. The relatively different vegetation at Tiadaghton was also detected by similar analyses of the overstory community (and site factors) during site selection (Long et al., 1991). This tends to validate our original approach that focused on the dominant vegetative stratum along with disturbance history, physiography and soil physical properties as a sufficient and practical basis for choosing ecological analogs.

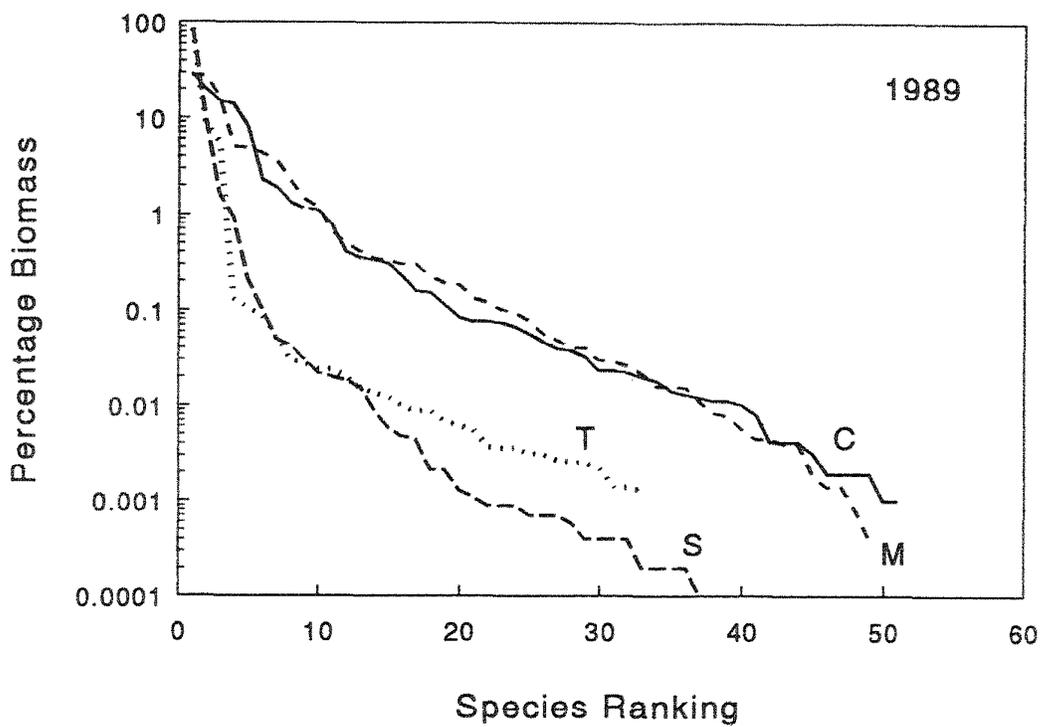
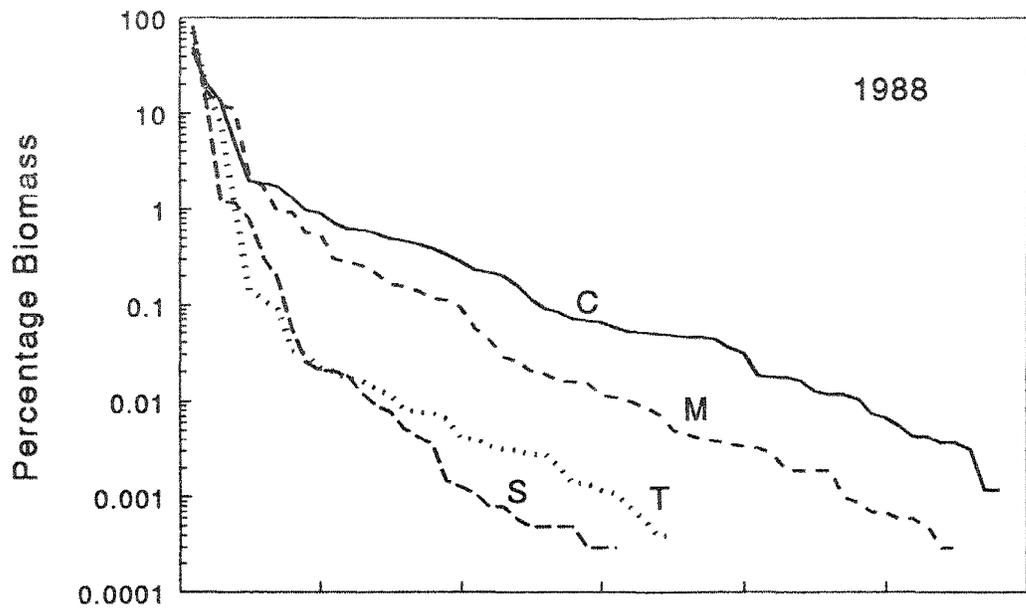


Figure 5. Dominance-diversity curves for core areas in 1988 and 1989.

SECTION:  West  Central  East

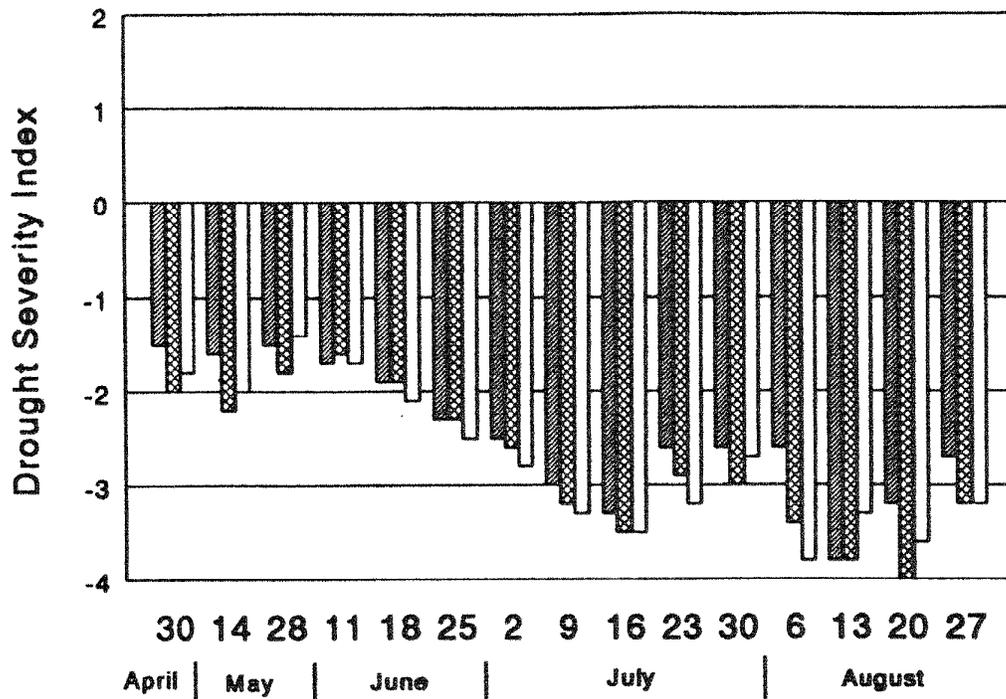


Figure 6. Palmer Drought Severity Indices during the 1988 growing season for climatic divisions corresponding to western, central and eastern sections of the study area (National Weather Service, 1988).

Two important temporal differences detected by classification and ordination were a reduction in mesic site indicator species and an increase in apparent vegetative similarity, particularly regarding Tiadaghton. Several investigators found inherent resistance to changes in spatial distribution among certain of the same species within herb-layer communities similar to ours (Hughes and Fahey, 1991; Collins and Pickett, 1988). Distributions of these species, especially the "stress-tolerators" (Grime, 1979), are hypothesized to develop under favorable conditions, and are maintained by a capacity to tolerate subsequent environmental stresses (Hughes and Fahey, 1991). Our results suggest that, despite any such resistance to broad-scale (successional) changes, this forest herb community can exhibit large annual-scale biomass variation, presumably in response to environmental fluctuation such as the 1988 drought.

Whatever the cause(s) of the annual biomass variation, mesic species were reduced in biomass to the extent that they were less useful for classifying (and ordinating) plots in 1989. The 1989 analyses were therefore less revealing of subtle variations in herb-layer community structure among these relatively analogous sites. This underscores the importance of considering the impact of recent climatic or other environmental perturbations when using the herb stratum to detect experimental effects or to compare sites at a single point in time. Also revealed is the capacity for large annual variability of this herb layer community.

Monitoring herb layer biomass in this oak forest ecosystem offers a sensitive means for detecting short-term environmental fluctuations such as annual climate variation. This short-term variability could have a large effect on interpretations of experiments that are based on single or infrequent measurements. Conversely, annual monitoring will eventually yield estimates of the short-term variability that can potentially be used to identify vegetation trends with statistical confidence.

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