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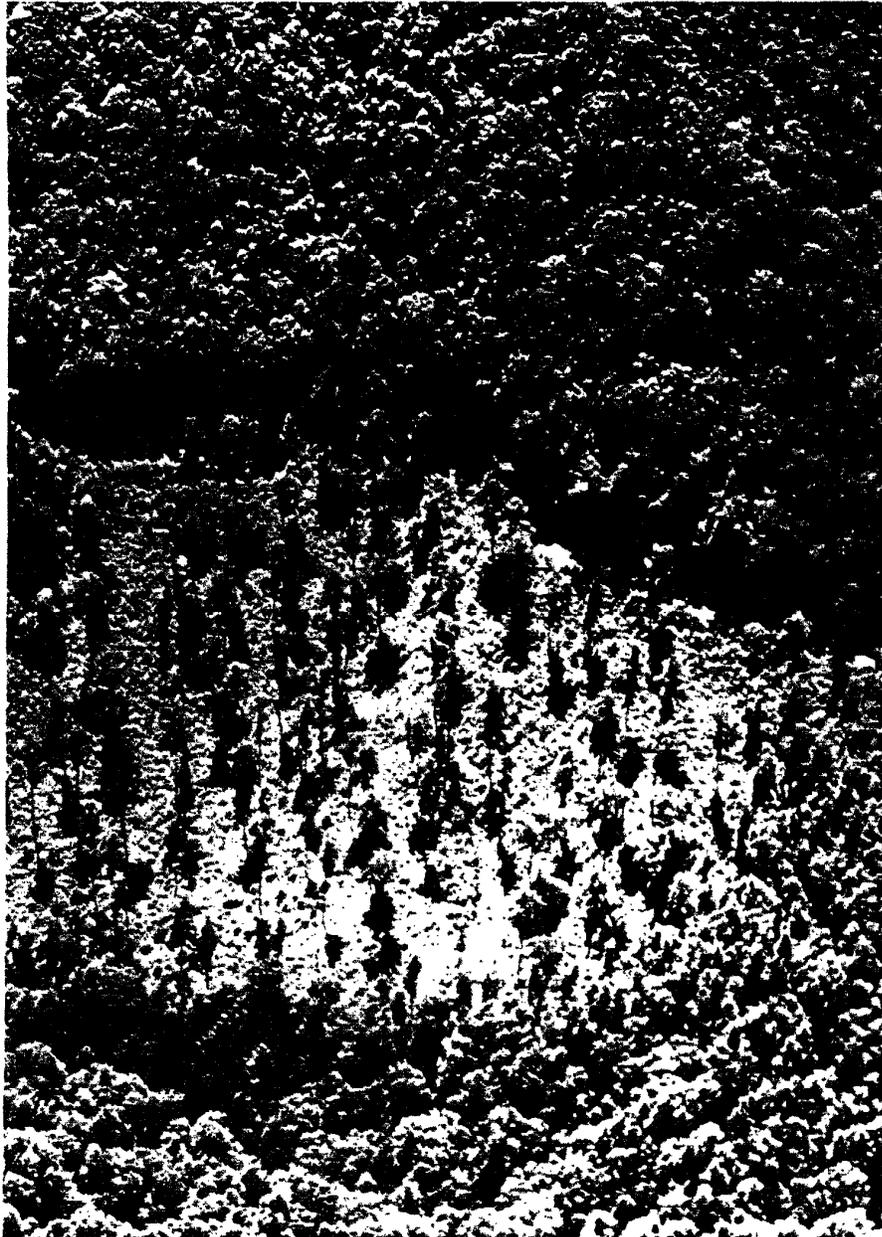
General Technical
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Proceedings

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

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

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10TH CENTRAL HARDWOOD FOREST CONFERENCE

Proceedings of a Meeting

Held at

Lakeview Resort and Conference Center

Morgantown, WV

March 5-8, 1995

Edited by

Kurt W. Gottschalk and Sandra L. C. Fosbroke

SPONSORED BY:

Division of Forestry, West Virginia University

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FOREWORD

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

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

REVIEW PROCEDURES

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

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AN ANALYSIS OF PHENOTYPIC SELECTION IN NATURAL STANDS
OF NORTHERN RED OAK (*QUERCUS RUBRA* L.)

Jeffrey W. Stringer, David B. Wagner, Scott E. Schlarbaum, and Daniel B. Houston¹

Abstract: Comparison of growth and stem quality parameters of 19-year-old progeny from superior and comparison trees indicates that rigorous phenotypic selection of trees in natural stands may not be an efficient method of parent tree selection for *Quercus rubra* L. Total tree height, dbh, number of branches in the butt log, fork height, and number of mainstem crooks of progeny from 11 phenotypic select trees and their co-occurring comparison trees were analyzed. Pooled data from 4 test sites indicated no difference in dbh or number of mainstem crooks among select and comparison families. However, comparison families were significantly ($p \leq 0.05$) taller, had significantly less branches in the butt log, and higher fork heights than select families. Similar patterns of variation were also found within test sites. The large degree of within-stand variation in growth and stem quality traits among families indicates that selecting several phenotypically above-average candidate trees may be more effective than rigorously selecting a smaller number of phenotypically superior *Q. rubra* trees.

INTRODUCTION

Mass selection of superior phenotypes is the most widely used method of obtaining material for the initial stages of tree breeding programs (Zobel and Talbert 1984). Regional *Quercus rubra* L. improvement programs have recently been initiated in both the central and southeastern U.S. (Cox and Schlarbaum 1991, Robison and Overton 1987). These programs have used mass selection to provide material for the establishment of seed orchards and test plantings. Results of relatively young provenance/progeny tests of *Q. rubra* have shown a large degree of intra-stand and provenance growth variation (Farmer and others 1981, Houston 1987). This suggests that gains through mass selection are possible however, gains from plus-tree selections have proved inconsistent (Robison 1988). Previous tests have focused primarily on growth characteristics which, for some hardwood species, have relatively low narrow-sense heritabilities (Zobel and Talbert 1984). The use of phenotypic selections in natural stands of *Q. rubra* remains appealing in light of potential stem quality gains, certain aspects of which may have high narrow-sense heritabilities (Zobel and Talbert 1984). Little information on potential stem quality gains is available for *Q. rubra* as previous analyses of provenance/progeny tests were completed in relatively young plantings (Kriebel 1993).

This paper addresses the question of whether mass selection criteria need be extremely rigorous to provide gains in the initial stages of *Q. rubra* tree improvement programs. Specifically, we were interested in comparing the performance of open-pollinated progeny from some of the best phenotypes in the region to the performance of open-pollinated progeny from several above-average phenotypes or "comparison" trees from the same stands as the select phenotypes. Results of our analysis may aid in designing effective selection strategies for *Q. rubra*.

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METHODS

Experimental Materials

We studied 19-year growth and stem quality data from 43 open-pollinated *Quercus rubra* L. families from a provenance/progeny test of 226 *Q. rubra* families established in 1973 by the Tennessee Valley Authority (TVA) (Farmer 1980). Mother trees were located throughout the Tennessee and lower Ohio Valleys between Long. 81°58'-89°00' W, Lat. 34°15' - 38°50' N, and 152 - 1402 m elevation. Acorns were collected in the fall of 1971 from dominant and co-dominant trees with good size and form. Twenty-two of the mother trees were selections made in the 1960's by the TVA. These mother trees were the best phenotypes in their stand, based on form and size, as well as being representative of the best phenotypes in the region (K. Taft, TVA, personal communication). Fifty-nine additional mother trees were located in stands with the select trees and could be considered "comparison" trees in the mass selection process (Zobel and Talbert 1984). The remaining 145 mother trees were above-average phenotypes located in stands where intensive selection had not been conducted by TVA personnel (D. Scanlon, TVA, personal communication).

Establishment and Measurement of Provenance/Progeny Tests

Acorns were planted in 2 replicates at a TVA nursery near Norris, TN (Lat. 36° N, Long. 84° W), in the fall of 1971. Seedlings were lifted in the spring of 1973 and graded for size. The 16 largest seedlings of each family were planted at test site I (Fig. 1), and the remaining ungraded seedlings were distributed to 11 other test sites. A randomized complete block design was selected for each test site. However, the number of blocks, trees per plot, and families differed by test site. By 1991, only 4 plantations remained intact for analysis (Fig. 1, Table 1). Total number of families, family plot size, number of replicate blocks, and number of select and comparison families included in our study are shown for each test site in Table 1.

Table 1. Description of *Quercus rubra* provenance/progeny test sites.

Test Site	Number of Families			Blocks	Plot Size (# of trees)
	Total	Select	Comparison		
I LBL, KY	226	10	30	8	2
II Parke Co., IN	134	8	17	3	2
III Ames, TN	80	3	2	6	4
IV Coshocton, OH	176	10	30	7	4

All test sites were evaluated during the dormant season of 1991-1992. Growth and stem quality measurements used in this analysis included total tree height (THT); diameter at 1.3 m height (DBH); number of branches (BR#), live or dead, in the butt log (0.32-5.3 m height); height to lowest fork (FKHT, fork defined as the occurrence of 2 crown branches resulting in a mainstem deviation $\geq 10^\circ$); and number of crooks below FKHT (CR#, crook defined as mainstem deviation $\geq 10^\circ$). Heights were measured with a clinometer (Suunto) positioned 15.2 m from each tree. A diameter tape was used for DBH determination, and a height pole was used to designate the butt log. A protractor was used to establish angle deviation for fork and crook identification.

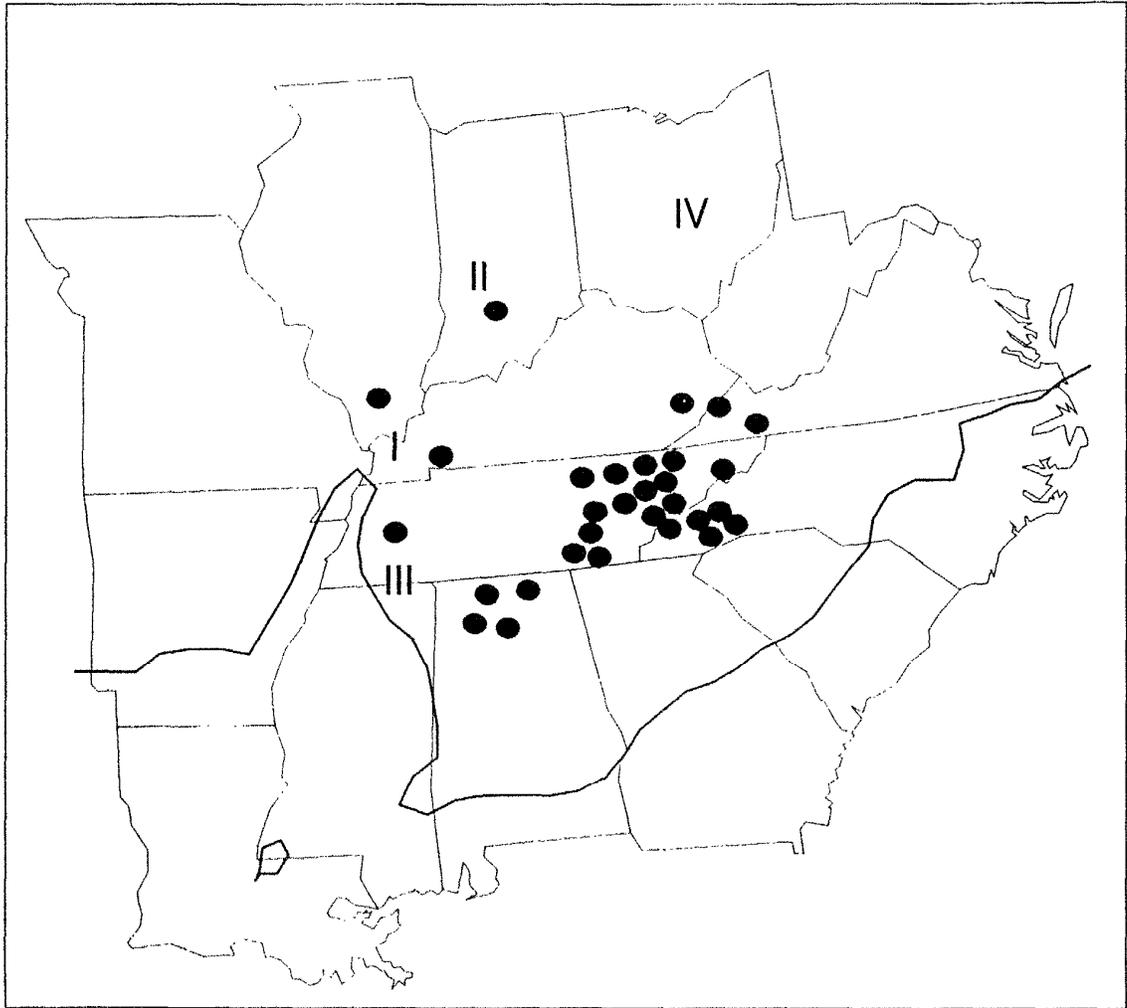


Figure 1. Stand location of mother trees (solid circles) and test site location (Roman numerals) of *Quercus rubra* L. genetic tests. Heavy lines indicate the natural range of *Q. rubra* L.

Data Analysis

Analyses were conducted on families from stands containing one select tree and at least one comparison tree. In the TVA test, several select trees were represented by a limited number of seedlings, and a small number of stands contained more than one select tree. Families of these trees were deleted from the analyses as were associated comparison tree families. The 145 families from stands lacking select trees also were deleted from the analyses. Measurements from families of the remaining 11 select trees and their 32 associated comparison trees formed the data set for our study.

Fork heights were converted to percent of total tree height (FKPER) and normalized using an arc sine transformation (Steel and Torrie 1980). All other variables were subjected to Wilk-Shapiro/rankit plots to check for normality. Data were subjected to a series of analyses and were analyzed untransformed. Pooled select and pooled comparison families were compared over all test sites as well as within test sites. Within-stand comparisons (i.e. analyses of select families and their associated comparison families) were also completed within test sites and for data pooled over all test sites. Two sample t-tests were used to detect differences at $p \leq 0.05$.

RESULTS AND DISCUSSION

Growth Variables

No significant differences ($p > 0.05$) in mean THT were found among pooled select and pooled comparison families within any of the test sites. Mean DBH of select versus comparison families was significantly different only at test site I (Fig. 2). Mean DBH for select families (12.05 cm) was 6.8% higher than comparison families (11.22 cm). None of the other test sites analyzed showed any differences among select and comparison families for DBH. While test site I was the location where the 16 largest seedlings of each family were planted, the importance of this in regards to a DBH difference among groups is not clear.

No significant differences ($p > 0.05$) were observed in analyses of data pooled over all test sites for mean DBH among select and comparison families, but mean THT's of select families were significantly less than those of comparison families (Fig. 3). However, the difference was relatively small, approximately 4 percent.

Stem Quality Variables

There were 12 possible variable/test site analyses evaluating pooled select versus pooled comparison family data within each test site. Of these 12 analyses, we found only 4 instances of significant differences ($p \leq 0.05$) for the stem quality variables (BR#, CR#, and FKPER) and only 2 instances where select families outperformed comparison families. Mean CR# was significantly less for select families (0.02) at test site I than for comparison families (0.12) but at test site II the opposite was true (Fig. 4). Differences for mean FKPER were also found at test sites I and II (Fig. 5). Only at test site II did select families perform better than comparison families, averaging 64.2 and 53.4 percent FKPER, respectively. No differences in select versus comparison families for mean BR# were found within test sites.

Data pooled over all test sites indicated no significant differences for mean CR# among select and comparison families. However, significant differences among groups in both BR# and FKPER were found ($p \leq 0.05$) (Fig. 6). Comparison families had the smaller mean BR# (7.14), compared to select families (7.99), representing a 10 percent difference. Comparison families also outperformed select families in FKPER having a mean of 70.7 compared to 66.0 for select families, representing a 7 percent difference.

Within-Stand Comparisons

Analysis of data pooled over all test sites found only 16 of the 51 within-stand comparisons of growth and stem quality variables significant ($p \leq 0.05$). Results of these analyses were expressed in terms of percent differences in means between select and comparison families (Table 2). Of the 16 significant differences, only 6 were positively associated with select families, while comparison families outperformed select families in 10 analyses.

The results of within-stand comparisons among select and comparison families within test sites were similar to the within-stand analyses that were pooled over test sites. Six significant differences ($p \leq 0.05$) were found out of 50 analyses performed on growth and stem quality variables for select versus comparison families in test site I. Only 2 of these significant results were positively associated with select families. Similar patterns occurred in within-stand analyses at each of the other test sites.

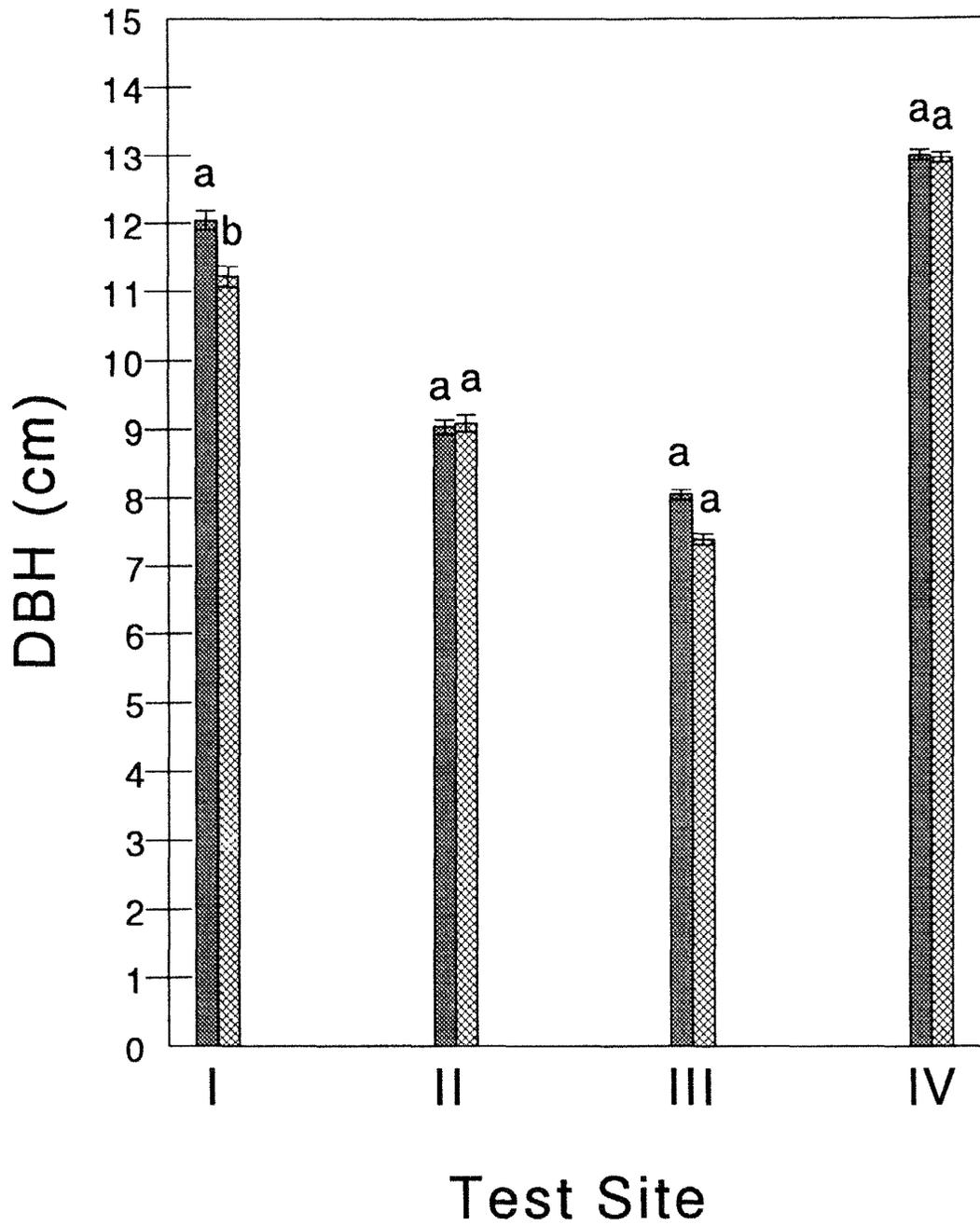


Figure 2. Contrasts of mean DBH among select (shaded) and comparison (hatched) families for each test site. Bars represent means with standard errors for each group. Significant differences ($p \leq 0.05$) are indicated by different letters.

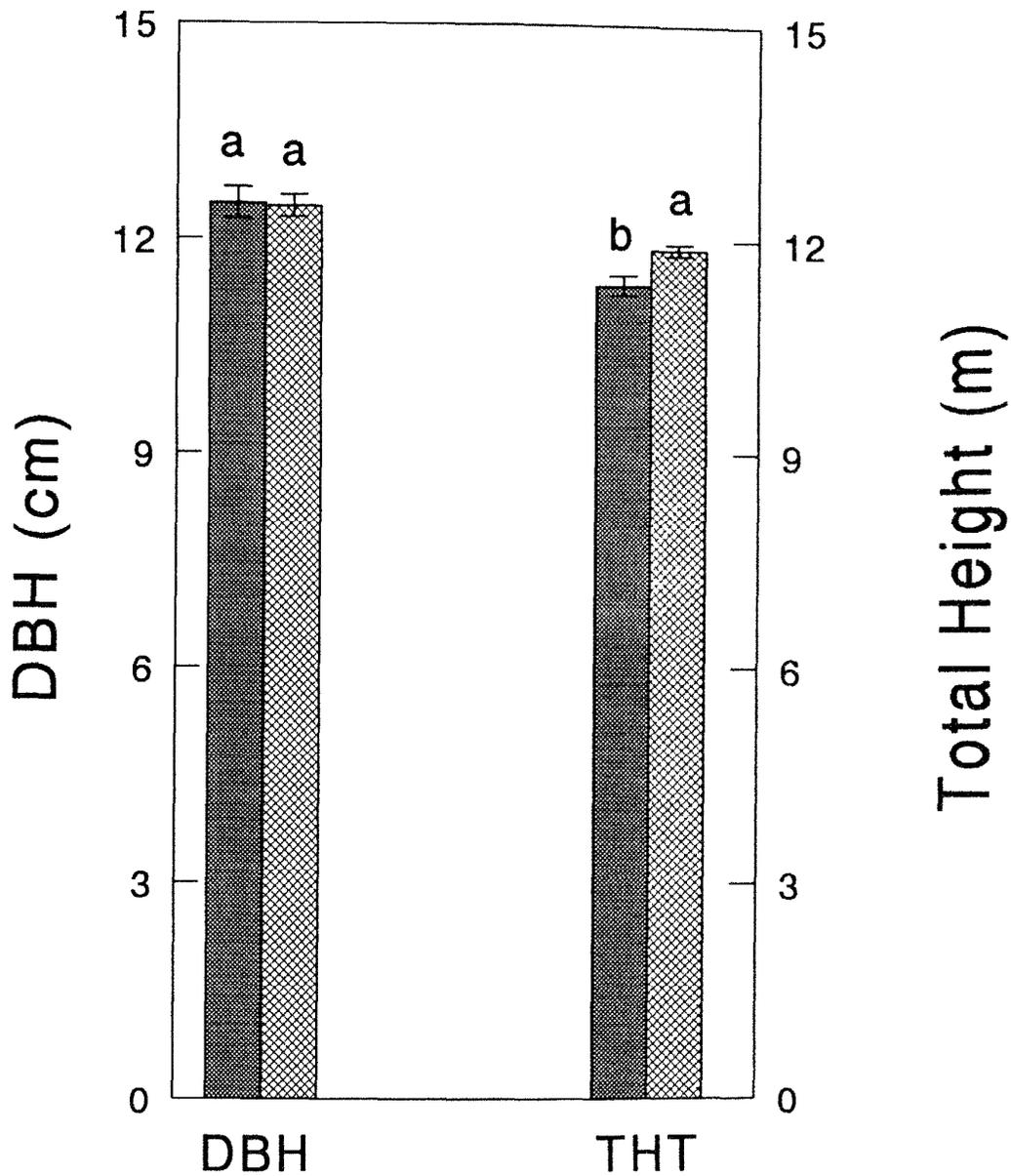


Figure 3. Comparison of mean DBH and mean THT among 11 select (shaded) and 32 comparison (hatched) families. Bars represent means with standard errors for each group pooled over all test sites. Significant differences ($p \leq 0.05$) are indicated by different letters.

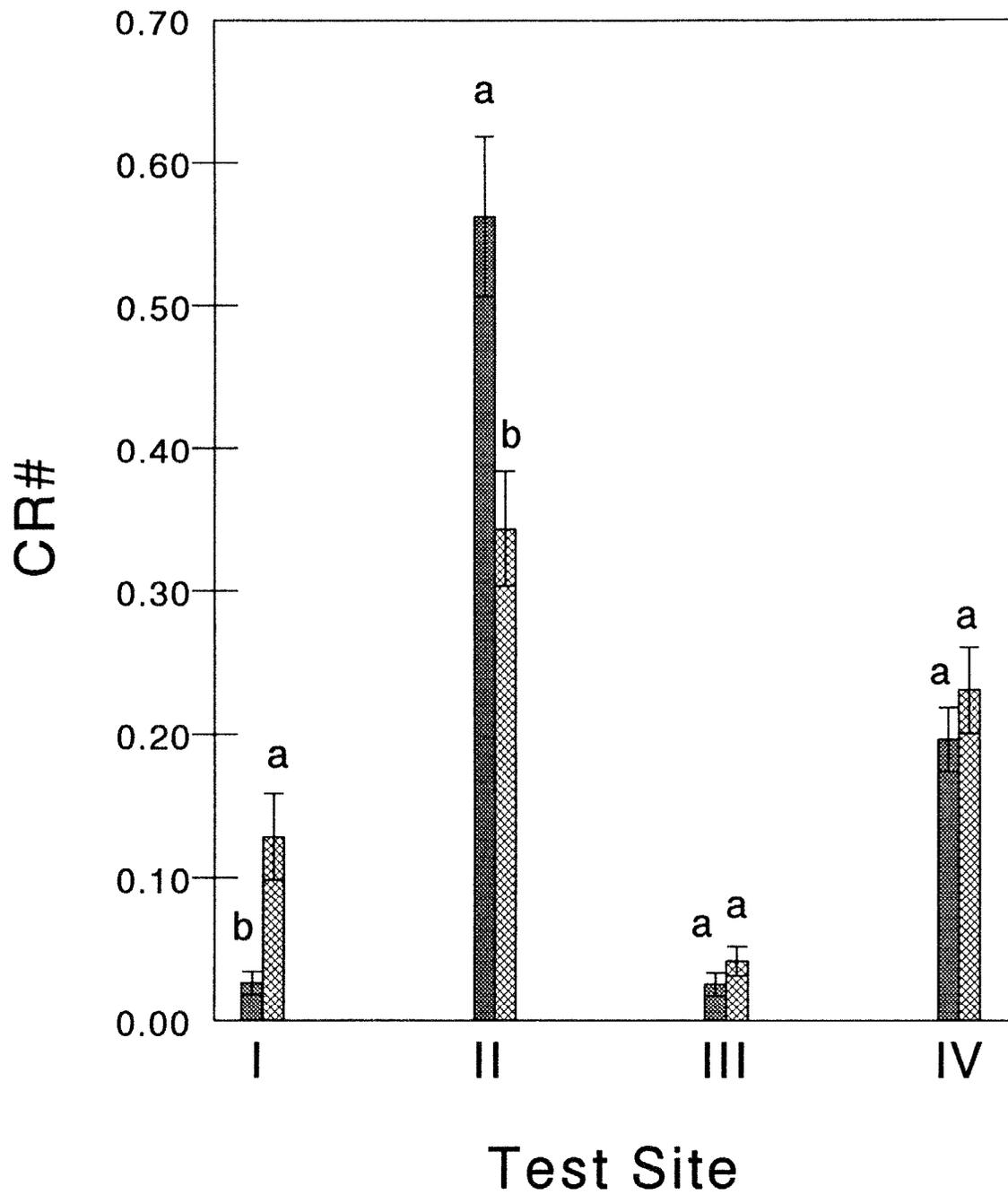


Figure 4. Contrasts of CR# (producing $\geq 10^\circ$ deviation of mainstem) among select (shaded) and comparison (hatched) families for each test site. Bars represent means with standard errors for each group. Significant differences ($p \leq 0.05$) are indicated by different letters.

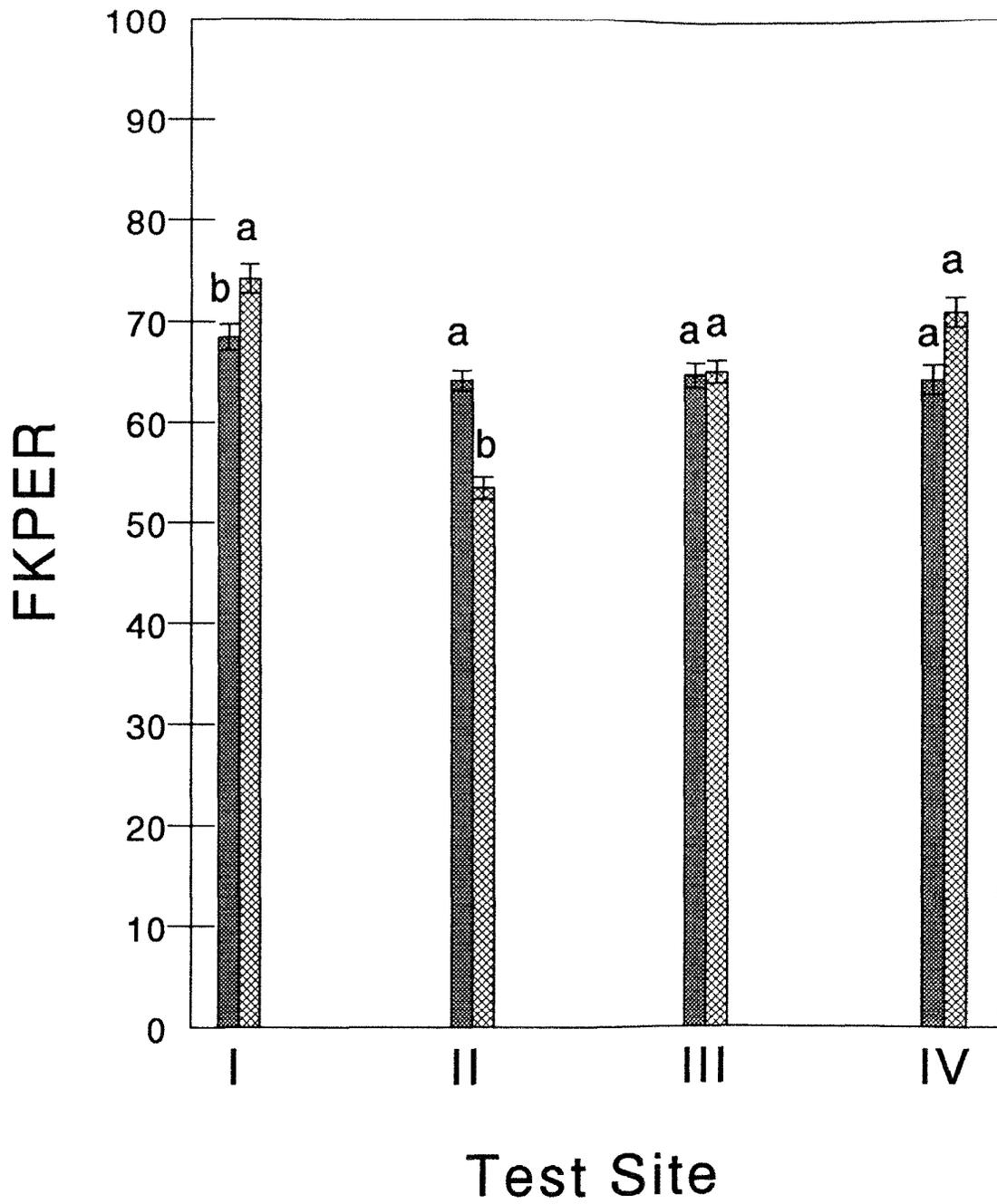


Figure 5. Contrast of FKPER (fork height, expressed as percent of total tree height) among select (shaded) and comparison (hatched) families for each test site. Bars represent means with standard errors for each group. Significant differences ($p \leq 0.05$) are indicated by different letters.

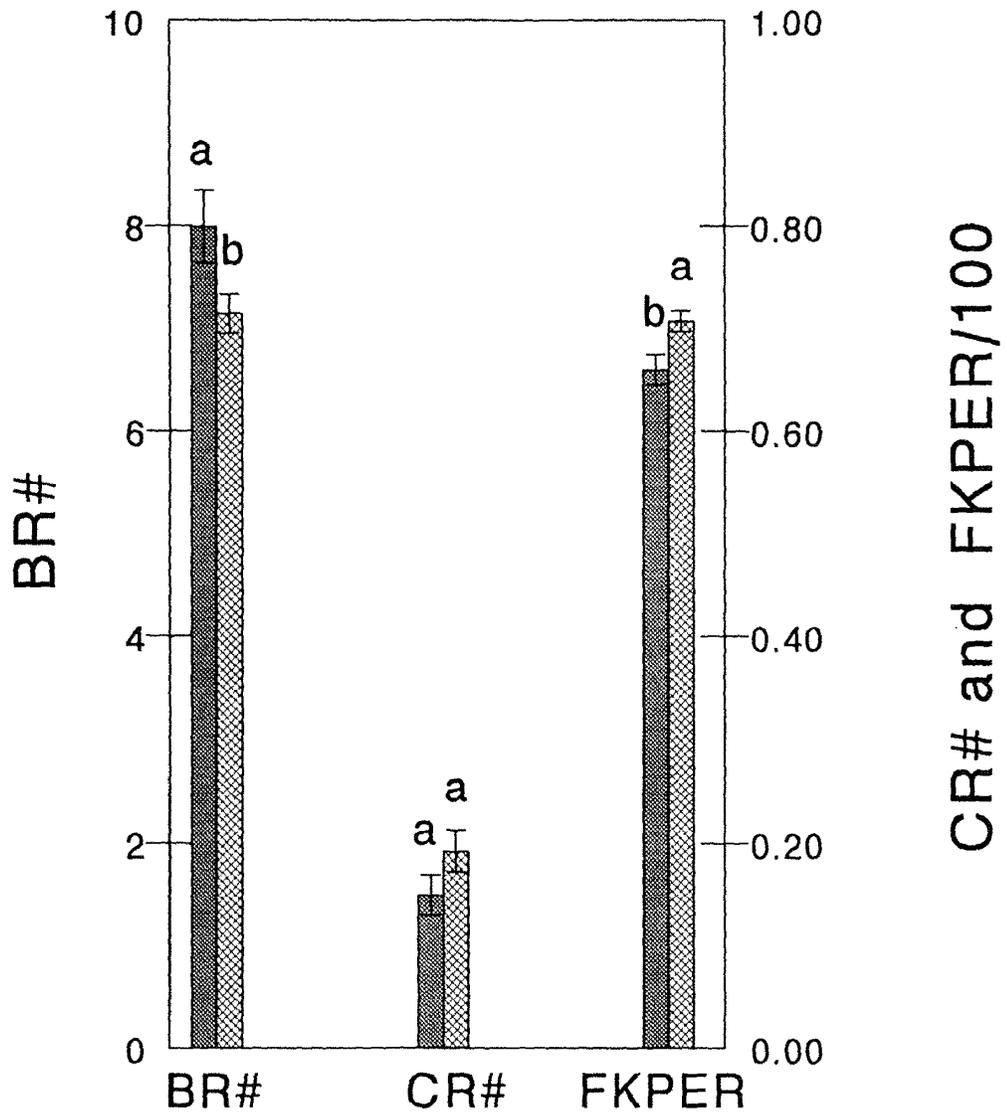


Figure 6. Comparison of BR#, CR#, and FKPER, among select (shaded) and comparison (hatched) families pooled over all test sites. Bars represent means with standard errors for each group. Significant differences ($p \leq 0.05$) are indicated by different letters.

Table 2. Percent differences in performance between select and comparison *Quercus rubra* families pooled over all test sites.

Select Family ID# (# progeny)	Number of Comparison Families (# progeny)	Percent Difference of Select Versus Comparison Families				
		DBH	THT	BR#	CR#	FKPER
2412 (22)	4 (82)	9.3	3.5	-24.6¹	-47.5	10.7
2419 (30)	3 (45)	3.5	-4.5	32.0	48.3	65.6
2421 (6)	4 (60)	19.2	-5.2	-21.0	---	-40.0
2427 (31)	1 (17)	---	---	-71.7	27.1	-18.9
2429 (24)	2 (43)	-0.4	-4.2	1.4	-35.0	-14.0
2451 (42)	2 (38)	-22.1	-22.1	48.2	-69.8	-7.5
2452 (18)	2 (28)	-4.8	-8.8	46.1	-92.6	-28.5
2457 (32)	4 (93)	-9.9	-11.4	-7.1	42.9	3.3
2458 (37)	2 (58)	-19.5	-16.3	22.0	-146.7	15.8
2462 (31)	6 (163)	15.2	8.3	-0.4	-14.8	-22.1
2471 (24)	2 (76)	-17.9	-10.4	20.4	---	11.6
(297)	32 (703)	-2.7 ²	-7.1	4.1	-32.0	-2.2

¹ Bold values represent a significant difference at the 95% probability level using a two sample t-test.

² Arithmetic means.

CONCLUSIONS

Our analyses indicate that selecting one tree per stand using rigorous phenotypic selection was no more effective in providing initial improvements in growth and stem quality of *Q. rubra* than selecting a number of good phenotypes in a stand. These results are similar to those obtained for *Q. alba* (Schlarbaum 1993). Similar results and recommendations have also been obtained for other species (e.g. Pitcher 1982). The relatively large differences among select and comparison families within stands, indicating large genetic variances, suggest that several of the best phenotypes in a stand should be used to obtain seed. Progeny testing should be used to establish rankings for candidate mother trees for future collections. However, our study focused on families from relatively large and well formed trees in each stand. We can not speculate on the relative gains possible from selection across the entire range of phenotypes.

Our analyses of select versus comparison progenies indicate low genotype-phenotype correlations in the parental trees, and thus provide little encouragement for rigorous phenotypic selection in natural stands. This may not be surprising given the nature of development of many oak dominated stands. Canopy tree recruitment comes predominately from advanced regeneration subjected to disturbance (Sander 1972, Watt 1979). Oak advanced regeneration developing in non-disturbed stands does so slowly. Many biotic and anthropogenic factors may

influence phenotype during this time. Disturbance which ultimately leads to rapid development of oak cohorts may also alter phenotype.

Selection of *Q. rubra* trees for tree improvement might successfully utilize a mother tree or candidate tree approach. This involves selecting a number of good phenotypes, relying on progeny testing to indicate superior or elite mother trees. Selecting a number of good individuals from a stand eliminates detailed grading procedures, but ensures that the best phenotypes are represented in collections. This approach would increase the number of initial selections and make identification of each selected tree easier compared to a more rigorous regional grading system. Widening the options for individual tree selection may be especially advantageous in years with little mast production. While the nature of *Q. rubra* may necessitate this approach, it may be possible to accelerate gains through juvenile trait selection (Bailey and Steiner 1989, La Farge and Lewis 1987). However, the time interval necessary to determine reliable estimates of family rankings for growth parameters in this species is still under scrutiny (Houston 1987, Kriebel and others 1988).

ACKNOWLEDGMENTS

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POLLINATION BIOLOGY OF NORTHERN RED AND BLACK OAK

Robert A. Cecich and William W. Haenchen¹

Abstract: Pistillate flower abortion in northern red oak and black oak was evaluated in relation to pollination and fertilization. The presence, position, and characteristics of the pollen grains, pollen tubes, and ovules were determined with bright field and fluorescence microscopy. Flower survival counts were made weekly, from late April to mid-September. Both species have rudimentary ovules and small locules during the first growing season. Pollen tubes cease growth during the first growing season in mid-May at the level of the distal end of the perianth and juncture of the three stigmas. In the next growing season, meiosis in the mature ovules may trigger the advance of the pollen tubes into the locules. Fertilization occurred in mid-June for northern red oak and late June in black oak.

INTRODUCTION

Bumper crops of acorns are considered to be sporadic or episodic. Sork and others (1993) found that the size of a given acorn crop was determined by both flower abundance and survival of the flowers to maturation. Most of the potential seed crop is lost when the pistillate flowers abort before fertilization (Cecich 1991). As members of the subgenus *Erythrobalanus*, northern red oak (*Quercus rubra* L.) and black oak (*Q. velutina* Lam.) require two growing seasons between pollination and seed maturation; only pollination occurs in the first season. However, it is during the 6-8 weeks after pollination in that first season that most of the abortion occurs. In northern red and white oak (*Q. alba* L.), up to 100 percent of the flowers may abort during that 6-8 week period (Cecich 1991). The possible role of insects, especially the treehoppers (Membracidae), as factors in oak flower abortion has been previously addressed (Cecich 1993).

Because of the time that most of the flower abortion occurs, the pollination process should be examined. The success of the acorn crop can be related to pollen dispersal. Emergence of the catkins and shedding of pollen increase with rising temperatures (Romashov 1957). Rainy weather, often associated with decreased temperature, can reduce pollen dispersal. Sharp and Chisman (1961) concluded from field observations that pollen dispersal occurred when relative humidity dropped and remained below 45 percent for several hours, but they did not mention the success of the acorn crop. Sharp and Sprague (1967) found no correlation with relative humidity and acorn yields in their field studies and concluded that temperature was a primary factor in determining acorn crops. Using growth chambers, Wolgast (1972) and Wolgast and Stout (1977) demonstrated experimentally that relative humidity at the time of pollen shed and stigma receptivity can limit the size of an acorn crop in *Q. ilicifolia* Wangenh. No acorns matured when relative humidity exceeded 61 percent, but about half the flowers matured into acorns when relative humidity was lower.

Past observations of *Quercus* pollen tube growth are conflicting and incomplete. Benson (1894) first observed pollen tubes in *Q. robur* L., a member of the *Lepidobalanus* (white oak) subgenus, in the locules, just before fertilization. She did not see them in the stigma or style. Jovanovic and Tucovic (1975) observed that pollen germination in *Q. robur* was completed within 24 hours, but fertilization occurred 6-7 weeks later, and speculated that pollen tube growth did not proceed until the ovule had completed development. In contrast, Allard (1932) noted that "When pollen reaches the stigma of members of the white oak group, the growth of the pollen tube containing the male cells follows an uninterrupted advance into the tissues of the style until the ovules are fertilized." Allard (1932) also found that in the red oak group the pollen tubes ceased growth at the base of the style until the following spring when fertilization occurred. Unfortunately, no details of pollen tube growth were documented in any of these reports. Therefore, in this study, we provide the first details of the pollination biology of a Missouri population of northern red oak and black

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oak during the first and second growing seasons. Pollen tube growth is examined in relation to the time of pollen shed, fertilization, and flower survival.

METHODS

The trees in this study were located along a forest road in a closed stand on the Thomas S. Baskett Wildlife Research and Education Area, Ashland, MO (38°N, 92°W); operated by the University of Missouri in cooperation with the Missouri Department of Conservation. Sampling was done from a hydraulic lift truck equipped with a 40-foot boom and reaching a height of 50 feet.

The number of pistillate flowers, their survival and anatomical development, and the time of pollen shed were determined from 1990 to 1994. Data sets for 12 black oaks (BO) and 4 northern red oaks (NRO) from the growing seasons of 1990-1991, 1991-1992, and 1992-1993 were selected to demonstrate the variation in flowering and survival. Pistillate flowers, from the upper and middle crown regions, were counted on the current year's growth of five 2nd-year (one-year-old) branches per tree. Pistillate flowers are found in the axils of current year's leaves. The average number of flowers per 2nd-year branch ranged from about 3-63, depending on the tree and the year. These same trees and branches were used to count the 2nd-year flowers that matured into acorns. For microscopic examination, ten pistillate flowers were collected weekly from one BO and one NRO, during mid-April to Mid-September, from 1991 to 1994. In the spring of 1993 and 1994, two additional black oaks were sampled. Estimates of the dates of pollen shed were done on the same trees as the flower counts, but during the years of 1991-1994.

Flowers were fixed in FAA (formalin : acetic acid : alcohol), embedded in Paraplast-Plus, cut on a rotary microtome, and sections, both longitudinal and transverse, were attached to slides with Haupt's adhesive. For observation by bright field microscopy, sections were cut 10- μ m-thick, stained in safranin-fast green, and coverslips mounted in Permount. For fluorescence microscopy, sections were cut 20- μ m-thick and stained with 0.005% aniline blue in 0.15M K_2HPO_4 at pH 8.2 for 10-30 minutes to locate callose, a 1,4 β -glucan polysaccharide that fluoresces a bright yellow-green, in the pollen tube wall (Currier 1957). Coverslips were mounted in the staining solution. Sections were examined with a Zeiss Universal microscope, illuminated by an HBO 200 W mercury lamp, in conjunction with the exciter filters UG-1 and BG-38 and the barrier filters 44, 47, and 53. Photomicrographs were taken with a Wild-Heerbrugg MKa4 Photoautomat camera using Kodak Ektachrome 400 HC film.

RESULTS

Mean survival curves of NRO and BO pistillate flowers, from 1990 to 1993, are shown in Figures 1-3. In NRO, most of the flower loss occurred in the first 6-8 weeks after pollination. However, additional loss was recorded in conjunction with the overwintering period of the pollinated flower. Since observations were not made between September and April of the following year, we could not determine the timing or cause of this loss. Thus, the loss that occurred overwinter (between September and April) is expressed as the increment between April and May in those Figures.

Staminate flowers that produce the pollen are found on inflorescences or catkins. Catkins are found in buds that only produce catkins ("male buds") or in "mixed buds" (buds that contain vegetative shoots and catkins, or buds that contain vegetative shoots, pistillate flowers and catkins). Depending on the year, pollen of NRO is usually shed during the week of April 20 at the central Missouri site, and about one week later in BO (Table 1). Pistillate or female flowers are found in the axils of newly emerging leaves of the terminal bud or its subtending lateral buds. In NRO and BO, the pistillate flowers (Figure 4) tend to be distributed among the leaves of the central and basipetal portion of a branch. Based upon our weekly sampling schedule, the stigmas of the pistillate flowers (Davis 1966) seemed to be receptive for no more than one week. Our assessment of receptivity was based on the

flexibility and bright red coloration of the stigmas. Once the stigmas turned brownish in color and became rigid, we felt that receptivity had passed. Oak stigmas are classified as dry (Heslop-Harrison and Shivanna 1977), meaning that they do not produce visible secretions on the stigmatic tip.

Table 1. Annual variation in the beginning date of pollen shed. The duration of pollen shed for a species in the stand seemed to be less than one week.

YEAR	RED OAK	BLACK OAK
1991	0*	1 May
1992	24 April	1 May
1993	1 May	7 May
1994	22 April*	29 April

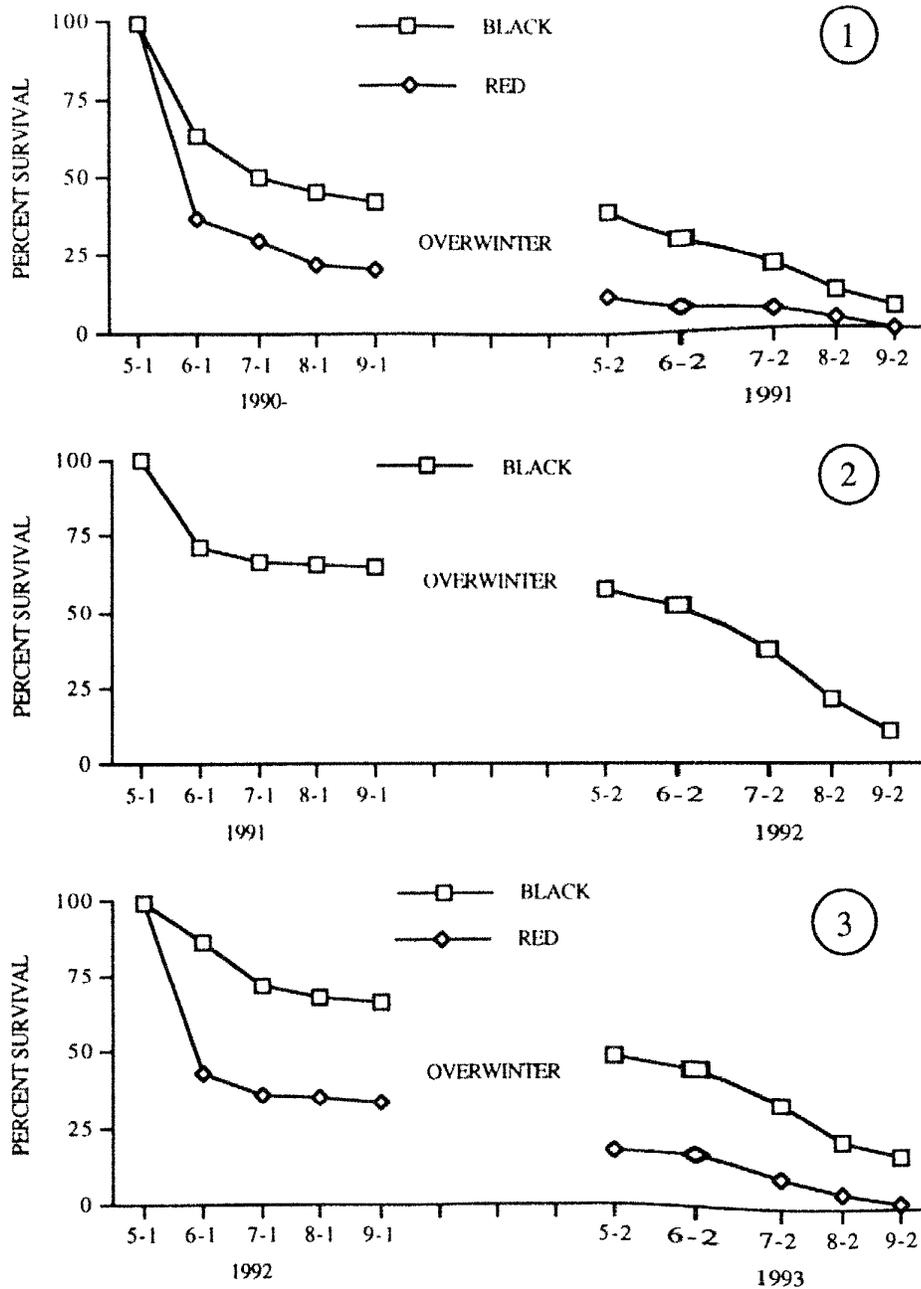
*No pistillate flowers in 1991 and few to none in 1994.

Pollen grains covered all surface tissues of the flowers, but it was only those that landed on the stigma surfaces that affected pollination (Figure 5). Heslop-Harrison and Heslop-Harrison (1985) have reviewed pollen-stigma interactions that specifically promote the germination and penetration of the pollen tube into the stigmas. Germination of oak pollen has been shown to occur within 24 hours of landing on the stigma (Jovanovic and Tucovic 1975). Our weekly collections did not permit verification of that timing. Pollen tubes were so numerous in some styles that accurate counts were not possible.

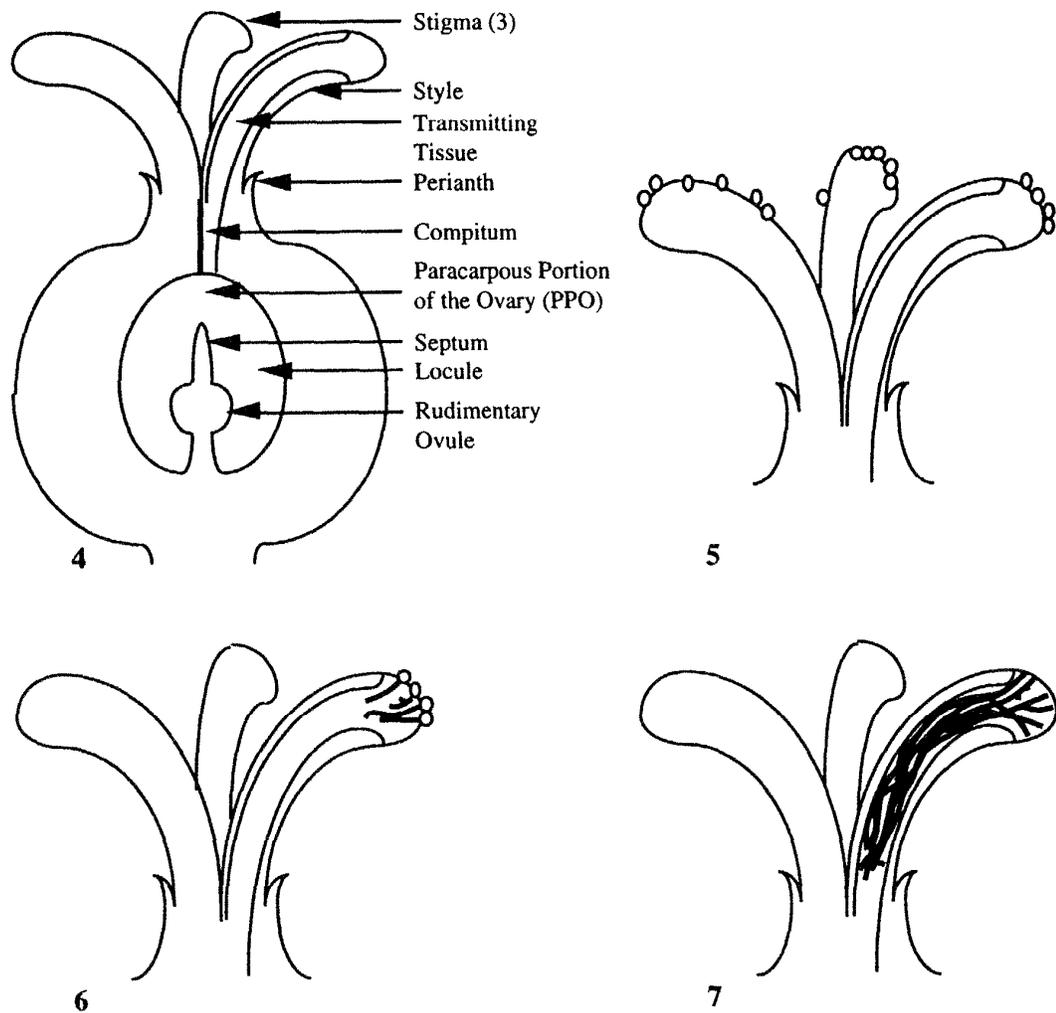
Both NRO and BO had the same pattern of pollen tube growth after the grains landed on the stigmas. The pollen tubes penetrated the stigmatic epidermis and synthesized a callose plug within the pollen tube, effectively isolating the contents of the tube from the now-empty pollen grain (Figure 6). One common feature of oak pollen tubes was the occurrence of several callose plugs within a single pollen tube. Callose plugs were generally amorphous masses. The pollen grains fell off the stigma within the week. Some pollen tubes produced numerous branches upon penetrating the stigma epidermis into the transmitting tissue of the style. Pollen tubes grew through the "central core" of the style in the parenchymatous, transmitting tissue toward the ovules (Figure 7).

The pollen tubes of both species penetrated downward, through the transmitting tissue until they reached the level of the perianth, just above the juncture of the three stigma/styles, on or about May 15. Thus, both species ceased penetrating on the same date, even though NRO began pollen tube growth at least one week before BO. No further pollen tube growth occurred during the first growing season. The ovary tissues of NRO and BO pistillate flowers are not well-developed in the first growing season. The three locules are small and contain a few hairs that surround the rudimentary ovules. From mid-May until the following spring, there were no observable changes in the structure of the pistillate flower or the position of the pollen tubes.

During the second growing season, pollen tubes of NRO resumed elongation on or about the May 21 collections. By that date, the ovary tissues had greatly enlarged. The ovules became organized into a nucellus that was surrounded by inner and outer micropyles. The locules enlarged and the number of hairs in the locules increased. In the next specimen collection (about May 28), pollen tubes were seen in the compitum (Carr and Carr 1961), the narrow "cylinder" of empty space that separates the three styles within the flower (Figure 8). After leaving the basipetal end of the compitum, the pollen tubes entered the paracarpous portion of the ovary (PPO) (Carr and Carr 1961). The central axis of the ovary is formed by the fusion of three septae. Each septum gives rise to a pair of rudimentary ovules. The septae are incompletely developed toward the top of the locules, creating a free space (the PPO) that connects each locule to the other two. Thus, as pollen tubes enter the compitum and PPO, they can fertilize any of the six ovules. Pollen tubes were randomly oriented and interwoven in the PPO.



Figures 1-3. Survival of pistillate flowers in the first growing season and developing acorns in the second growing season. Fig. 1. 1990-1991 growing seasons. Fig. 2. 1991-1992 growing season. **There were no flowers on the red oak in 1991.** Fig. 3. 1992-1993 growing season. For purposes of plotting data, **we have** used an estimated value for the first day of each month, not the weekly data.



Figures 4-7. Line drawings of the pistillate flower and pollen tube growth. Fig. 4. A median-longitudinal section of an oak pistillate flower with pertinent parts labelled. Fig. 5. Pollen grains on the three stigmas. Fig. 6. Pollen tubes grow through the stigma epidermis and produce a callose plug. Branches may form on the tubes. Fig. 7. Pollen tubes cease growth in mid-May at the level of the perianth.

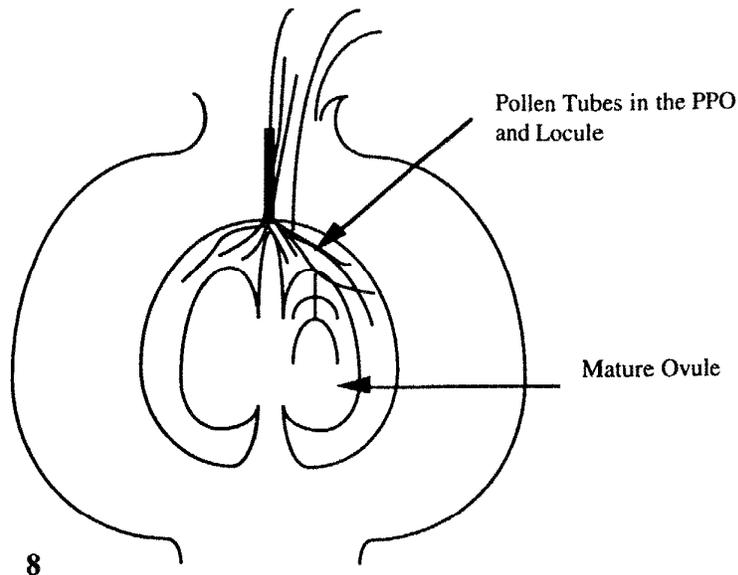


Figure 8. When pollen tubes resume growth, they leave the transmitting tissue and enter the compitum and paracarpous portion of the ovary (PPO), where they can randomly enter any of the three locules and fertilize any of the six ovules and their eggs. See Fig. 4 for additional labelling of flower parts.

Pollen tubes of NRO resumed growth in the May 21 collections and were observed in the locules, below the level of the PPO, in the June 4 and June 11 collections, as the megaspore mother cells were undergoing meiosis. The free nuclear endosperm stage was observed on June 18, indicating that fertilization had occurred after June 11. The BO pollen tubes were first seen resuming growth as they entered the compitum on June 4, two weeks after NRO. However, a free nuclear endosperm was not seen until July 2, indicating that fertilization occurred about two weeks after it did in NRO.

DISCUSSION

Our observations suggest several possible mechanisms for the control of pollen tube growth. Since both species ceased elongation on May 15, an external or environmental factor may be involved. This relationship has been demonstrated in a number of annual plants and grasses (Lyndon 1992). Pollen of *Q. pubescens* W. requires a higher temperature for germination (38° C) than pollen of *Q. robur* (20° C). Low and erratic fertility of *Q. pubescens* in cold habitats was attributed to the prevention of pollen germination (Jicinska and Koncalava 1978). However, the control over pollen tube elongation may be sporophytic, as manifested physiologically through the incomplete development of the ovules. For instance, the pollen tubes may stop penetrating the transmitting tissue because the rudimentary ovules may not be providing the correct signal, perhaps a hormonal gradient, for the pollen tubes to continue growing. This may be the type of feedback mechanism between pollen tubes and ovules that Owens (1992) cites. In addition, pollen tube growth may have stopped on May 15 because some portion of the ovary was producing an inhibitory substance that prevented the pollen tubes from elongating past the stylar juncture, and that this product was removed or neutralized with the approach of megasporogenesis. It may only be when the ovules reach a critical or threshold stage of development, for instance in the second growing

season, that the proper stimulus for continued pollen tube growth is produced. This is especially evident in these two red oak group species that have only rudimentary ovules in the first growing season. It was observed in this study that the pollen tubes entered the compitum and PPO just as the megaspore mother cells were undergoing meiosis and not before. Thus, the putative "signal" for pollen tube growth resumption could have been produced shortly before meiosis was visible.

We have found no evidence of late spring frosts at our study site. Sharp (1958) concluded that low temperatures in the spring did not affect flowering unless there was a freeze sufficient to damage shoots and leaves. Goodrum and others (1971) also concluded that the influence of low temperatures on flowering, setting of fruit and subsequent acorn yield was inconclusive. However, low air temperatures were associated with a delay in the development, but not the number, of pistillate inflorescences of *Q. robur* near Moscow (Minina 1954).

The role of various pollen sources must also be considered as factors in the success of an acorn crop. For instance, NRO is the first oak species to flower at our relatively dry ridgetop site. The fast abortion rate of the pistillate flowers in May (Fig. 1-3) could reflect a lack of available outcrossed NRO pollen or a high degree of self pollination. Oaks are relatively self incompatible (Cottam, Tucker, and Santamour 1982). Since there are few NRO trees in our stand, the chance for cross pollination is reduced. But, there is an increased opportunity for a greater proportion of self pollinated flowers. Schwarzmann and Gerhold (1991) reported that northern red oak is a highly outcrossed species with a low level of self fertilization. Their study was done with acorns, the product of successful fertilizations. Our results, to a large extent, deal with flowers that have a high likelihood of aborting. Thus, a comparison may not be completely valid. The black oaks in our study have a slower rate of flower abortion during the first 6-8 weeks, compared to NRO. There are many more trees in the stand, allowing a greater likelihood of cross pollination. Any selfing would occur in less proportion and lead to a higher survival rate of those flowers.

One speculated role for callose plugs is as an incompatibility reaction, either from interspecific pollen or from self pollination (Dumas and Knox 1983). Thus, the callose plugs in these oak pollen tubes could indicate that many of the pollen tubes are from selfing. However, we have occasionally observed callose plugs in pollen tubes that had reached the locules and were apparently ready to fertilize the ovules in the second growing season. We expect that a self-pollinated flower would have aborted early in the first growing season. An alternate hypothesis is that callose plugs are a regulator of turgor pressure in the pollen tube (Dumas and Knox 1983). Callose plugs are formed sequentially as the tubes grow, perhaps allowing turgor pressure to be maintained in the cytoplasm at the tip of the pollen tube and facilitating penetration. Controlled pollination experiments are planned to examine the relationship between various types of crosses and the occurrence of callose plugs in oaks.

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AGE TRENDS IN GENETIC CONTROL OF *JUGLANS NIGRA* L. HEIGHT GROWTH

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Abstract: Age-related trends in narrow-sense and family heritabilities for black walnut height and dbh from a southern Illinois open-pollinated progeny test are evaluated through age 20 years. Narrow-sense heritability for height tends to be relatively stable between ages 10 and 20 at 0.55 - 0.65 with similar patterns and values for family heritabilities for both height and dbh. Individual phenotypic age-age correlation coefficients increased from approximately 0.1 at age 1 to 0.8 at age 8 and remained above this level through age 20.

INTRODUCTION

Genetic gain, the quantitative estimate of the amount of improvement per generation resulting from selection, is the product of heritability and selection intensity. Thus, precise estimates of heritability are needed for calculating gain. Although such estimates are available for juvenile black walnut (Rink 1984, Rink and Clausen 1989), precise estimates of heritability for growth traits from mature trees are not available. Since it is known that heritabilities differ with tree age, changes in these genetic parameters need to be evaluated over the course of a generational rotation. Also, relationships between early and later estimates of heritabilities need to be explored along with phenotypic age-age correlations. The objective of this study is to evaluate heritabilities for black walnut tree height and dbh and age-related growth trends.

METHODS

Open-pollinated seeds collected in 1971 from 54 trees were used to produce 1-0 seedlings for the Pleasant Valley progeny test in southern Illinois. Parent trees were selected from within a 250-mile radius south of the plantation location (Fig. 1), the area most frequently cited as the optimum provenance for obtaining a growth stimulus from geographic seed source selection for artificial regeneration in southern Illinois (Bresnan et al., in press). This included an area bounded by southern Illinois, western Kentucky, western Tennessee, and southeast Kansas. However, most of the seed collections were from west Kentucky and west Tennessee. In most cases seed was collected from one tree per stand. Although trees of better than average form were sought at the time of collection, no rigid minimum selection criteria were applied. Open-pollinated progeny of these trees were planted in 5-tree row plots at a spacing of 1.8 m within rows and 3.7 m between rows, in a randomized complete block design with 10 blocks.

The test was established in early spring 1973 on a Haymond silt loam on the floodplain of Sexton Creek, Alexander County, Illinois. The Haymond loam is characterized as a coarse-silty, mixed, nonacid, mesic Typic Udifluent classified as suitable for walnut culture (site index 50 at age 70) (Losche et al. 1980). The site was an abandoned fescue pasture on which 1.2 m strips were machine sprayed with a simazine, dalapon, 2,4-D mix before planting, spot sprayed in spring 1974 and 1975, and mowed annually. In addition, the test was rogued (thinned) after the 10th growing season to remove 3 of the smallest trees per 5-tree plot and again after the 14th growing season to retain the most vigorous, best formed tree per family-row plot. The trees were measured for total height 14 times and dbh

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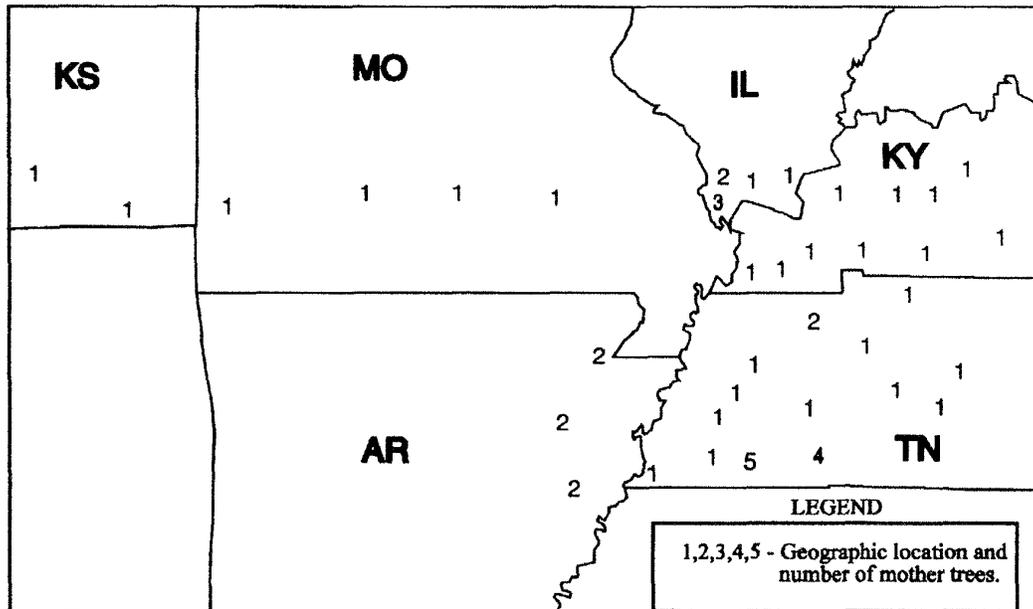


Figure 1. Location of mother trees from which seed were collected for Pleasant Valley open-pollinated progeny test.

11 times during the 20-year period through the 1992 growing season. Statistical analyses were applied to data sets which included only the trees present at age 20 (i.e., the earlier data sets were censored to include only one tree per family-row-plot retained after the last thinning).

Annual measurements were subjected to univariate analysis of variance on an individual tree basis using the following model:

<u>Source of Variation</u>	<u>Mean Square</u>	<u>Expected Mean Square</u>
Blocks (b)	MS_b	$\sigma_a^2 + 0.099 \sigma_f^2 + 47.277 \sigma_b^2$
Family (f)	MS_f	$\sigma_a^2 + 9.076 \sigma_f^2$
Error (e)	MS_e	σ_e^2

Variance components were generated from the Type I sums of squares in the General Linear Model of the Statistical Analysis System (SAS Institute 1982). The Type I method was used in order to obtain an unbiased estimate of the family variance component; by this method all ambiguous variance is assigned to the first variance component entered into the estimation procedure (in this case the block term). Resulting variance components were used to generate narrow-sense and family heritabilities. Pearson correlation analysis was also used to develop phenotypic age-age correlations on an individual tree basis, but only correlations of height at age 20 with height at earlier ages are presented.

RESULTS AND DISCUSSION

Mean cumulative height of black walnut trees in the Pleasant Valley progeny test was contrasted for the ten tallest and ten shortest families (Fig. 2). The group of 10 families which were tallest and shortest at outplanting remained tallest and shortest, respectively, at age 20; the cumulative growth curves never cross. Analyses of variance of the three family groups (10 tallest families, average families, and 10 shortest families) indicated significant differences in height every year beyond the first year, and Duncan's Multiple Range tests consistently separated the three groups of mean heights after age 8. Growth of the 10 tallest families exceeded the plantation average by 8 percent every year beyond age 2. The average height at age 20 was 9 meters.

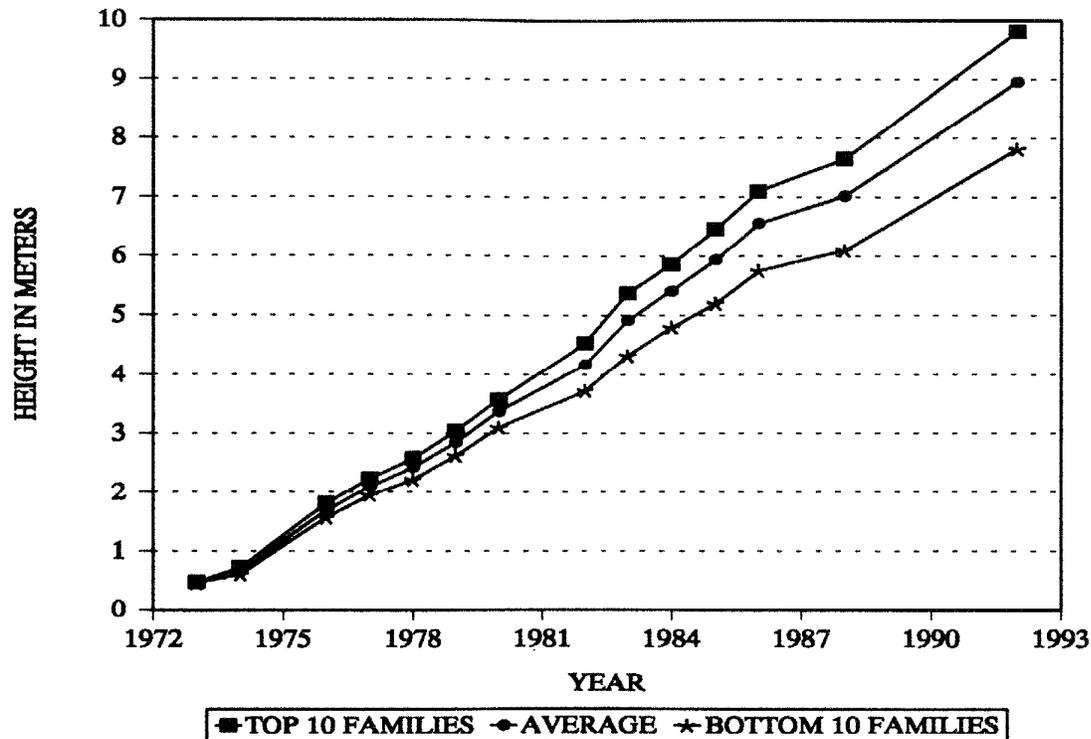


Figure 2. Average cumulative black walnut tree height in Pleasant Valley progeny test, from establishment in the winter of 1973 through the 20th growing season, including averages of the ten fastest and ten slowest growing families.

The distribution of mean annual height increment was less uniform during this period (Fig. 3). The low height increment during the 1986-1988 period corresponded to a 3-year drought in which growing season precipitation was below average. Similarly, the 1982-1983 high mean annual height growth corresponded to above average precipitation during the 1983 growing season. Differences between the family groups (10 tallest, average and 10 shortest families) were significant during these dry and very wet periods, although significant height increment differences were inconsistent in other years. Patterns of cumulative dbh and mean annual dbh increment were very similar to the patterns displayed for tree height.

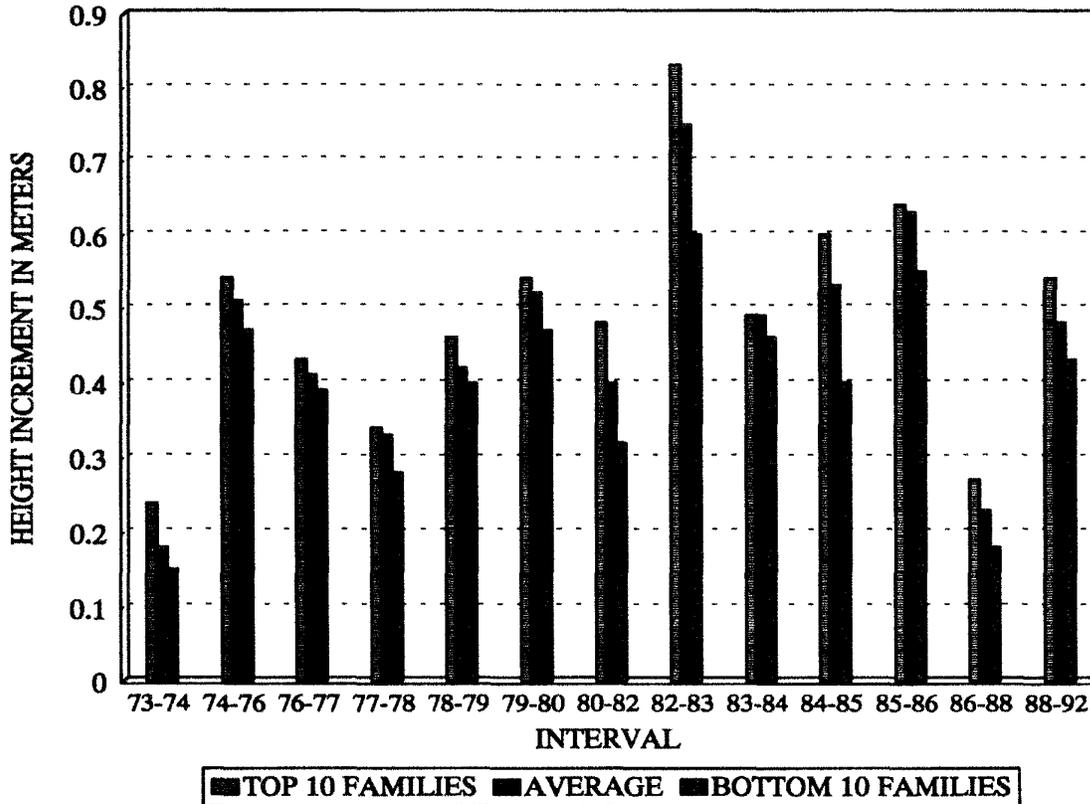


Figure 3. Mean annual height increment in Pleasant Valley black walnut progeny test, including averages of the ten fastest and ten slowest families.

Results from analyses of variance of height and diameter data indicated significance for both block and family effects in all 14 measurement years. Such results are common in experiments with large numbers of families and blocks and reflect an efficient experimental design. Due to missing plots a trivial coefficient (0.099) for the family variance component in the block effect was indicated; this reflected only minor confounding of the block effect.

The absolute magnitude of the family variance components consistently increased throughout the 20-year period of this progeny test (Table 1). However, on a percentage basis, in relation to total variance, the family variance component was at a maximum the year after establishment and decreased consistently during this 20-year period (Table 1). By the end of the 20th growing season, the family component accounted for 2.7 percent of total variance. The trend for family variance components was consistent with that reported by Rink and Clausen (1989) for this experiment through age 13 years and prior to thinning. Block variances, both absolute and as a percentage of total, increased over time, accounting for approximately 80 percent of total variance by the end of the 20th growing season (Table 1). Such a trend of rising block variance components may reflect intensified site occupancy over time by growing root systems of a site-sensitive tree species such as black walnut.

Table 1. Mean height (m) and dbh (cm), variance components, narrow-sense and family heritabilities¹, and respective standard errors for black walnut trees in Pleasant Valley progeny test.

Yr	Age	Mean	Std	Variance Components				Heritability ¹			
				Block	Family	Error	Total	Ind.	SE	Family	SE
HEIGHT											
73	1	0.48	0.13	0.0002	0.0041	0.0127	0.0170	0.97	0.251	0.74	0.063
74	2	0.66	0.20	0.0032	0.0044	0.0344	0.0420	0.46	0.154	0.54	0.039
76	4	1.69	0.39	0.0280	0.0142	0.1100	0.1523	0.46	0.136	0.54	0.034
77	5	2.10	0.50	0.0812	0.0146	0.1608	0.2566	0.33	0.100	0.45	0.025
78	6	2.43	0.65	0.1696	0.0320	0.2318	0.4333	0.48	0.104	0.56	0.026
79	7	2.86	0.79	0.3057	0.0394	0.3074	0.6525	0.45	0.089	0.54	0.022
80	8	3.38	0.94	0.5353	0.0499	0.3561	0.9413	0.49	0.075	0.56	0.019
82	10	4.19	1.35	1.2477	0.0981	0.6147	1.9605	0.55	0.066	0.59	0.017
83	11	4.93	1.60	1.8299	0.1475	0.7600	2.7374	0.65	0.066	0.64	0.017
84	12	5.41	1.66	2.0336	0.1429	0.7715	2.9481	0.63	0.061	0.63	0.015
85	13	5.94	1.96	3.0129	0.1772	0.9337	4.1238	0.64	0.053	0.63	0.013
86	14	6.57	2.14	3.7270	0.1899	1.0293	4.9463	0.62	0.048	0.63	0.012
88	16	7.03	2.34	4.3719	0.2118	1.3177	5.9014	0.55	0.047	0.59	0.012
92	20	8.98	3.19	8.8437	0.2981	1.9031	11.0449	0.54	0.036	0.59	0.009
DBH											
77	5	1.73	0.84	0.1431	0.0588	0.5168	0.7187	0.41	0.127	0.51	0.032
78	6	2.33	1.14	0.4594	0.1077	0.7895	1.3566	0.48	0.113	0.55	0.028
79	7	3.14	1.53	1.0079	0.1490	1.2835	2.4405	0.42	0.094	0.51	0.023
80	8	4.17	1.90	1.8367	0.2508	1.6958	3.7833	0.52	0.091	0.57	0.023
82	10	5.65	2.38	3.2980	0.3481	2.3499	5.9960	0.52	0.080	0.57	0.020
83	11	6.69	2.68	4.3814	0.4602	2.7617	7.6034	0.57	0.079	0.60	0.020
84	12	7.67	2.87	5.1486	0.4903	3.1269	8.7658	0.54	0.075	0.59	0.019
85	13	8.51	3.17	6.6255	0.5264	3.5360	10.6880	0.52	0.067	0.57	0.017
86	14	9.34	3.38	7.9461	0.5681	3.7849	12.2992	0.52	0.063	0.58	0.016
88	16	10.53	3.81	9.7916	0.6471	5.0398	15.4785	0.46	0.061	0.54	0.015
92	20	13.46	4.89	17.3099	1.0297	7.2604	25.6001	0.50	0.056	0.56	0.014

$$^1 \text{Narrow-sense individual tree heritability} = \frac{4\sigma_f^2}{\sigma_e^2 + \sigma_f^2}$$

$$\text{Family heritability} = \frac{\sigma_f^2}{\frac{\sigma_e^2}{9.076} + \sigma_f^2}$$

Between ages 1 and 5 years, narrow-sense individual tree heritabilities for height declined from 0.97 to 0.33. This was followed by steady increases to a maximum of 0.65 at age 11, remaining relatively stable until age 20 (Table 1, Fig. 4). Family heritabilities for height were slightly higher than for individual tree heritabilities, but the overall trend over time was nearly identical. Heritabilities for diameter at breast height were also similar in magnitude and had similar age trends (Table 1, Fig. 5).

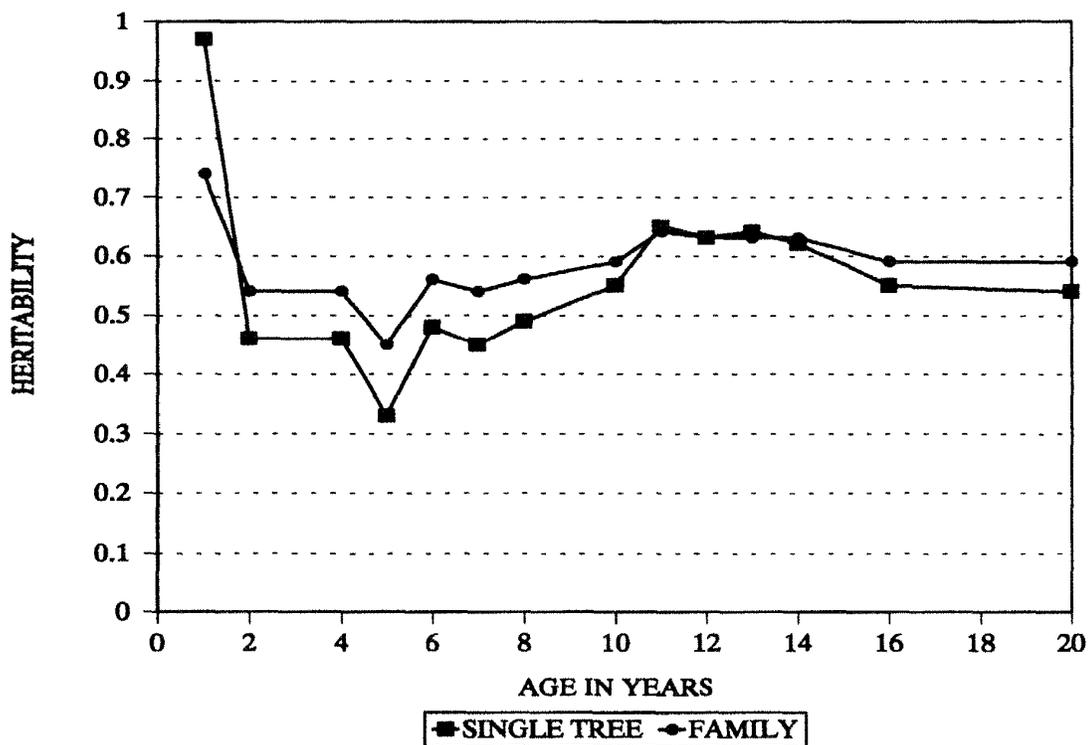


Figure 4. Narrow-sense (single-tree) and family heritability values for height at various ages of the Pleasant Valley black walnut progeny test.

The age-related pattern of heritability for black walnut tree height is similar to that described for North American conifers. Franklin (1979) proposed a hypothetical model with three genetic phases developed on the basis of heritability and additive genetic variance. The model consisted of a juvenile genotypic phase with a peak in heritability in the early to middle part of the phase, a mature genotypic phase with another peak in heritability occurring early in the phase, and a codominance-suppression phase characterized by rapidly declining heritability. The transition between juvenile and mature genotypic phases is characterized by a low in heritability (e.g., in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) France) at age 16, $h^2 < 0.005$) and a mature genotypic phase which extends from age 15 to age 40 (Namkoong et al. 1972).

Although the absolute values for black walnut differ from values for coniferous species, the pattern of heritabilities is similar. Peak heritability was found at age 1 ($h^2 = 0.97$) with a low estimate at age 5 ($h^2 = 0.33$), corresponding to a juvenile phase. Heritabilities gradually increase to a high at age 11 ($h^2 = 0.65$) and diminish slightly to 0.54 by age 20. Although the black walnut heritabilities in this study tend to be substantially higher than those reported for North American conifers, there is a resemblance in the distribution of heritabilities with that of the conifers. Thus, the low

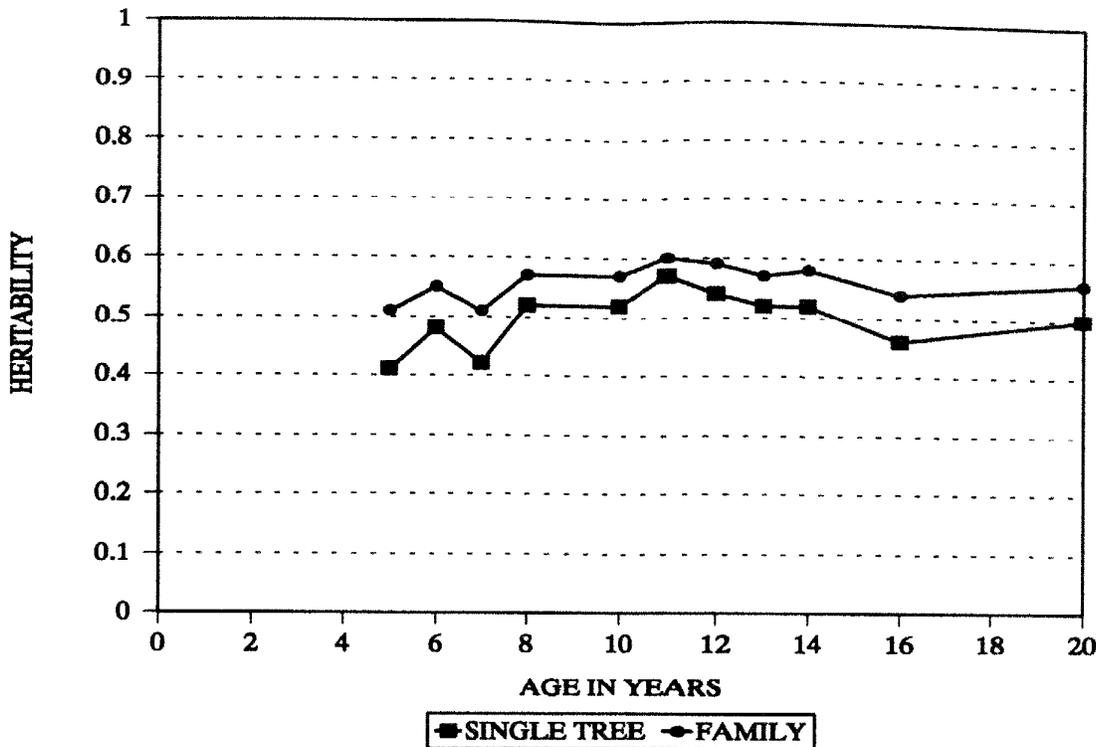


Figure 5. Narrow-sense (single-tree) and family heritability values for dbh at various ages of the black walnut progeny test.

heritability at age 5 may correspond to black walnut crown closure at this age and spacing and apparently occurs earlier than the age 15 in Douglas-fir (Franklin 1979).

It is possible that individual tree heritabilities presented here are overestimated due to potential confounding with a seed source effect (i.e., non-random mating within local seed sources) and a genotype x environment interaction, neither of which could be estimated from these data. Although age 13 genotype x environment interaction estimates presented elsewhere were very low (Rink and Clausen 1989) and would not have a great impact, the provenance effect potentially could have a substantial influence on these heritability estimates if trees represented in this study were in fact from more than one provenance. Thus, Squillace (1974) reported that overestimates of heritability result when data from unrelated families (e.g., such as from distant localities) are used for calculations. Strictly speaking, heritabilities should be estimated using data from open-pollinated families representative of a random-mating population in genetic equilibrium.

The curve of phenotypic age-age correlations between individual tree height in 1992 (at age 20) and individual tree height in earlier years is presented in Figure 6. By 1980 (age 8), the curve of age-age correlations appears to have attained a somewhat horizontal plateau; at this age, the correlation between 1992 height and 1980 height is 0.809, and the individual tree narrow-sense heritability is estimated at 0.49.

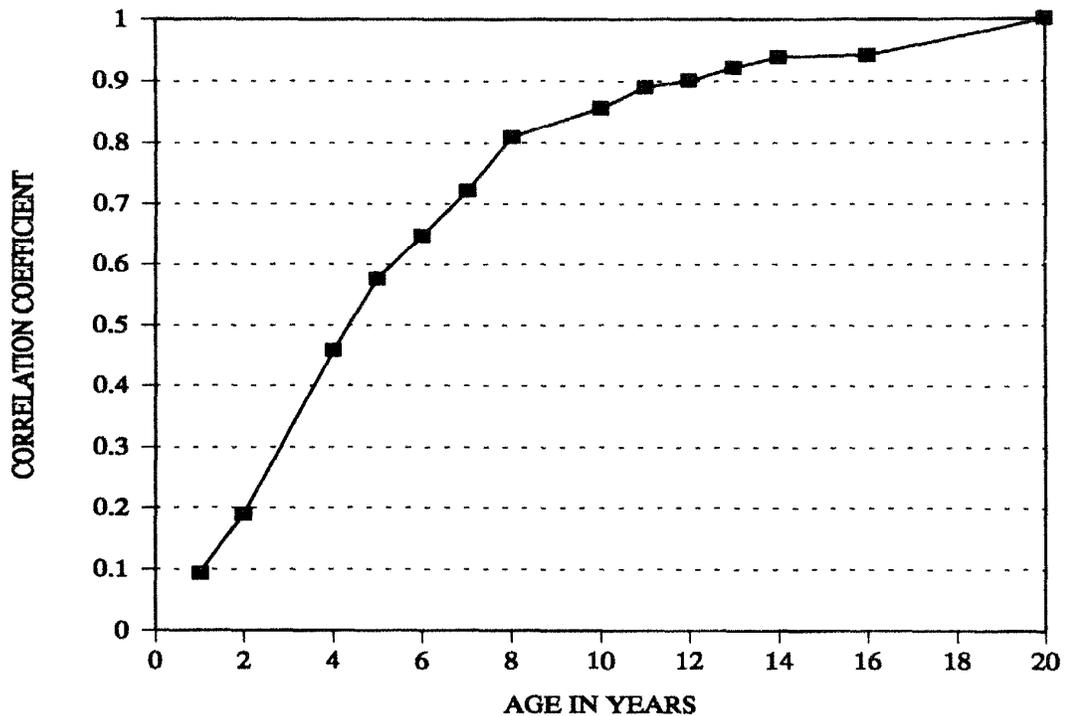


Figure 6. Age-age correlations of height of black walnut trees in 1992 (i.e., age 20) with height in other measurement years, on an individual tree basis.

Although the distribution of these heritability and phenotypic correlation values over time is based on a progeny test on only one site in southern Illinois, it would appear that selection of black walnut for improved height growth could be carried out with a high degree of confidence beyond age 8. Phenotypic correlations appear to have attained a plateau and seem to remain relatively stable. These results support the Indiana Division of Forestry (Coggeshall and Pennington 1982) effort in establishing close-spaced, short-term black walnut progeny tests for the purpose of juvenile testing and selection. Such approaches accelerate progeny testing and increase gain per unit time.

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EFFECTS OF HAYSCENTED FERN DENSITY AND LIGHT
ON WHITE ASH SEEDLING GROWTH

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Abstract: Communities of hayscented ferns [*Dennstaedtia punctilobula* (Michx.) Moore] are present in many forested areas of Pennsylvania. These ferns can reduce the number and height growth of desirable tree seedlings. A study was conducted to determine the effects of fern frond density on the stem growth and leaf development of bare-root planted white ash (*Fraxinus americana* L.) seedlings. Treatments of 0, 25, 50, and 100% frond density created conditions of 0, 151, 271, and 448 g/m² of oven-dry frond biomass in August. Amount and quality of sunlight passing through the fronds was measured. Shoot growth of the white ash seedlings was greatest in the 0% frond density (21 cm) and lowest in the 100% frond density (12 cm). A study using simulated fern fronds to alter sunlight conditions where root competition was not a factor was also conducted. White ash seedling stem growth was 23 to 45 cm for frond densities ranging from 80 to 0%. Reduced seedling shoot growth and changes in seedling leaf tissues associated with increased frond density were, in-part, due to changes in sunlight quality and quantity.

INTRODUCTION

In Pennsylvania and in other areas of the Northeast, the presence of hayscented fern [*Dennstaedtia punctilobula* (Michx.) Moore] often results in seedling establishment failure in hardwood stands. Hayscented fern can form a dense, nearly monospecific, ground cover beneath hardwood overstories following reproduction cuts. Dense ground covers of hayscented fern can reduce the number of desirable seedlings by 50-90% and inhibit seedling height growth by 40-60% (Horsley, 1983). When seedling growth is reduced, the seedlings are exposed to deer browsing for a longer period of time, seriously arrested advance regeneration development. Horsley (1993) recently has shown that reduced availability of light was the key factor preventing establishment and growth of black cherry (*Prunus serotina* Ehrh.) in Allegheny hardwood stands. We conducted two field studies to determine the effects of light altered by fern foliage on growth and development of planted white ash (*Fraxinus americana* L.) seedlings.

LITERATURE REVIEW

Competition for Light

Competition for light occurs when one species because of more rapid growth, taller stature, or established presence casts shade on another species, thereby limiting its growth. Competition for light differs in several ways from competition for other resources needed for plant growth. Basically, this difference arises from the nature of the supply of the resources. With water or nutrients there is a reservoir from which all competitors draw. It may be a virtually limitless supply or it may be a fluctuating or inadequate supply, such as occurs when soil moisture alternates between field capacity and wilting point. The situation for light is quite different; there is no reserve. Instead, light energy is instantaneously available and it must be instantaneously intercepted by leaves or it will be lost as a source of energy for photosynthesis. Light cannot accumulate in the environment for later use.

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A vital relationship in competition for light is one of physical position, the position of the foliage relative to the foliage of its competitors. Allocation of carbohydrate to new photosynthetic surface area will result in an exponential increase in growth. Increased growth may allow the development of a plant canopy that will shade a competitor, thereby reducing its growth and ability to exploit available resources. Allocation to below ground structures, although necessary for water and nutrient uptake, increases respiratory demand and decreases carbohydrates available for canopy development.

As one plant overtops another, not only is the quantity of light changed but also the quality. Plant canopies act not only to weaken but to filter sunlight. For plants growing under a vegetative canopy, there are three spectral changes which are of potential physiological significance. First, the quantity of photosynthetically active radiation is drastically reduced; second, a marked reduction in the quantity of radiation in the blue waveband; and third is the strong depletion of the red waveband and relatively weak reduction of the far-red waveband. These spectral changes occur as a result of the selective spectral absorption of leaves (Federer and Tanner, 1966). Light arriving at a green leaf is absorbed selectively, the remainder being scattered (reflected or transmitted). The blue and red (450-500 nm and 650-700 nm, respectively) wavebands are absorbed strongly, the green waveband is less strongly absorbed and the far-red is almost entirely reflected or transmitted (Holmes, 1981). The ratio of red to far-red radiation is expressed by R:FR which is the ratio of the photon fluence rate in 10 nm wide wavebands centered at 660 nm and 730 nm respectively (Holmes, 1981). Red:far-red during daylight, irrespective of time of year and weather conditions, remains remarkably constant, averaging 1.15 ± 0.02 (Smith, 1982).

The first person to make accurate measurements of the radiation spectrum on a forest floor was Knuchel (1914) who used a spectrophotometer. Unfortunately his measurements did not extend beyond 650 nm.

Seybold (1936) and Engle (1937) made measurements with glass filters which extended to 720 nm, but the wave bands were not sharply defined. These measurements clearly showed that the light in a forest is relatively rich in far red and near infrared. Only recently have suitable interference filters become available which make satisfactory field measurements possible.

Dirmhirn (1964) made measurements (between 400 nm and 1100 nm) under a group of walnut trees using a monochromator with interference filters. Federer and Tanner (1966) made measurements with a similar instrument under different stands in a wavelength range of 400-740 nm. Goodfellow and Barkham (1974) used an ISCO Spectroradiometer to measure quantity of radiation in the range 380-1100 nm in a beech forest. More recently, the LI-COR Spectroradiometer has become available and is capable of a similar range of readings (300 nm-1100 nm).

As early as 1936, Meischke drew attention to the fact that germination of many seeds is inhibited by far-red light, the wavelength band which is very strongly transmitted by green leaves. He concluded that under natural conditions this inhibition might occur under dense vegetation and showed in an experiment that light filtered through a leaf could inhibit seed germination (Stoutjesdijk, 1972).

Smith (1982) found that low R:FR light led to increased petiole length, reduced leaf area, increased stem dry weight, reduced branching, and changes in chlorophyll content. Thus there is strong evidence that plants are able to detect and react to both light quantity and R:FR levels associated with vegetation shade.

A typical spectral photon distribution for daylight between 400 nm and 800 nm at a station at 53°N latitude, under a clear midsummer sky and near midday, is shown in Figure 1 (Holmes and Smith, 1977a). There is some decrease in fluence rate at the blue end, but between 450 nm and 850 nm the photon fluence rate is remarkably uniform, being interrupted only by O₂ and H₂O absorption troughs.

Under a vegetative canopy, Figure 1 (Holmes and Smith, 1977b), highest transmission occurs beyond 700 nm which is maintained to 900 nm or 1100 nm. The transmission curve for the visible region shows a slight minimum being found between 425 nm and 475 nm and at 675 nm, with a maximum at 550 nm. This is explained by the absorption and reflection spectra for deciduous leaves. Within the visible spectrum a certain amount of radiation will be

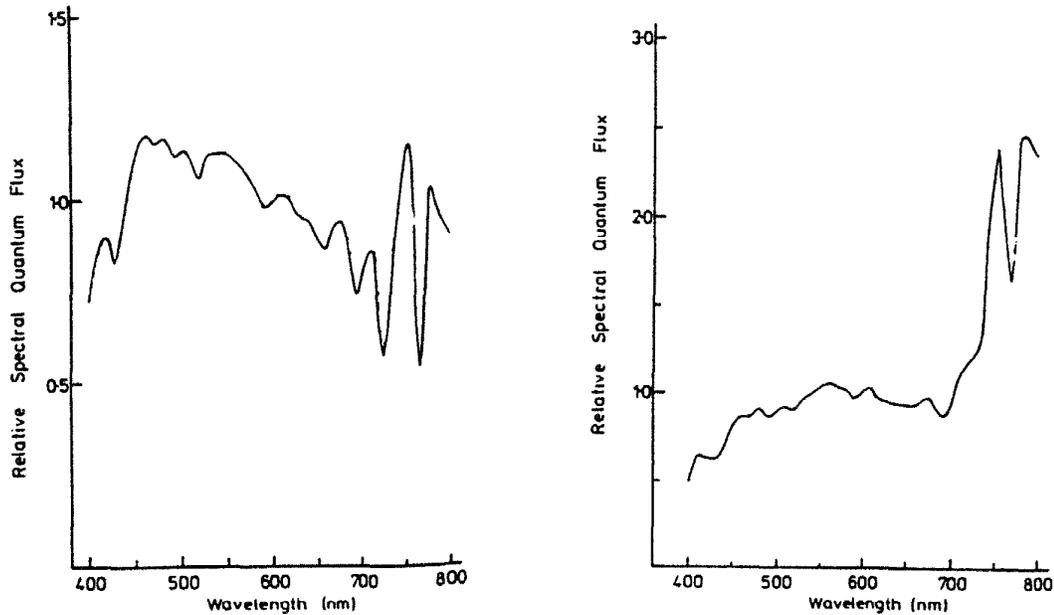


Figure 1. Light quality spectrum under clear skies, left (Holmes and Smith, 1977a); and light quality spectrum under a wheat canopy, right (Holmes and Smith, 1977b).

absorbed in all wavebands, but at 440 nm and 670 nm, the peaks of the photosynthetic action spectra, absorption is strongest. Other wavebands will be subjected to greater amount of transmission and reflection by the canopy. At 550 nm absorption is at a minimum, and the amount of radiation reflected and transmitted will be high. Similarly, beyond 700 nm in the far red and near infrared wavebands, absorption is low and these wavelengths therefore figure prominently under vegetative canopies.

Hayscented Fern

Hayscented fern [*Dennstaedtia punctilobula* (Michx.) Moore] is a native perennial fern of North America with its range centered in the Appalachian region and extending into adjacent parts of eastern Canada and eastern United States (Cody et al., 1977).

It reproduces both sexually and asexually. Sexually it produces spores which are released in late summer. Several million spores may be produced by a single well developed frond (Cody et al., 1977). These minute spores can travel through the air, depending on wind and other conditions, several hundred feet from the mother plant. These spores, given the correct conditions, generally bare, moist mineral soil, in a protected microsite will germinate and eventually produce a new fern plant (Groninger, 1991). Fern spores are known to be capable of germination under a very wide range of light intensities (Page, 1979). Light quality may also be of significance. In the wild, the vast majority of forest fern spores must be able to germinate successfully under low light conditions. The highest temperatures which permit germination are 30-35°C (Page, 1979). Most species of fern succeed between 10-20°C in high humidity and shade (Page, 1979). Once mature, spore production takes place regularly from year to year, showing very little

fluctuation with annual variations in climate such as those that may produce good and bad seed years in Angiosperms (Page, 1979).

Asexually, ferns can reproduce by an extensive rhizome or root system which generally occurs in the mineral and organic soil layers generally 5-15 cm below the surface (Cody et al., 1977). The rhizome system produces frond buds which may remain dormant for one or two years and then develop into mature fern fronds. Two to five fronds is the common annual growth from each branch of the rhizome (Cody et al., 1977). The rhizome overwinters and produces new fronds in the spring and throughout the growing season. Where a single plant can spread its rhizomes and occupy an entire area, a frond density as high as 55,000 per hectare may occur (Page, 1979).

Horsley (1984), in a study comparing fern rhizome development in uncut and thinned Allegheny hardwood stands, found that rhizomes from thinned stands elongated more, and produced more nodes between forks than those from uncut stands. In the uncut stands 10-15% of the frond petioles bore rhizome buds and these did not grow into new rhizomes unless the parent rhizome was injured. In the thinned stands, 55% of the frond petioles had rhizome buds and many of these grew into rhizomes the same year they were formed. This can possibly explain its rapid expansion in thinned or cleared areas.

There are three main stages in the annual development of the aerial part of the fern plant. The first stage is the fiddlehead stage which is characterized by a short straight rachis with a small curled top. This stage is visible from mid-April to mid-May. The second stage is the frond stage and is characterized by an increase in growth of the fiddlehead and the uncurling of the fern fronds to their full size. This stage occurs between mid-May and mid-September. The last stage is the dead frond stage. This stage is characterized by frond senescence, leaving the dried rachis which generally lies down on the soil and may persist for several years before degrading.

The only known method of totally eliminating hayscented fern is through the use of herbicides. The herbicides glyphosate (Roundup) and sulfometuron (Oust) are used in the northern hardwood forests of Pennsylvania to control hayscented fern (Groninger, 1991). Glyphosate must be applied to photosynthesizing foliage and has no soil residual activity. Sulfometuron, though, applied to exposed mineral soil may prevent the establishment of hayscented fern through spore germination (Groninger, 1991).

White Ash

Fraxinus americana (L.) grows most commonly on fertile soils with high nitrogen content and moderate to high calcium content. The absence of nitrogen reduces seedling dry weight by 38% (Schlesinger, 1990). Soil moisture is an important factor affecting local distribution. Natural regeneration from seeds will occur if the soil, humus, or leaf litter is wet in the spring. Best growth occurs in moderately well-drained soil. Tolerance to pH varies from 5.0 to 7.5 (Schlesinger, 1990). Seedlings are capable of withstanding protracted periods of soil drought and are intermediately tolerant to temporary flooding (Rink and Sambeek, 1987).

Young white ash exhibit strong apical dominance. Open-grown seedlings 2 m tall often have only two or three pairs of lateral branches. If the terminal bud is removed, apical dominance is altered and new branches develop from the uppermost pair of lateral buds. Generally one of these grows faster than the other and assumes dominance.

Seedlings develop best in 45% full sun or greater (Logan, 1973). Therefore, silvicultural systems that provide sunlight, such as shelterwood or clearcutting, have been recommended for white ash. When seedlings are young, they are shade tolerant but with age they become more intolerant. Seedlings are capable of survival under a canopy with less than 3% full sun, but they show very little growth at these light levels (Schlesinger, 1990). Under good conditions, they complete 90% of their height growth in 30 days and complete 100% in 60 days. Diameter growth continues until August (Schlesinger, 1990).

Despite its low shade tolerance, white ash is characteristic of intermediate as well as early stages of plant succession. Throughout its range it is a minor but constant component of both the understory and overstory of mature forests on

suitable soils. It owes its position in the final overstory to its ability to persist for a few years in moderately dense shade and to respond quickly to openings in the canopy.

White ash was chosen for the studies based on its behavior in a study by Kolb et al. (1990). They studied the influence of light intensity on weed-induced stresses of tree seedlings (white ash, red oak, and white pine). They found that white ash produced the greatest height growth in interference-free environments but also showed the greatest reduction in growth in a fern environment. These results suggest that white ash has a lower tolerance to herbaceous interference than either red oak or white pine. For this reason white ash was chosen as the study species.

METHODS

The study site was located in the Rothrock State Forest, Huntingdon County, PA, in the Ridge and Valley Province of central Pennsylvania. The area chosen had a southeastern aspect with soils derived from sandstones. The soils were mapped as a Hazelton-DeKalb association having moderately rapid permeability, low to moderate water availability, severe erosion hazard, and medium runoff (Soil Survey of Huntingdon County, PA). Soil pH averaged 4.6 for the site. A shelterwood cut was made in the late 1960's prior to clearcutting during the 1984 growing season. The site index prior to any cutting activity was approximately 70 for oak. Oak species dominated the stand. The site now consists of 80-100% fern and grass communities.

Four areas measuring 8 m by 8 m were selected which contained a dense fern population. The 8 m by 8 m areas were divided into 4 m by 4 m sections with each section representing a fern treatment.

Four areas measuring 2 m by 8 m were selected adjacent to the fern treatment areas and were herbicided with glyphosate (Roundup) at a rate of 1.1 ai/ha one year prior to study initiation. The 2 m by 8 m areas were divided into four 2 m by 2 m sections with each section representing a shade treatment. All areas were cleared of brush and logging debris in the spring of 1991.

On April 19, 1991 one year old bare root, white ash (*Fraxinus americana* L.) seedlings obtained from the Pennsylvania Bureau of Forestry's Penn Nursery at Potters Mills, PA, were planted randomly in the designated areas. White ash was selected for this study because it had a substantial response to ferns in an earlier study (Kolb et al., 1990). The seedlings were top clipped to 10 cm and root clipped to 15 cm before planting. Each fern treatment received 24 seedlings with either one or two seedlings per meter square, a total of 384 seedlings for the fern treatment areas. Each shade treatment received 5 seedlings in each replication for a total of 80 seedlings for the shade treatment areas.

Each treatment in the fern plots was randomly assigned one of four density treatments; 100% fern, 50% fern, 25% fern, and 0% fern. The treatments assigned 100% fern were left untouched with the ferns being allowed to grow to their natural density. The 50% fern treatments were marked off with parallel lines every 0.25 m. The 25% fern treatments were marked off by a combination of parallel and perpendicular lines every 0.25 m.

Shade frames were built over the shade plots with each replication receiving four different shade treatments: 0%, 30%, 60%, and 80% shade. White PVC pipe was used as a frame to support black polypropylene shade cloth 1.2 m above the ground. The shade cloth also extended halfway down the side of the frame to eliminate large amounts of sidelighting but to allow for air circulation under the frames. A four-foot-high wire mesh fence was erected around each area to exclude deer.

Four gypsum moisture blocks and two copper-constantan thermocouples were installed at random locations at 7 cm depth in each fern treatment areas. Two gypsum blocks and one thermocouple were installed at random locations in each of the shade treatments. Soil moisture readings from the gypsum blocks and soil temperature readings from the thermocouples were taken once a week beginning in June and continuing throughout the study. The readings were taken between 11:00 AM and 1:00 PM.

Seedling heights from root collar to top of stem and stem diameters were measured after all treatment preparations had been made. Seedling growth (shoot growth from site of initiation on original stem) was measured every six weeks until mid-September. Any herbaceous vegetation which grew in the shade plots during the study was removed.

The fern treatments were clipped after the fern fronds had grown to about 50% of full size (May 25, 1991), but before bud break in the seedlings. In areas designated 0% fern, all of the fern fronds were cut off at the soil surface. In treatments designated 25% fern, every other 0.25 m wide strip was cut in both directions leaving 0.25 m² per 1.0 m² patch of fern. In areas designated 50% fern every other 0.25 m wide strip was cut leaving alternating strips of 0.5 m² fern and 0.5 m² of non-fern. In treatments designated as 100% fern, no ferns were cut. Since the seedlings were located randomly in the plots, some occurred in the fern strips whereas others occurred in the cut strips. Two 1.0 m² samples of fern fronds were collected from each treatment in each replication for a total of 8 samples for each treatment. The dry weight of the ferns per 1.0 m² were measured for each treatment and are shown in Table 1. Several days after the cutting treatments were completed the fern fronds leaned over and filled in the non-fern spaces in a somewhat uniform manner with the fronds facing in all directions. The areas were re-clipped once a month to maintain the cut strips.

Table 1. Average fern biomass per square meter \pm SE as compared to 100% fern treatment. Ferns were collected from two 1.0 m² areas in each treatment of each replication for a total of 8 samples for each treatment. The ferns were then oven dried, weighed, and averaged among treatments.

Treatment	Dry Weight (g)	% Biomass
100% FERN	448 \pm 28.1 g/m ²	100%
50% FERN	271 \pm 18.2 g/m ²	60%
25% FERN	151 \pm 21.9 g/m ²	30%
0% FERN	0 g/m ²	0%

Light quantity readings were taken under all treatments on July 10, 1991 with a LI-COR 191SA Line Quantum Sensor, Lincoln, NE. Two light quantity readings were taken in each treatment of each replication for a total of 8 readings per treatment. The line sensor is 1 m long and approximately 5 cm in height. The sensor was placed under the ferns in the fern treatments perpendicular to the cut strips so that fern/no fern strips were uniformly distributed across the sensor. The sensor was placed in the center of the shade treatments for the readings.

Light quality readings were taken randomly under each fern treatment with a LI-COR 1800 Spectroradiometer Lincoln, NE. Light quality readings were taken on two consecutive days (September 7th and 8th, 1991) with two readings per treatment per replication for a total of eight measurements for each fern treatment and one reading was taken in each treatment of each replication for a total of 4 readings for each shade treatment. The sensor was located approximately 18 cm off the ground and was approximately 4 cm in diameter. Readings were taken in both fern and cut areas of the fern treatments to try to get an average. All light readings were taken within two hours of midday in order to eliminate variations in light intensity and quality due to rapidly changing zenith angle of the sun. Readings were taken in reference to the horizontal surface under clear-sky, calm weather conditions.

The study was conducted for a single growing season and seedlings were harvested at the soil surface on September 17, 1991. Shoot growth was measured at this time and the leaves from each plant were removed and leaf area

measured with a LI-COR Area Meter Lincoln, NE. The stem and leaves were then dried in a drying oven for 5 days and then weighed to obtain dry weights.

The data were treated as a randomized block experiment and analysis of variance (ANOVA) was run on the following parameters to test for significant treatment effects; shoot growth, dry weight of the stem, number of leaves, leaf area per plant, area per leaf, dry weight of the leaves, dry weight per leaf, and specific leaf area. Root length was not measured because the hardness of the soil due to lack of rain did not permit the extraction of the entire root system. Mean separations were performed on those parameters which showed significant treatment effects with Tukey's Method of Multiple Comparisons (0.05 was the level of alpha considered significant).

RESULTS AND DISCUSSION

Fern Treatments

Light Quantity. The range of light quantity readings, their averages and percentages are shown in Table 2. Light quantity readings taken in full sun were the basis for comparison. One would not expect this much variability in the ranges of light quantity as the Line Quantum Sensor is designed to reduce variability. The wide range in values for each treatment could be due to the variability of the fern populations and the nature of the treatments (fern/no fern strips). Another explanation is that in some areas the ferns were thicker (more fern fronds per unit area) than in other areas. Also the fern appeared more 'transparent' in some areas than in others, so more light may get through the more 'transparent' ferns.

Table 2. Light quantity ranges, averages, and percentages in the four fern treatments. The measurements were taken with a LI-COR Line Quantum Sensor under the ferns. Values are in μmol . The shade percentages were calculated relative to full sun (0% fern). The measurements were made within two hour of mid-day on July 10, 1991, with clear-sky conditions.

TREATMENT	RANGE (μmol)	AVERAGE	% SHADE	RANGE
0% FERN	1570-1985	1778	0%	-----
25% FERN	201-1413	545	70%	21-89%
50% FERN	136-781	277	84%	56-92%
100% FERN	5-162	53	97%	91-100%

Light Quality. Plants need light in the red and blue region (650-700 nm and 450-500 nm respectively) of the spectrum to carry out photosynthesis. The R:FR ratios (ratio of the photon fluence rate in 10 nm bands centered at 660 nm and 730 nm respectively) showed the reduction in red light as the fern densities increased. In the open the ratio was 1.13, under 25% fern the ratio was 0.84, under 50% fern was the ratio was 0.31, and under 100% fern the ratio was 0.20. The averaged light quality measurements are shown in Figure 2. The graph shows not only a reduction in light quantity but a large change in light quality in the wavelength range from 300-700 nm for the 100% fern and 50% fern treatments. This graph is similar to Figure 1 shown previously. So light penetrating a fern canopy is almost entirely far-red in quality, unusable by plants.

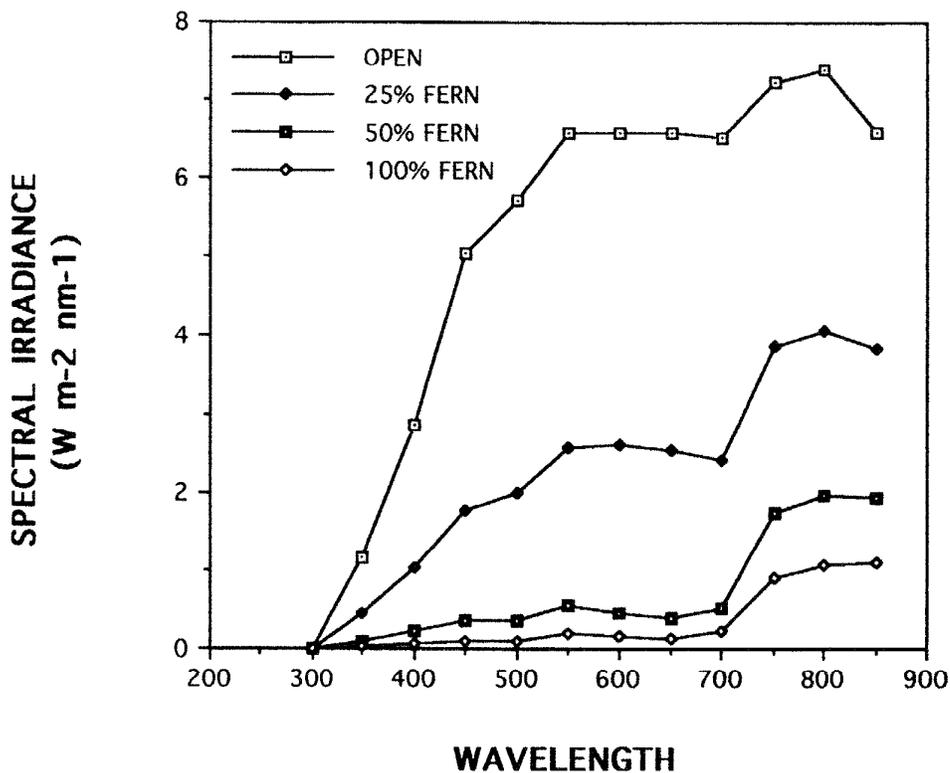


Figure 2. Average spectral irradiance values for the four fern treatments by wavelength. The measurements were made with a LI-COR Spectroradiometer. Each point is an average of 8 measurements.

Soil Moisture. Measurements taken with the gypsum blocks in all four treatments showed no significant difference between the treatments. Soil moisture fluctuated by month with rainfall events as recorded by The Agricultural Research Center at Rock Springs located approximately 12 km northwest of the study site. In general percent soil moisture increased after rainfall events as would be expected. Overall the soil moisture percentages seem much higher than would be expected in the field. The reason for this is unknown. Lower readings would be expected because of the low amounts of rainfall received in the 1991 growing season.

Soil Temperature. Soil temperature measurements showed that 0% fern treatments had significantly higher average soil temperatures at 7 cm depth than the 100% fern treatments. This difference averaged 2.5°C. The other treatments did not differ significantly. Kolb et al. (1989) found soil temperatures to be 4°C greater in fern free environments. In general, the 0% fern treatments had higher soil temperatures than the average air temperature for that particular day and 100% fern had lower average soil temperatures than the average air temperature for that day. The soil temperature difference between the 0% fern and 100% fern would be expected because there is less radiation reaching the soil surface beneath the ferns and so less soil heating.

Shoot Responses to the Treatments. Seedlings growing in the 0% fern treatment were significantly taller than all the other treatments averaging 20.6 cm of shoot growth (tallest stem measured from site of growth on initial stem) Table 3. Shoot growth of the seedlings growing in 25% fern, 50% fern, and 100% fern were not significantly different from each other. The average shoot growth was 12 cm in these treatments. So shoot growth was reduced

Table 3. Growth responses of white ash seedlings to different levels of hayscented fern cover. Means \pm SE followed by the same letter are not significantly different at the $P < 0.05$ level ($n=96$).

RESPONSE	TREATMENT			
	0% FERN	25% FERN	50% FERN	100% FERN
Shoot growth (cm)	20.6a \pm 1.2	13.0b \pm 0.60	11.3b \pm 0.50	11.8b \pm 0.60
Dry weight stem (g)	2.0a \pm 0.27	0.65b \pm 0.05	0.40b \pm 0.03	0.33b \pm 0.03
# Leaves/plant	16a \pm 0.68	11b \pm 1.08	8c \pm 0.30	8c \pm 0.33
Leaf area (cm ²)	503a \pm 48.5	213b \pm 13.3	156b \pm 8.6	144b \pm 9.3
Area/leaf (cm ² /leaf)	28.5a \pm 1.5	19.9b \pm 0.95	19.6b \pm 0.89	18.8b \pm 0.93
Dry weight leaves (g)	3.1a \pm 0.30	1.0b \pm 0.07	0.7b \pm 0.04	0.5b \pm 0.03
Dry weight/leaf (g/leaf)	0.18a \pm 0.01	0.1b \pm 0.005	0.08c \pm 0.004	0.07c \pm 0.003
Specific leaf area (cm ² /g)	167d \pm 2.7	213c \pm 3.9	241b \pm 4.2	284a \pm 6.1

40% in the presence of any amount of fern. Others have studied seedling height growth under fern and have also found that height growth is severely inhibited by the presence of ferns (Drew, 1988; Horsley and Marquis, 1983; Kolb et al., 1990).

Reasons for the reduced growth of seedlings under fern canopies have been proposed and studied by some authors. Allelopathic studies have been done on hayscented fern by Horsley (1977). He demonstrated that black cherry seedlings watered with nutrient solutions containing foliage extracts from hayscented fern reduced their growth. In future studies though, he dismisses the allelopathic effects of hayscented fern (Horsley, 1986).

Drew (1988) in his paper on the interference of seedling growth by hayscented fern and whorled aster suggests competition for soil nitrogen and forest microsite as the possible cause of reduced growth under the ferns and also suggests the reduced light environment under the ferns as a cause.

Stem (new growth taken from site of initiation on initial stem) dry weights showed results similar to shoot growth with the 0% fern treatment producing the most stem biomass; averaging 2.0 g (Table 3). The three fern treatments did not differ significantly; averaging 0.5 g per stem.

Leaf Responses to the Treatments. The seedlings growing free from above ground competition (0% fern) had larger leaves than the trees with above ground competition (Table 3). The 0% fern treatment averaged 28.5 cm²/leaf and the 25% fern, 50% fern, and 100% fern did not differ and averaged 19.4 cm²/leaf.

The largest dry weight per leaf averaged 0.18 g/leaf and was measured in the 0% fern treatment. This was significantly greater than all other treatments. The 25% fern treatment (0.10 g/leaf) differed significantly from the 100% fern treatment (0.07 g/leaf), but did not differ from the 50% fern treatment (0.08 g/leaf). The 50% fern treatment dry weight per leaf did not differ from that of the 100% fern treatment.

Specific leaf area (SLA) is a measurement of area per unit weight and gives an indication of leaf expansion. Generally SLA increases in low light as a result of the formation of thinner leaves with a higher water content (Corre, 1983; Morgan and Smith, 1981; Nygren and Kellomaki, 1983). The results of this study produced similar results with all treatments being significantly different. The seedlings in the 0% fern treatment with the lowest SLA averaging 167 cm²/g and seedlings in the 100% fern treatment with the highest SLA averaging 284 cm²/g.

One reason for the general reduced shoot growth under the ferns was both a reduction in the amount and a change in quality of light passing through the ferns. The amount of light was reduced to 3-30% of full sun in the presence of 25-100% ferns. From Figure 2, it is clear that the R/FR ratio has changed significantly. Studies show that white ash is capable of survival but not growth under a canopy with less than 3% full sun, but they show very little growth under these circumstances (Schlesinger, 1990). In this study light varied from 100% sun to almost 0% sun and the seedlings survived, but showed very little growth. Only the above ground portion of the fern plant was manipulated, leaving the entire rhizome system intact. Perhaps the rhizomes have more of an influence on seedling growth than the fronds, since the rhizome system remained constant in all the treatments.

Shade Frame Treatments

Light Quantity. The light quantity readings taken under the shade treatments were consistent with the shade ratings of the nylon shade cloth used (30%, 60%, 80%), varying only 2-3% from the rating.

Light Quality. Light quality readings under the shade treatments (Figure 3) show the reduction in quantity but also show that the general shape of the spectra remained constant. Wavelength quantities were proportionately reduced, but all wavelengths remained in the spectrum. There was no reduction in the proportion of red light to far red light. The R:FR ratios under the shade treatments remained constant averaging 1.10 which is very similar to readings taken by Smith (1982) whose R:FR ratio in daylight averaged 1.15.

Soil Moisture. Measurements taken with the gypsum blocks in all four treatments showed no significant difference among them. Overall soil moisture remained fairly high throughout the study despite the low amounts of rainfall. Again soil moisture percentages seem very high for unknown reasons.

Soil Temperature. Soil temperature measurements showed that 0% shade treatments had significantly higher soil temperatures than all the other treatments. The 30%, 60%, and 80% shade treatments did not differ significantly. There was an average of 3°C difference between 0% shade and 30% shade, and average of 3.5°C between 0% shade and 60% shade, and average of 4.5°C between 0% shade and 80% shade. In general, 0% shade treatment produced the highest soil temperatures which averaged above the average air temperature. Generally, the 30%, 60%, and 80% shade treatments averaged below the average air temperature.

Since the shade cloth produces an artificial environment some of its affects on the environment beneath it needs to be discussed. First there is reduced air circulation and so less evaporation of soil moisture. Second, there is less radiation reaching the soil surface and so cooler temperatures both beneath the cloth and in the soil. Rainfall amounts reaching beneath the shade cloth were probably different for all treatments since the shade cloth trends to intercept rainfall (different rainfall amounts were intercepted depending on the density of the shadecloth) and direct it off of the plots, running down the sides of the frames. Despite this redirection of rainfall, it seemed definitely damper under the shade cloth than in the open. This is probably due to the lack of air circulation and radiation under the cloth which would increase evaporation.

The shade cloth environments would compare to the different levels of shade cover in the following ways; first, under the ferns there would also be reduced air circulation, especially in the 100% fern. Second, the ferns also intercept radiation and rainfall much in the same manner as the shade cloths, with different levels of fern intercepting different amounts of each. So although different in composition and appearance, the shade cloth and the fern cover do produce similar results in the way of reducing air circulation, reducing radiation, and intercepting rainfall. The main difference being the selective spectral absorbance of the ferns.

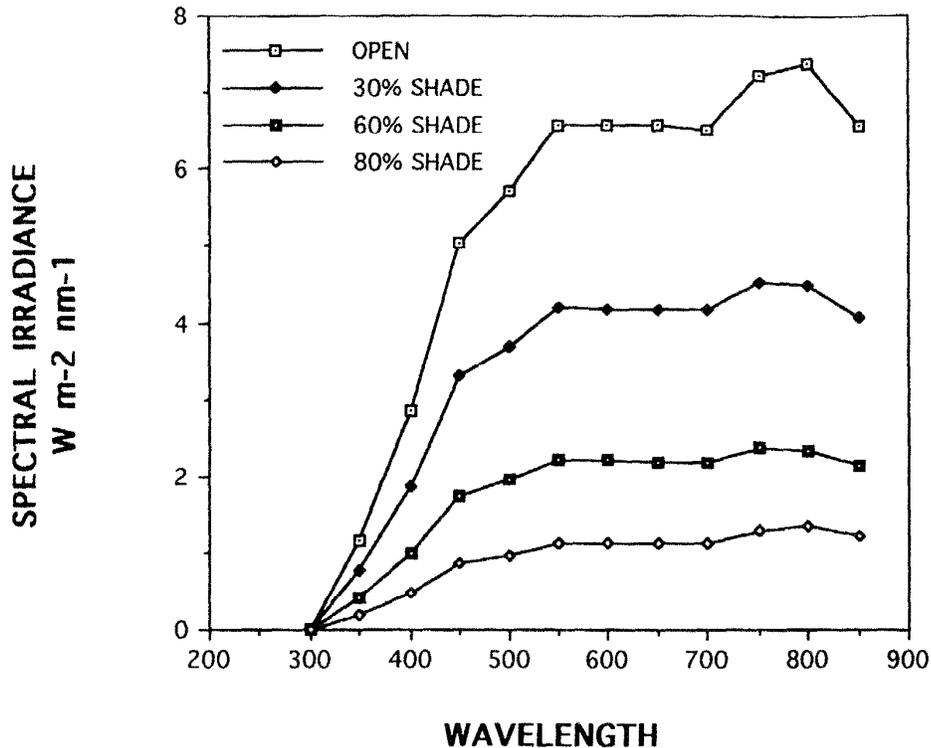


Figure 3. Average spectral irradiance values for the four shade treatments by wavelength. The measurements were made with a LI-COR Spectroradiometer. Each point is an average of 4 measurements.

Shoot Responses to the Treatments. Analysis of shoot growth (Table 4) shows that seedlings in the 30% shade treatment produced the best height growth averaging 44.7 cm in height (tallest stem). The 30% and 0% shade treatments did not differ significantly though and average growth between the two was 42.2 cm. The 0% shade treatment did not differ from the 60% shade treatment which averaged 34.4 cm in height. The 60% shade treatment did not differ from the 80% shade treatment averaging 26.0 cm. Schlesinger (1990) found that white ash seedlings grow best in 45% full sun.

The dry weight of the stems show that 0% shade, 30% shade, and 60% shade were not significantly different averaging 6.8 g. The 60% shade treatment did not differ from the 80% shade treatment and averaged 3.1 g.

Leaf Responses to the Treatments. The number of leaves produced did not differ significantly between 0% shade, 30% shade, and 60% shade and averaged 23 leaves per plant. The 60% shade treatment and the 80% shade treatment did not differ and averaged 19 leaves per plant (Table 4).

Total leaf area per plant exhibited a similar trend as the number of leaves per plant. Generally the more leaves a plant has, the greater the total leaf area. The 0%, 30%, and 60% shade treatments did not differ significantly and averaged 1331 cm². The 60% shade treatment and the 80% shade treatment did not differ and averaged 875 cm² (Table 4).

Table 4. Growth responses of white ash seedlings to varying shade treatments. Means \pm SE followed by the same letter are not significantly different at the $P < 0.05$ level ($n = 20$).

RESPONSE	TREATMENT			
	0% SHADE	30% SHADE	60% SHADE	80% SHADE
Shoot growth (cm)	39.7 ab \pm 3.8	44.7a \pm 3.3	29.2cb \pm 3.2	22.9c \pm 3.4
Dry weight stem(g)	7.9a \pm 1.5	8.5a \pm 2.1	4.0ab \pm 0.78	2.3b \pm 0.44
# Leaves/plant	24ab \pm 1.9	26a \pm 2.1	21ab \pm 1.7	18b \pm 1.4
Leaf area (cm ²)	1468a \pm 252	1498a \pm 227	1037ab \pm 142	713b \pm 112
Area/leaf (cm ² /leaf)	55.4ab \pm 6.0	59.4a \pm 6.7	51.1ab \pm 6.3	37.0b \pm 3.9
Dry weight leaves (g)	8.9a \pm 1.5	8.3a \pm 1.7	5.2ab \pm 0.83	2.9b \pm 0.45
Dry weight/leaf (g/leaf)	0.34a \pm 0.04	0.33a \pm 0.05	0.23ab \pm 0.02	0.15b \pm 0.02
Specific leaf area (cm ² /g)	165a \pm 11.0	215a \pm 28.0	284a \pm 89.0	252a \pm 8.5

Area per leaf measurements show the seedlings in the 30% shade treatment to have the largest leaves with 59.4 cm²/leaf average. The 30% shade treatment though did not differ from the 0% shade treatment or the 60% shade treatments. The 0% shade, 30% shade, and 60% shade treatments averaged 55.3 cm²/leaf. The 80% shade treatment though did not differ significantly from 0% shade or 60% shade either averaging 47.8 cm²/leaf overall.

Dry weight per leaf shows that 0% shade, 30% shade, and 60% shade did not differ averaging 0.30 g/leaf. Again, 60% shade does not differ from 80% shade averaging 0.19 g/leaf.

Specific leaf area (SLA) surprisingly did not differ significantly between treatments but the expected trend is shown in the results (Table 4). Plants growing in low light intensity have a higher SLA than plants growing in a higher light intensity (Corre, 1983; Nygren and Kellomaki, 1983). In this study 60% shade had the highest SLA averaging 252 cm²/g and 0% shade had the lowest average of 165 cm²/g. Why 80% shade treatment did not produce the highest SLA is unknown. One possible explanation is that 80% shade is past the threshold for shade tolerance of white ash and so shading decreased leaf area instead of increasing it. Huxley (1967) and Wassink and Stolwijk (1956) found similar results where leaf area increased with increased shading up to a certain point and then decreased.

Comparison of the two field studies results shows some interesting points that warrant further research. Overall, all of the shade treatments showed better growth than any of the fern treatments. The 0% fern treatments showed 100% lower growth than the 0% shade treatments despite the fact that they received equal amounts of sunlight. The only difference between the two treatments was the presence of active fern rhizomes in the 0% fern treatments. So obviously light is not the only factor reducing the growth of the seedlings, there is also some sort of soil effect (Drew, 1988). Comparison of soil moisture in both treatments, indicate a difference in percent soil moisture between 0% fern and 0% shade, with 0% shade having greater soil moisture than 0% fern. Perhaps the fern rhizomes are still utilizing soil resources without the fern fronds being present. Perhaps this difference in soil moisture is one explanation for the difference in growth between these two treatments.

It is also possible that the fern litter produced by herbiciding the shade plots enhanced the nutrient supply in the shade treatments, thereby influencing growth. Soil nutrient levels were not intensively studied here so no definite conclusion can be drawn.

CONCLUSIONS

It is obvious from the results of these studies that hayscented fern [*Dennstaedtia punctilobula* (Michx.) Moore] definitely influences the growth of tree seedlings. These studies indicate that hayscented fern produces not only an above-ground influence through changes in light quantity and quality, but a below-ground influence where the causal factors are unknown.

The fern cover study showed that a range of levels of fern cover; 25%, 50%, or 100% did not produce significantly different growth of white ash. Again only the above ground portion of the fern plant was manipulated leaving the entire rhizome system intact. Removing all of the fern fronds produced a significant increase in growth, probably due to increased light.

The shade frame study brought out some interesting points. First, all of the shade frame treatments showed better growth than all of the fern treatments. The seedlings growing in the 80% shade treatments showed better growth than the seedlings growing in the 0% fern treatments, despite the fact that the seedlings in the 80% shade treatments are receiving 80% less light than the 0% fern treatments. Light cannot be the only limiting factor. Second, the seedlings in the 0% shade treatment grew 100% taller than the 0% fern treatment although both were receiving the same amount of sunlight. There must be a below ground influence, whether it be soil moisture differences, nutrient differences, or another means. Although this study focused on light, it was shown that light has perhaps only a very small influence. Further studies are needed to determine what influence the rhizomes have on the seedlings and the soil environment in general. At this point it can be concluded that fern-free conditions are necessary to attain the maximum height growth of seedlings.

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THE INFLUENCE OF SHADE ON NORTHERN RED OAK SEEDLINGS

GROWTH AND CARBON BALANCE

Jennifer L. Jennings¹

Abstract: One management problem of the Southern Appalachian mixed hardwood forest is the lack of development of northern red oak (*Quercus rubra* L.) seedlings on high quality sites. Regeneration of red oak is not the problem. Following the removal of a stand, a combination of new seedlings, advanced reproduction and stump sprouts ensure red oak's initial presence. However, seedlings and sprouts cannot compete with other hardwoods, specifically yellow-poplar (*Liriodendron tulipifera* L.). Advance reproduction is the exception-if present before harvest, it will usually be present in the new stand. A modified shelterwood cut, in which the understory is removed from below, has been shown to assure the development of this advance reproduction.

Light quantity is thought to be a major factor inhibiting the rapid development of northern red oak. Changes in light intensity will affect biomass partitioning and physiological parameters such as photosynthesis and respiration. To test this hypothesis, seedlings located in the Pisgah National Forest were shaded at 95%, 90%, 60% and 0% full sunlight. Height, diameter and photosynthesis readings were taken throughout the growing season. Seedlings were then destructively sampled and the oven dry weight was found for the leaves, stems and roots of all seedlings. Preliminary data suggest that seedlings shaded at 60% full sun have an increased growth response.

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CHARACTERISTICS OF A LONG-TERM FOREST SOIL PRODUCTIVITY RESEARCH SITE IN MISSOURI

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Abstract: Problems with soil quality and maintenance of soil productivity occur when management activities are improperly planned and carried out. To ensure that Forest Service management practices do not reduce long-term soil productivity (LTSP), a network of coordinated long-term experiments is being established across the United States. The first LTSP study in the Central Hardwood Region is being established in the Ozark Region of southeastern Missouri, in Shannon County. The study area contained mature upland oak-hickory forest with some oak-pine communities. Within the 17.4-ha (43-acre) study area are 27 plots that are approximately 0.4 ha (1 acre) each. The national study plan calls for three levels of organic matter removal (stem only, whole tree, and whole tree plus litter layer) and three levels of compaction (none, moderate, and severe). Logs were lifted from the uncompacted treatment (9 plots) using a skyline yarder system instead of entering plots with a skidder. The remaining plots were harvested conventionally. Pre-treatment data collected include census, height, diameter, and nutrient measurements of overstory, understorey, and herbaceous plants; litter and forest floor weights as well as chemical composition; and chemical and physical (porosity and bulk density) soil properties. These data will be used to investigate the effects of treatments on growth, composition, and spatial distribution of woody and herbaceous vegetation, physical and chemical soil properties, and nutrient cycling.

INTRODUCTION

Developing forest management practices to ensure the long-term sustainability of forests is becoming a research and management priority. Interest in sustaining productivity of forest lands has steadily increased since the use of heavy equipment (Woodbury 1930) and whole tree harvesting (Hornbeck and Kropelin 1982). Public concern about the impacts of forest management activities has resulted in legislation (USDA Forest Service 1983) and policies (U.S. Code of Federal Regulations 1985) that mandate research and monitoring (USDA Forest Service 1987) of management systems to protect the productivity of the land.

Before these policies and legislation, there was the National Forest Management Act (NFMA) of 1976, which requires the research and monitoring of federal lands to safeguard the productivity of forest soils (Powers and others 1990). This requirement has led to a nationwide research and monitoring program to define the effects of management practices on long-term soil productivity through the establishment of coordinated, long-term experiments on major timber species, soils, and regions across the United States (Powers and others 1989). The objectives of the program are to: (1) quantify the effects of soil disturbance from management activities on long-term productivity; (2) validate soil monitoring standards developed in compliance with the NFMA of 1976; (3) learn more about the fundamental relationships between soil properties, long-term productivity, and forest management practices; and (4) evaluate the potential for mitigating the adverse effects of disturbance.

The soil properties believed to be primarily responsible in controlling forest productivity are soil porosity and soil organic matter content. These are also the soil properties greatly impacted by forest management activities. The experimental design used creates an artificially imposed factorial gradient in soil porosity and organic matter content to generate a productivity response as a function of these two soil properties rather than the impact of operational practices. The response relating changes in growth potential to changes in site organic matter and soil porosity will

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allow us to estimate the magnitude of damage to forest productivity that has been generated by disturbance. Except for treatments producing minimal soil disturbance, the remaining treatments sometimes greatly exceed the degree of disturbance caused by normal logging operations.

The national long-term soil productivity (LTSP) study plan calls for three levels of compaction (none, moderate, and severe) and three levels of organic matter removal (stem only, whole tree, and whole tree and litter layer). Most harvesting operations currently being conducted in the Central Hardwood Region fall into the lowest levels of compaction and biomass removal. The long rotation length (approximately 80 years), high installation cost, and commitment to maintain, measure, and report on study progress are not small matters. The present study (LTSP in Missouri) is being led by Forest Service Research, with cooperation from the Mark Twain National Forest, Missouri's Department of Conservation and Department of Natural Resources, Natural Resource Conservation Service, and the University of Missouri.

This paper describes pretreatment data collection and treatment installation; and it presents pretreatment data to characterize the first LTSP in the Central Hardwood Region.

METHODS

The Study Site

Site selection, plot criteria, experimental design, and treatments for the Missouri LTSP are based on information in the national LTSP study plan (Powers and others 1989). The study is located on the Carr Creek State Forest (Missouri Department of Conservation) in Shannon County. Mean annual precipitation there is 112 cm (44 inches), and mean annual temperature is 13.3°C (56°F). The site occupies the upper sideslopes of two northeastern ridges that extend from north to south in the southeastern Missouri Ozarks. It contained a well-stocked, mature, second-growth oak-hickory forest. Site index ranges from 74 to 80 based on black oak (*Quercus velutina* Lam.) at 50 years (Hahn 1991). The oak-hickory timber type is the major timber type in the Central Hardwood Region occurring over a variety of soils, relief, and stand conditions.

The sloping topography (20-28% slopes) has small shallow streams that contain exposed cobbles and stones. The area is underlain mainly by Ordovician dolomite, and areas of Cambrian dolomite and Precambrian igneous rocks are also present (Missouri Geological Survey 1979).

The weathering of the Ordovician and Cambrian dolomite has resulted in a deep mantle of cherty residuum (Gott 1975). Soils derived from this residuum are primarily of the Clarksville series (Loamy skeletal mixed mesic Typic Paleudults). Water drains freely through the soils into subsurface channels.

Treatments

A preliminary soil survey was made to locate the study area on relatively uniform soil. Soil pits were dug and soils were described and analyzed with cooperation from the Missouri Department of Natural Resources, the Natural Resources Conservation Service, the Mark Twain National Forest, and the University of Missouri. Field examination included estimation of depth to restrictive layer, horizon thickness, texture, and gravel content. After estimating that the key soil properties did not vary significantly across the areas, we established boundaries for plots. Three replicates of nine treatment plots approximately 0.4 ha (1 ac.) in size were laid out in the summer of 1993. Four-meter-wide buffer strips were laid out around all plots. Treatments include a nine-plot factorial of three levels each of organic matter removal and soil compaction. Organic matter removal consists of: (1) stem only, (2) whole tree, and (3) whole aboveground biomass including the forest floor. Soil compaction levels are none, moderate, and severe. Severe compaction is defined as 80% of the difference between the hypothetical growth-limiting bulk density (Daddow and Warrington 1983) and the bulk density of the uncompacted soil. Moderate is midway between the extremes.

Inventory

The pre-harvest inventory of the overstory, understory, herbaceous layer, and dead and downed woody material was completed in the summer of 1993 by the Missouri Forest Ecosystem Project (MOFEP) botany crew of the Missouri Department of Conservation. Overstory measurements were made on 0.2-ha (0.49-ac.) circular plots. All trees living and dead standing 11.5 cm (4.5 in.) dbh and greater were identified, and dbh was measured. All live saplings between 3.8 cm (1.5 in.) and 11.2 cm (4.4 in.) dbh were identified and measured on four circular 0.02-ha (0.05-ac.) plots located 17.25 m (56.4 ft.) from the center point in each cardinal direction (N, S, E, and W). Understory woody vegetation 1.3 cm but less than 3.8 cm dbh and greater than 1 m tall was measured on 0.004-ha (0.01-ac.) plots that were located within sapling plots. Dead and downed woody material greater than 5 cm dbh and 0.6 m long was inventoried (species, maximum diameter, length, and decomposition class) along each of four line intercepts 17.25 m (56.4 ft.) in length. Herbaceous vegetation was identified and counted on four 1-m² plots that were located 6.1 m from the sapling plot center along NE, SE, SW, and NW transects; a total of 16 herbaceous plots were sampled within each 0.2-ha plot.

Biomass and Nutrient Sampling

Biomass samples were collected for overstory canopy trees, understory saplings, ground vegetation, and leaf litter/humus layer. All samples were dried at 105°C for 72 hr or until a constant weight was achieved. Each sample was then ground to a fine powder in a Wiley Mill and analyzed for macronutrient and micronutrient content.

Leaf litter/humus samples were collected from eight 0.125-m² plots that were located 5 and 15 m from each plot center along N, S, E, and W transects. Leaf litter was separated from humus material, and all eight samples were combined for biomass and nutrient analysis. Woody and herbaceous ground cover was clipped separately on four 2.5-m² plots located at 5 m from plot center along the same cardinal transects. Plot centers for these samples correspond to each of the 27 treatment plots but not necessarily with all MOFEP inventory plot centers. Samples were collected before leaf drop in the fall of 1993.

A total of 54 trees were selected, felled, and weighed in the field during the spring of 1994. Twenty-six saplings (dbh < 10 cm) and 28 midstory and overstory trees (dbh > 10 cm) were selected for measuring total tree biomass. Individual trees were selected based on the following criteria: 1) one of the major species present in the overstory; i.e., black oak, scarlet oak, hickory spp., white oak, and shortleaf pine, 2) sapling with a dbh between 2.5 and 10 cm, at least one for each 2.5-cm size class, 3) midstory and overstory trees with a dbh between 10 and 50 cm, when possible, one for each 5-cm size class, and 4) trees that appeared vigorous and healthy with no outward signs of rot or limb damage. The dbh of trees sampled covered the range from 5 cm to 50 cm. Total height, dbh, basal diameter, and specific crown dimensions were measured on each tree. Trees with merchantable logs were sectioned in appropriate lengths: others were cut to 2-m lengths. Sawdust samples and wood disks were collected from the end of each log section up to the 10-cm diameter. Tree crowns were sectioned into <2 cm, 2 to 10 cm, and 10+ cm size classes. Fresh weights of all tree logs and crown portions were measured in the field. Some merchantable logs were too large to be weighed in the field (scale limit = 500 lbs). Thus, detailed log dimensions were taken to estimate volume: weight was later predicted from laboratory samples. Samples were also collected from each crown size class for further analysis. Fresh weights of all sawdust samples, wood disks, and crown subsamples were measured separately.

Soil Sampling

In addition to soil pits, soil samples were collected with a two-person power-driven coring device in a systematic design. Four intact cores (7.6 cm diam. x 40 cm long) of soil per plot were collected and partitioned according to soil horizon before determination of bulk density, pH, organic matter content, hydraulic conductivity, and macronutrient content (Soil Survey Staff 1984, Page and others 1982, Black 1965).

Timber Harvesting

Trees and biomass were removed according to protocols in the national LTSP study plan (Powers and others 1989) by means that minimize soil disturbance. Trees were harvested over a 4-month period in 1994, beginning in February and ending in May. On plots designated as uncompacted, merchantable trees were directionally felled and removed with a skyline cable logging system. Merchantable trees on remaining plots, plot borders, and the area within the study boundary were directionally felled and removed with a skidder that traveled only on designated paths within the plots and in plot borders. Remaining crowns, unmerchantable trees, dead and live snags, dead and down, leaf litter layer, and other debris were removed manually according to protocols. Depending on treatment, it was necessary to replace these materials (except the leaf/litter layer) after compaction was completed in some plots.

Tree crowns were retained on the stem only plots. On plots where the whole tree and leaf/litter layer were removed, the total aboveground biomass was removed. All understory vegetation was clipped and removed, and the forest floor was raked away to the mineral soil. The raking of the forest floor began in August and was completed by mid-November. Skidders and tractors were not permitted on uncompacted plots, but they were permitted on compacted plots.

After plots are compacted with a 14-ton vibrating sheep-foot roller, each 0.4-ha treatment plot will be regenerated with the appropriate timber species. Half of each plot will be kept weed free to permit target trees to grow freely. The other half will be allowed to develop naturally into a more complex community of trees and other vegetation. Net primary productivity in these two plant communities will provide direct measures of productivity as influenced by the degree of soil disturbance.

RESULTS AND DISCUSSION

The values for chemical properties, bulk density, and percent organic matter in Table 1 are typical for soils in the Clarksville series (Gott 1975). There is concern that the high gravel content in the soil could reduce the depth to which the soil can be effectively compacted. However, principal investigators of some LTSP studies have had problems in achieving a distinct difference between the moderate and severe levels of compaction in soils with low gravel content (Personal communication).

Table 1. Mean chemical properties and bulk density of soil in the Missouri LTSP study*.

Depth cm	Extractable bases				Extr. Al	Organic C %	pH H ₂ O	Bulk density g/cm ³
	Ca	Mg	K	Na				
0-10	4.6	0.8	0.3	Tr	0.8	5.4	5.5	1.54
10-20	0.5	0.4	0.2	Tr	1.1	0.5	5.3	1.58
20-30	0.6	0.5	0.1	Tr	1.2	0.1	4.8	1.70
30-40	1.1	2.3	0.2	Tr	3.1	0.1	4.9	1.71

*N and P analyses are not complete and are not presented.

Census Data

Overstory species composition by diameter class is shown in Figure 1. The red oak group consists primarily of black and scarlet (*Quercus coccinea* Muenchh.); the white oaks include white (*Quercus alba* L.) and post (*Quercus stellata* Wangenh.); the hickory group includes black (*Carya texana* Buckl.), mockernut (*Carya tomentosa* Nutt.) and pignut

(*Carya glabra* Mill.); the other category is composed of black walnut (*Juglans nigra* L.), blackgum (*Nyssa sylvatica* Marsh.) and dogwood (*Cornus stolonifera* L.); and the predominant native pine species is shortleaf pine (*Pinus echinata* Mill.). Average height of co-dominants for each class were: 25.9 m for red oaks, 23.2 m for white oaks and hickory, and 23.8 m for pine. Red oaks, white oaks, hickory and pine made up 47.5, 26.1, 17.3 and 4.2 percent, respectively, of the overstory. Species composition of the sapling understory is shown in Figure 2. Hickory, white oaks, and dogwood accounted for 80 percent of all stems; the red oaks represented less than 3 percent. Seedling composition (less than 3.8 cm dbh) is shown in Figure 3. Total number of stems per hectare in this group was 1,905.

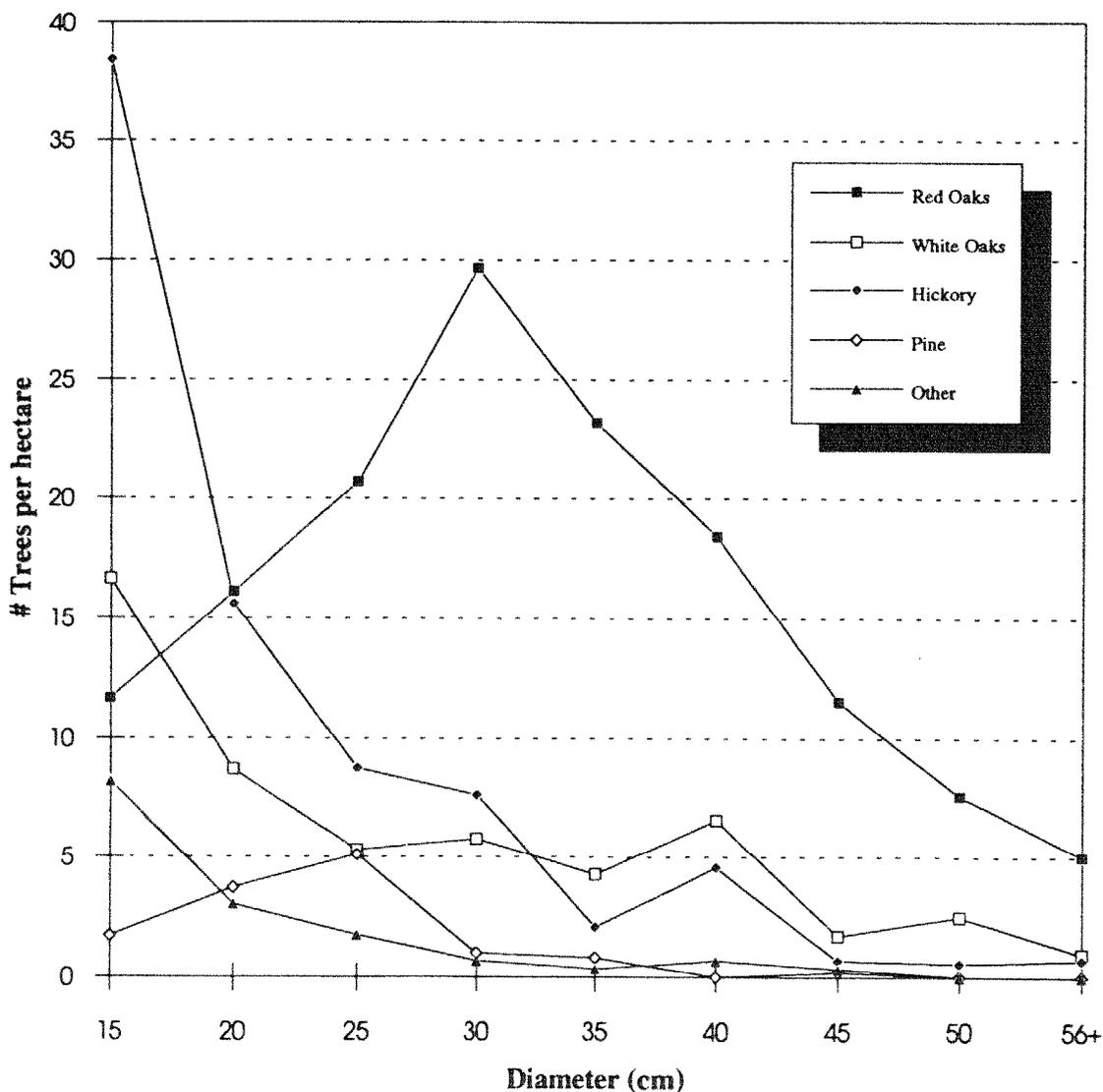


Figure 1. Overstory diameter frequency distribution by species for LTSP study site.

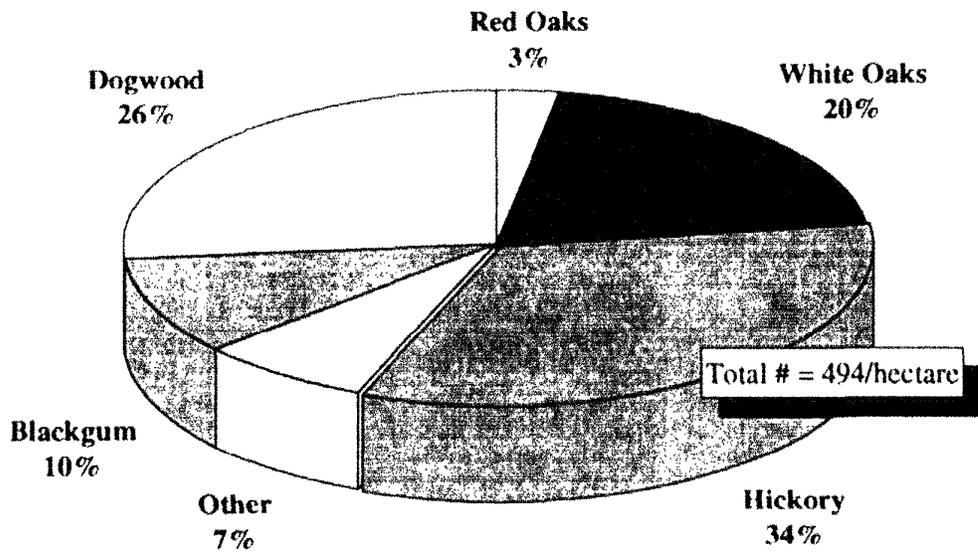


Figure 2. Sapling understory (3.8 to 12.5 cm dbh) species composition.

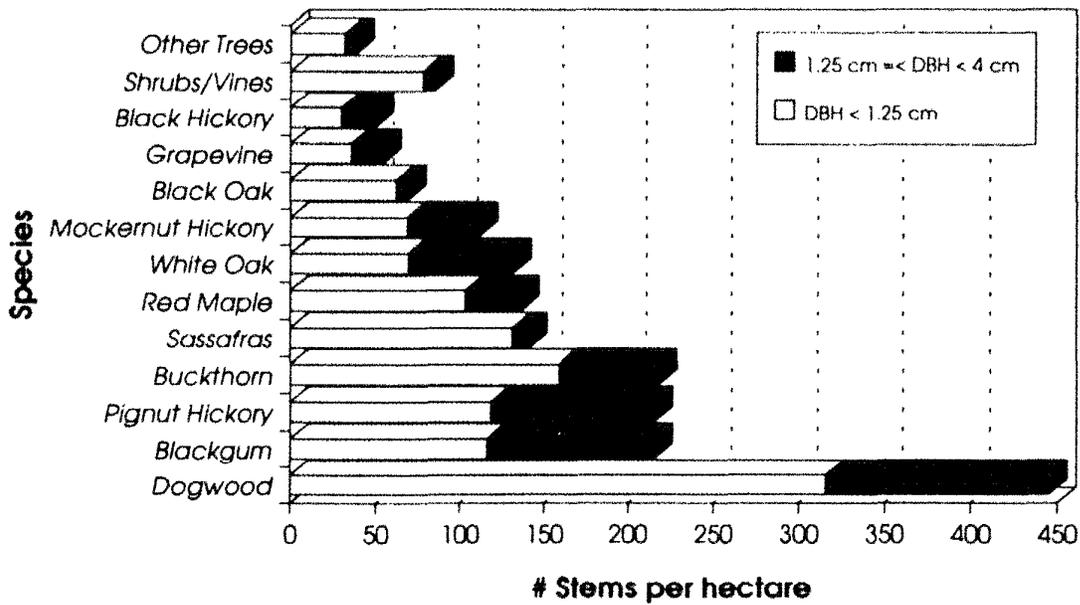


Figure 3. Number of stems per hectare of understory woody species at least 1 m tall.

The total number of dead standing trees is shown in Figure 4. The average number per hectare was 30. Most of the dead stems (74%) were either black or scarlet oak. Decay stage was recorded but is not presented here. The stages range from recently dead to highly decomposed but still standing.

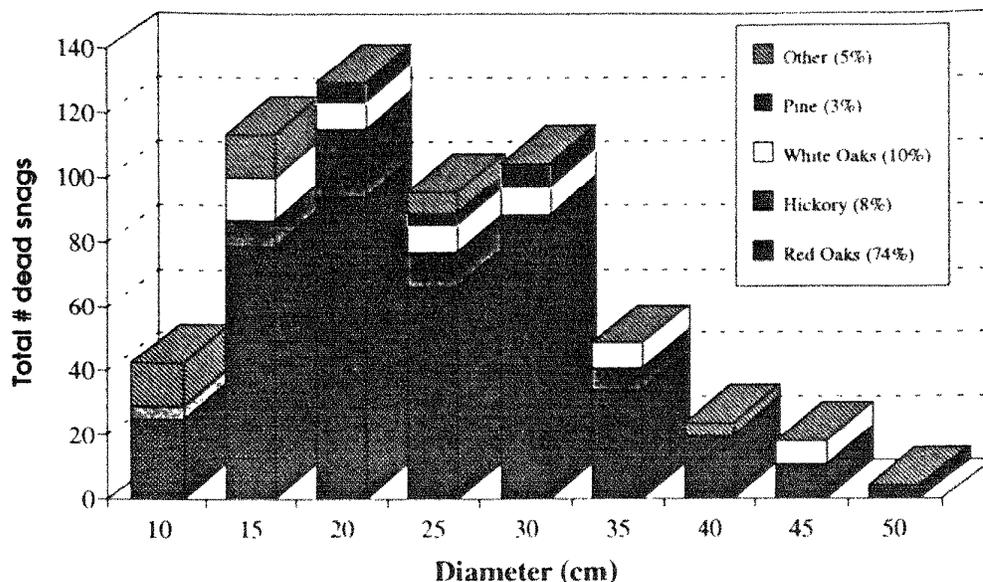


Figure 4. Total number and percent composition of dead standing trees on LTSP study site.

Biomass and Nutrient Data

Total dry weight biomass was calculated for all individual trees that were sampled. Dry weight was then plotted against dbh for each species, and biomass at each 5-cm diameter class was extrapolated from an eye-fitted curve. Combined with the number of trees per acre, total dry weight of the overstory (>4 cm) was estimated to be 175.5 tons per hectare (1,016 kg/ton). Figure 5 depicts the total amount of biomass estimated to be removed by each of the three organic matter treatments. Of the 175.5 tons of woody dry matter, red oaks comprised 63%, white oaks 15%, hickory 16.5%, pine 2%, and other species 3.5%.

Allometric regression equations of the form $Y = a(DBH)^{**}b$ were also developed and compared to these estimates. Additionally, the literature on biomass equations for the species found on our site was reviewed and used for comparison. Dry weight estimates for white oak and hickory by Clark and others (1985); black, scarlet and white oak and hickory equations by Wiant and others (1977); and black oak sawlog biomass equations by King and Schnell (1972) were compared to the dry weight estimates from our regression.

In general, estimates for dry matter for all species compared fell within one standard deviation of our estimates for size classes below 25 cm dbh, but estimates of dry matter above 25 cm ranged from 1.3 to 9.5 standard deviations from our data. One exception was the white oak estimates from Wiant and others (1977), in which all size classes were within 1.1 standard deviations of our data.

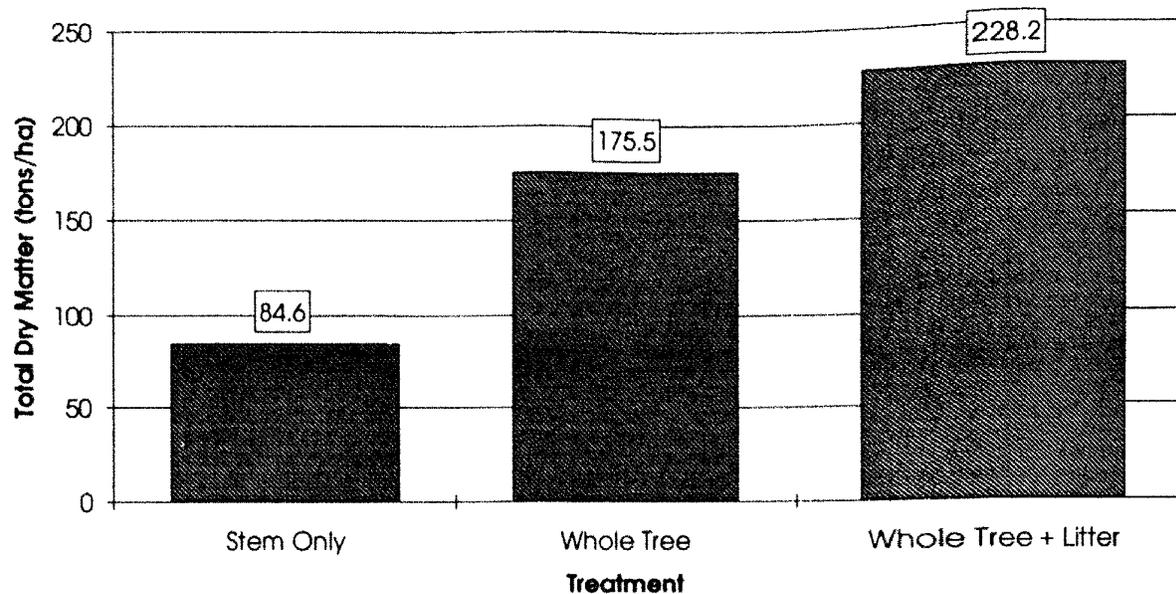


Figure 5. Total dry matter removed from plots relative to treatment.

Nutrient analysis was completed for all subsamples of ten individual trees, two of each dominant overstory species and dogwood. Crown, wood, and bark components were analyzed separately and multiplied by the proportion of the biomass they represented. Total macronutrient and micronutrient content is summarized in Table 2. The amount of nutrients removed in the biomass increased considerably when the leaf/litter layer was included.

The whole tree plus leaf/litter layer treatment removed 33% more N, 46% more P, 10% more K, 18% more Ca, and 35% more Mg than the whole tree treatment. Among micro-nutrients, considerably more Mn, Fe, and Al were removed in the whole tree plus leaf/litter treatment than in the whole tree treatment. Branches and unmerchantable tree parts also have large amounts of nutrients as shown when the whole tree treatment is compared to the merchantable stem only treatment. Removing the whole tree removed 3 times more N and P, 2 times more K, 3 times more Ca, and 2.6 times more Mg than did removing only the stem. Similar trends were apparent in micronutrients between whole tree and stem only treatments.

Table 2. Macronutrient and micronutrients removed from the site relative to organic matter treatment.

Nutrient	TREATMENTS		
	Stem only	Whole tree ----- kg/hectare-----	Whole tree + litter*
Macro	195.26	540.04	810.80
N	7.41	25.96	48.30
P	108.65	255.61	284.90
Ca	774.24	2303.11	2819.22
Mg	19.97	52.59	81.20
Micro			
Mn	7.08	18.00	49.37
Fe	1.01	2.56	17.48
Zn	0.53	1.55	2.61
Al	2.10	7.61	81.12
Na	0.48	1.08	1.63
Cu	0.11	0.32	0.58
B	0.38	1.13	1.50

*Excluding snags and dead woody debris.

SUMMARY

This is a long term study that is in the latter part of the installation phase. It will be several years before answers about the relationships between management practices and long-term soil productivity are available. Data from this study will provide information for evaluating the effects of soil disturbance on long-term productivity of several Central Hardwood tree species and their associated flora and fauna communities. The results will help us better understand the joint role of soil porosity and site organic matter in their effect on site processes that control productivity. Combining information from the network of LTSP studies with other ecological information is expected to provide managers with more complete information with which to manipulate soil properties to either increase productivity or prevent reductions.

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A SUMMARY OF WATER YIELD EXPERIMENTS ON HARDWOOD FORESTED
WATERSHEDS IN NORTHEASTERN UNITED STATES

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Abstract: This paper summarizes and compares long-term changes in annual water yield following cutting experiments at four locations in northeastern United States. Substantial increases in water yield of up to 350 mm yr⁻¹ were obtained in the first year by clearfelling hardwood forest vegetation and controlling regrowth with herbicides. Commercial clearcutting of hardwoods with natural regrowth resulted in smaller initial increases in water yield of 110 to 250 mm yr⁻¹. This range in response was due to differences in precipitation and configuration of cuttings. Unless regrowth was controlled with herbicides, yield increases declined quickly after cutting, seldom persisting for more than 10 years. However, yield increases were readily extended over 20 years or more with intermediate cuttings and/or repeated control of regrowth with herbicides. Nearly all increases in water yield occur during summer and early autumn. Changes in species composition after forest cutting on several study watersheds eventually resulted in decreased water yields compared to those from uncut, control watersheds. Results are discussed in terms of implications for surface water supplies, global climate change, nutrient cycling, hydrologic modeling, and long-term research.

INTRODUCTION

Long-term paired watershed studies at four locations in the northeastern United States are analyzed in this paper: Fernow Experimental Forest in north-central West Virginia, Leading Ridge Experimental Watersheds in central Pennsylvania, Marcell Experimental Forest in north-central Minnesota, and Hubbard Brook Experimental Forest in central New Hampshire (Fig. 1). These locations span the diverse geography of the northeastern United States. At each site, one or more watersheds have been calibrated against a nearby control, then treated experimentally. Changes in water yield were then determined with results in some cases spanning up to 3 decades.

Two of the study locations, Fernow and Leading Ridge, are forested with central hardwoods. This provides an opportunity to compare streamflow responses in central hardwood forests with 2 other important forest types in the Northeast: northern hardwoods at Hubbard Brook and aspen-birch at Marcell.

Results from these studies have special significance for the northeastern United States. Forests cover >60% of the landscape, and forested watersheds serve as sources of water for more than 1,000 municipalities ranging from small, rural communities to large urban centers such as New York, Baltimore, and Boston. Although the region is well watered with 1,100 mm average annual precipitation, water shortages are not uncommon. A knowledge of how both abrupt and gradual changes in forest cover affect water yield over time periods on the order of decades is needed to manage forested watersheds for optimum water production.

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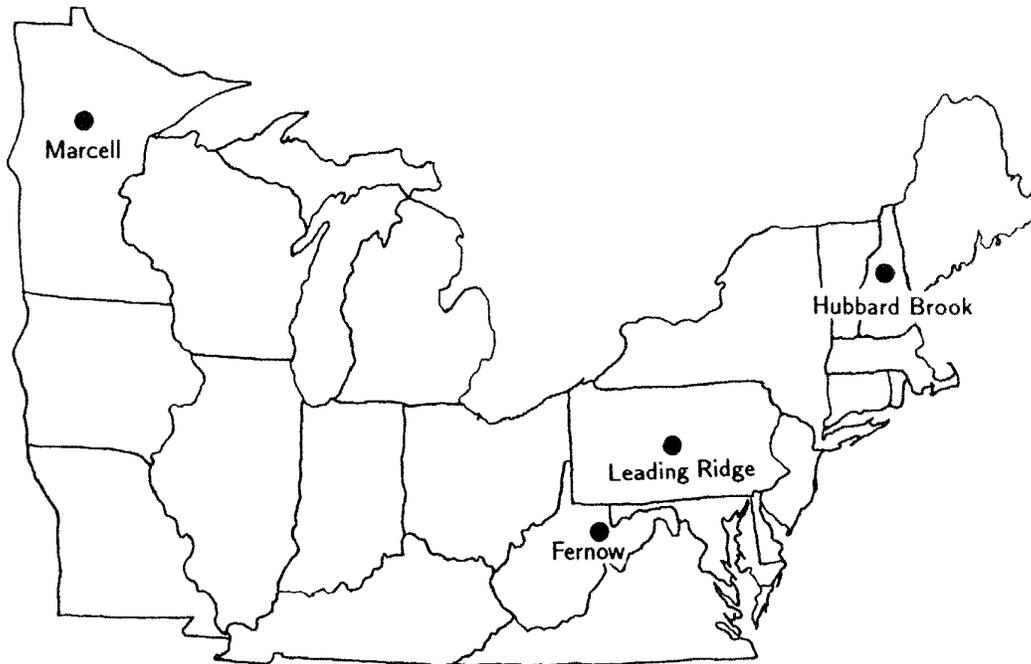


Figure 1. Northeastern United States showing study site locations.

METHODS

Results from 11 separate, treated watersheds are summarized and compared in this paper (Table 1). Record collection on many of these watersheds began in the 1950s, followed 5 to 10 years later by initial treatments of vegetation. At the time of these initial treatments, the northeastern United States was experiencing an extended period of below average precipitation and there was widespread interest in the potential for increasing water yield from forested watersheds. Also, controversies over the use of herbicides and forest clearcutting had not begun to escalate. Thus, some of the initial treatments at Fernow, Hubbard Brook, and Leading Ridge were designed to obtain benchmark information on maximum possible yield increases, and treatments included complete forest clearing and control of regrowth with herbicides. Later experiments performed in the 1970s and 1980s focused more on determining impacts of commercial harvesting operations. These treatments tended to be less drastic and did not include herbicide applications.

The longevity of the studies has in many cases allowed for determining impacts of multiple treatments on the same watershed. For example, watershed 3 on the Fernow Experimental Forest was first harvested in 1958-59 by intensive selection, a silvicultural practice that was in common use in the region and which involves cutting a relatively small fraction (in this case, 13%) of total basal area. In keeping with the silvicultural prescription, the treatment was repeated 4 years later with an additional 8% of total basal area being cut. The prescription was changed in 1968 to patch cutting, and 6% of the existing basal area was felled. Then in late 1969, to obtain information relative to a developing controversy over impacts of clearcutting (Horwitz 1974), the watershed was subjected to a commercial clearcutting during which 91% of existing basal area was cut.

Table 1. Descriptions of catchment studies in northeastern United States

Catchment	Area-ha	Mid eleva- tion-m	Vegetation (before treatment) and soils	Mean annual precipitation-mm ¹	Mean annual streamflow-mm ¹	Descriptions of treatment	Year(s) of treatment	Basal area cut - % ²	Reference
Fernow Experimental Forest, West Virginia									
1	30	755	Central Appalachian hardwoods, Typic Dystrachrepts	1,460	640	Clearcut to 15cm dbh except culls.	1957-58	74	Kochenderfer and others 1990
2	15	780	same			Diameter limit cut to 43 cm. Diameter limit cut to 43 cm.	1958 1972	32 12	same
3	34	505	same			Intensive selection. Intensive selection. Patch (0.2 ha) cuttings. Clearcut.	1958-59 1963 1968 1969-70	13 8 6 91	same
6	22	805	same			Clearcut lower half Herbicides on lower half Clearcut upper half Herbicides on entire catchment Plant Norway spruce. Herbicides on entire catchment	1964 1965-69 1967-68 1968-69 1973 1967-69	51 49	Patric & Reinhart (1971, Kochenderfer and others 1990)
7	24	801	same			Clearcut upper half Herbicides on upper half Clearcut lower half Herbicides on entire catchment.	1963-64 1964-69 1966-67 1967-69	49 51	same
Leading Ridge Experimental Watersheds, Pennsylvania									
2	43	360	Central hardwoods, Typic Dystrachrepts and Typic Hapludults	1,060	440	Clearcut lowest 9 ha. Clearcut mid-slope 11 ha. Herbicide lower and mid-slope areas. Clearcut 17 ha on upper slope. Herbicide all clearcut areas.	1967 1971-72 1974 1975-76 1977	24 27 40	Lynch and others 1980
3	104	340	same			Clearcut on 45 ha.	1976-77	43	Lynch and Corbett 1989
Marcell Experimental Forest, Minnesota									
4	34	433	Aspen-birch upland, black spruce peatland, Typic Glosoboralfs, interspersed with bog wetlands	760	1:0	Aspen-birch upland portion (26ha) clearcut (all trees >3 m height)	1970-71	100	Verry, 1987
Hubbard Brook Experimental Forest, New Hampshire									
2	16	595	Northern hardwoods, Typic Haplorthods	1,240	880	Clearfelled. Herbicides on entire catchments.	1965-66 1967-69	100	Hornbeck and others 1970
4	36	606	same			Progressive strip cut, 1st 3rd harvested. 2nd 3rd harvested. Final 3rd harvested.	1970 1972 1974	33 33 33	Hornbeck and others 1987
5	22	636	same			Whole-tree harvest	1963-84	95	None available

¹Long-term means for untreated, control catchments.

²Based on existing tree basal area on catchment at initiation of cutting.

Other forms of multiple treatments included a three-stage, progressive strip cutting on watershed 4 at Hubbard Brook, complete forest clearing in three stages on watershed 2 at Leading Ridge and in two stages on watersheds 6 and 7 at Fernow, and controlling vegetation with herbicides prior to or during species conversion or natural regrowth at Leading Ridge, Fernow, and Hubbard Brook (Table 1).

Impacts of treatment on water yield were determined using the paired watershed approach described by Reinhart (1967). Linear regression was used to develop a calibration relationship between annual water yield from a control watershed (independent variable, X) and a watershed to be treated (dependent variable, Y). At locations with multiple watershed experiments, the same control was used in developing all regressions. The calibrations are based on 5 or more water years of record, and although most of the calibration periods ended at least 2 decades ago, we assume the relationships still apply. Forests on all control watersheds are mature and reasonably steady-state with regard to biomass and leaf area (Bormann and Likens 1979) and annual evapotranspiration (Federer and others 1990). Thus, water yield relationships for control watersheds should be unchanging, except during a 2-year period of severe insect defoliation at Leading Ridge (Corbett and Heilman 1975).

After treatment, deviations from the calibration regressions were considered to be statistically significant and attributed to treatment if they exceeded 95% confidence intervals about the regressions. The deviations, which indicate increases and decreases in annual water yield from the treated watersheds, are presented in both graphical and tabular form in this paper. Statistical significance is not indicated when using graphs. However, on average for all sites, deviations greater than $\pm 30\text{mm yr}^{-1}$ from the calibration regressions were statistically significant.

RESULTS

The array of forest treatments across the four study locations caused a variety of responses in water yield (Fig. 2, Table 2). However, three generalizations can be used as a framework for discussing results: (1) initial increases in water yield occur promptly after forest cutting, with the magnitude being roughly proportional to percentage reduction in basal area, (2) the increases can be prolonged for an undetermined length of time by controlling natural regrowth; otherwise increased streamflow diminishes rapidly, usually within 3 to 10 years, and (3) small increases or decreases in water yield may persist for at least a decade, and probably much longer, in response to changes in species composition and climate.

Initial Increases in Water Yield

Only Hubbard Brook and Marcell Experimental Forests normally have continuous winter snowpacks. Snowmelt runoff occurred earlier at both sites, but volume of snowmelt runoff was unchanged (Hornbeck 1975, Verry and others 1983). Thus, increases in annual yield at all four study sites resulted primarily from reductions in transpiration and canopy interception. Simply stated, soils were wetter on recently treated watersheds and more water was available for streamflow. Flow-duration curves for posttreatment periods at each site show that nearly all changes in water yield result from increases at low flow levels, or as augmented baseflow or delayed flow, and that flood flows were not greatly affected (Hornbeck and others 1970, Lynch and others 1980, Patric and Reinhart 1971, Verry 1972). Further, the yield increases occurred primarily in the growing season. Complete recharge of soil moisture on both forested and treated watersheds usually occurs soon after the start of the dormant season, thus limiting further opportunities for treatment effects until the start of the next growing season.

As found in previous summaries (Bosch and Hewlett 1982, Douglass and Swank 1972), increases in yield for the first water year after treatment were roughly proportional to percentage reductions in stand basal area. Moreover, a comparison for all sites (Fig. 3) supports previous findings that reductions in basal area must approach 25% to obtain measurable responses in annual water yield (Douglass and Swank 1972). Above this threshold, there is some variability in first-year responses among watersheds with similar basal areas cut, but differences usually can be explained by factors such as configuration and timing of the cutting, and whether regrowth was controlled with herbicides.

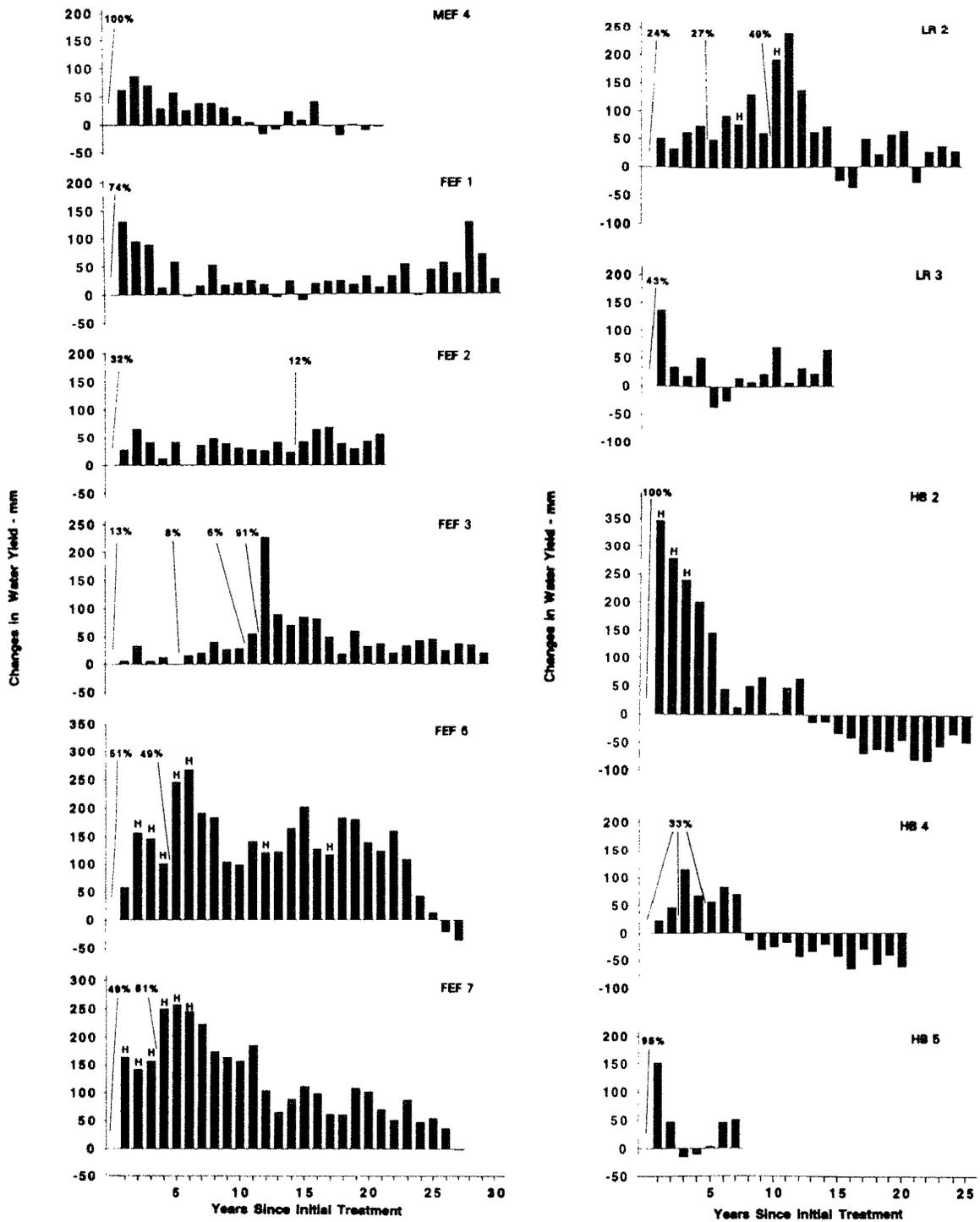


Figure 2. Changes in water yield for 11 experimental watersheds studies. MEF is Marcell Experimental Forest, FEF is Fernow Experimental Forest, LR is Leading Ridge Experimental Watersheds, and HB is Hubbard Brook Experimental Forest. Percentage values denote existing basal area cut during experimental treatments and H signifies herbicide application to cut portions of watersheds.

Table 2. Changes in annual water yield for selected watersheds.

Marcell Experimental Forest #4

Year after initial treatment	Estimated streamflow if untreated ¹ mm	Change due to treatment ²		Precipitation mm	Estimated streamflow if untreated ¹ mm	Change due to treatment ²		Precipitation mm
		mm	%			mm	%	
1	209	81*	39	871	715	165*	23	1,316
2	195	114*	58	817	390	142*	36	1,057
3	130	92*	70	779	669	157*	23	1,231
4	188	38*	20	862	658	251*	38	1,215
5	227	77*	34	780	637	258*	40	1,217
6	76	34*	45	458	738	246*	33	1,332
7	152	51*	34	935	675	224*	33	1,268
8	246	52*	21	882	869	175*	20	1,481
9	276	40*	15	786	1,030	164*	16	1,557
10	108	19	18	662	919	157*	17	1,553
11	198	6	3	821	944	187*	20	1,551
12	282	-22	-8	799	628	104*	17	1,243
13	100	-9	-9	748	607	65	11	1,170
14	202	33*	16	744	755	89*	12	1,328
15	286	12	4	920	988	112*	11	1,628
16	217	56*	26	796	828	99*	12	1,451
17	178	-1	0	744	755	62*	8	1,397
18	296	-25*	-8	995	987	61	6	1,587
19	281	1	0	839	801	109*	14	1,470
20	125	-12	-10	587	852	103*	12	1,529
21	89	-4	-4	711	842	71*	8	1,487
22					1,073	52	5	1,745
23					694	88*	13	1,389
24					516	48	9	1,191
25					766	55*	7	1,435
26					958	37	4	1,561
27					936	-2	0	1,583

Continued on next page

Fernow Experimental Forest #7

Table 2. (continued) Changes in annual water yield for selected watersheds
 Leading Ridge Experimental Watershed #2

Year after initial treatment	Estimated streamflow if untreated ¹			Change due to treatment ²		Precipitation		Hubbard Brook Experimental Forest #2		
	mm	mm	%	mm	%	mm	mm	mm	%	mm
1	433	51*	12	967	41	347*	851	967	41	1,279
2	302	32*	11	897	29	278*	954	897	29	1,394
3	401	63*	16	1,008	26	240*	919	1,008	26	1,271
4	562	76*	14	1,167	22	200*	902	1,167	22	1,294
5	507	50*	10	1,061	17	146*	840	1,061	17	1,225
6	940	94*	10	1,435	6	44	787	1,435	6	1,221
7	462	79*	17	1,018	1	12	1,059	1,018	1	1,504
8	529	132*	25	1,104	4	52	1,469	1,104	4	1,832
9	658	61*	9	1,210	8	67*	832	1,210	8	1,240
10	606	193*	32	1,214	0	3	1,305	1,214	0	1,659
11	682	239*	35	1,285	5	48	884	1,285	5	1,323
12	648	138*	21	1,220	6	64*	996	1,220	6	1,431
13	687	63*	9	1,255	-1	-13	902	1,255	-1	1,287
14	260	73*	28	877	-2	-13	764	877	-2	1,139
15	570	-25	-4	1,089	-4	-34	807	1,089	-4	1,261
16	528	-37	-7	1,060	-3	-41*	1,179	1,060	-3	1,530
17	570	49*	9	1,091	-8	-70*	885	1,091	-8	1,328
18	559	22	4	1,121	-6	-62*	1,099	1,121	-6	1,522
19	500	56*	11	1,106	-9	-64*	715	1,106	-9	1,087
20	558	64*	11	1,178	-5	-44*	958	1,178	-5	1,310
21	422	-28	-7	964	-9	-80*	872	964	-9	1,210
22	410	26	6	964	-10	-82*	790	964	-10	1,190
23	584	36*	6	1,163	-8	-56*	708	1,163	-8	1,149
24	777	27	3	1,139	-3	-34	1,109	1,139	-3	1,468
25					-4	-48*	1,194		-4	1,590

¹Determined from calibration regression

²Determined by subtracting estimated streamflow from actual streamflow

³Change exceeded 95% confidence interval about the calibration regression

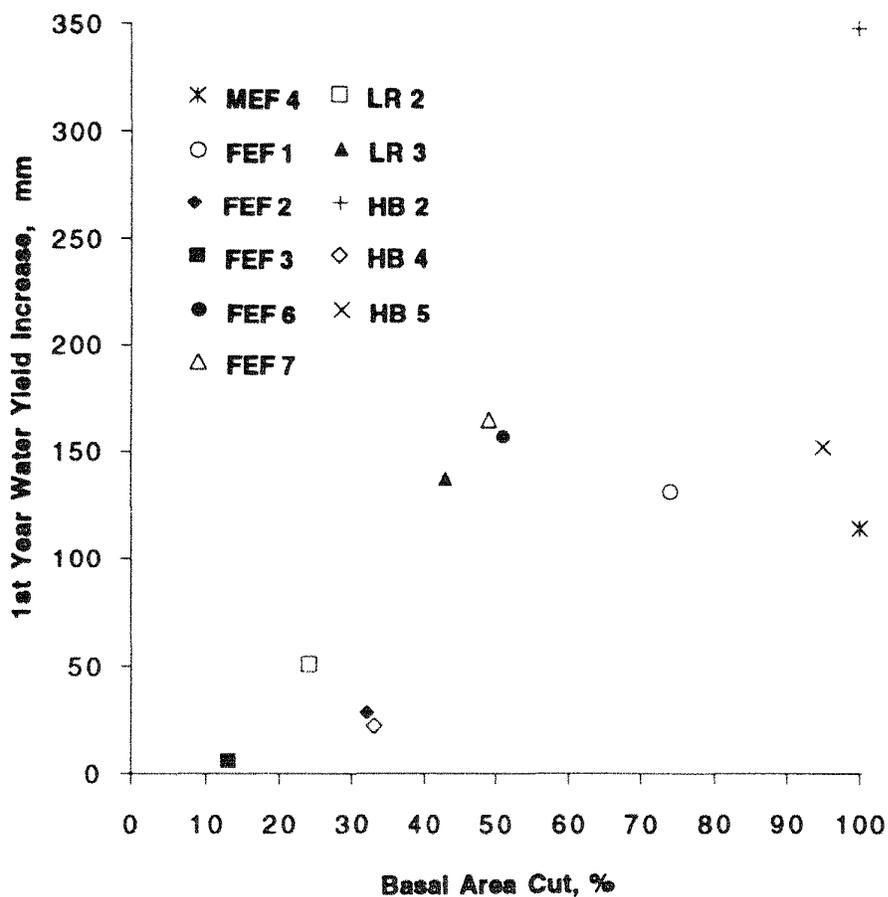


Figure 3. First-year increases in water yield in response to forest cutting.

As an example of the role of configuration, the cutting of 24% of the basal area on watershed 2 at Leading Ridge produced a nearly twofold larger increase than cutting one-third of the basal area on watershed 4 at Hubbard Brook and watershed 2 at Fernow (Fig. 3). The cutting at Leading Ridge was in a single block on the lowest portion of the watershed, the cutting at Hubbard Brook was in a series of strips spaced equidistant from bottom to top of the watershed, and the cutting on the Fernow involved harvesting individual trees scattered about the watershed. The cutting of strips and individual trees increases crown exposure and transpiration rate of residual trees, especially those bordering openings (Federer and Gee 1974). A portion of the added transpiration may be drawn from the extra water

available in the cut strips or individual tree openings, or from soil water moving downslope from cut to uncut areas. As a result, increases in streamflow were smaller than had the areas been cut like the single, low-elevation block at Leading Ridge. Larger increases for the first water years after cutting the second and third sets of strips at Hubbard Brook watershed 4 (Fig. 2) support this explanation.

The importance of timing of cutting and control of regrowth are demonstrated by comparing Hubbard Brook watersheds 2 and 5. On watershed 2, 100% of the basal area was clearfelled during the dormant season, and herbicides were applied early in the next growing season. This combination proved optimum for increasing water yield and resulted in a first-year increase of 347 mm, the maximum for all experimental treatments (Figs. 2, 3). By contrast, 95% of the basal area on watershed 5 was felled during a whole-tree harvest that spanned nearly a full year, and natural regrowth was uncontrolled. The first-year increase in water yield from watershed 5 was only 152 mm, or 44% of that from watershed 2. The difference in first-year increases from the watersheds is due largely to greater transpiration and interception by regrowth on watershed 5.

Impacts of Controlled Versus Natural Regrowth

Herbicides were used to control regrowth on watersheds 6 and 7 at Fernow, watershed 2 at Leading Ridge, and watershed 2 at Hubbard Brook (Table 1). In all cases, the effect was to prolong and substantially increase annual water yields compared to treated watersheds on which natural regrowth was uncontrolled. The use of herbicides for 3 successive growing seasons after felling all trees on watershed 2 at Hubbard Brook resulted in average annual yield increases of 288 mm for the 3-year period (Table 2). Herbicide applications to completely cleared watersheds at Fernow and Leading Ridge resulted in maximum annual increases of about 250 mm (Fig. 2, Table 2). Upon cessation of herbicide applications, sizable increases in water yield persisted for about 7 years at Fernow. However, natural regrowth quickly cut into increases in water yield at Hubbard Brook and Leading Ridge (Fig. 2).

Transpiration and interception by natural regrowth also quickly reduced increases in water yield in experiments where herbicides were not used. This was especially true for Hubbard Brook watersheds 4 and 5 where increases in water yield either disappeared or were greatly reduced within 3 or 4 years after cessation of intensive harvests (Fig. 2).

The increases appeared to decline equally rapidly on watershed 3 at Leading Ridge. Small decreases in water yield occurred by years 5 and 6 after harvest (Fig. 2). However, these decreases were anomalies resulting from a natural disturbance. During both of these years the mature forest on the control watershed was defoliated for part of the growing season by gypsy moth (*Porthetria dispar*). Such defoliations reduce transpiration and cause small increases in water yield (Corbett and Heilman 1975). Regeneration on the harvested watershed was not defoliated, resulting in greater transpiration from the harvested watershed and decreases in water yields compared to the control.

The decline with regrowth was less rapid on Fernow and Marcell watersheds (Fig. 2, Table 2). Yield increases persisted for two decades on watershed 2 at Fernow, but these were partly due to a follow-up diameter limit cut that was part of the prescribed treatment. Small increases of $<50 \text{ mm yr}^{-1}$ persisted for up to a decade or more after clearcuttings on watershed 4 at Marcell (Fig. 2). For years 12 through 21 since harvest at Marcell, the relatively small and inconsistent changes in water yield have been closely related to amount and distribution of spring and summer precipitation; increases in water yield occurred with above average precipitation and decreases occurred with drier weather conditions (Verry 1987). The same response was found for watershed 3 at Leading Ridge. The larger increases that occurred in years 10 and 14 after harvest (Fig. 2) were accompanied by growing season precipitation values that exceeded long-term means by more than 100 mm. Such findings reinforce an axiom expressed by Hewlett (1967) regarding forest cutting and increases in water yield: "It takes water to fetch water."

While above-average precipitation stimulates increases in water yield from cutting, excessive amounts can create problems with statistical procedures used in paired watershed studies. When precipitation and streamflow are well above the range normally encountered, calibration statistics must be extrapolated to accommodate resulting extremes in streamflow, providing a potential source of error in determining treatment effects (Hornbeck 1973). A case in point may be the 28th and 29th years after harvest on Fernow watershed 1. The increases in water yield were about the

same magnitude as those for the 1st and 2nd years after cutting (Fig. 2). Since the regrowing forest on watershed 1 is similar in species composition to that before harvest and there have been no recent changes in forest condition, there is no reason to expect such increases to suddenly occur late in the postcutting period. As it turns out, both the 28th and 29th years after harvest had extreme precipitation values. The calibration regressions had to be extrapolated substantially to test the resulting extremes in streamflow, and probably gave erroneous results. Obviously, the evaluation and interpretation of extreme events must be handled with caution.

Long-term Changes Related to Species Composition

Long-term changes of some consequence occurred on Fernow watersheds 6 and 7 and Hubbard Brook watersheds 2 and 4. The Fernow watersheds are recovering from clearcutting and several years of herbiciding. Watershed 6 also was planted to Norway spruce 9 years after the initiation of clearcutting, and herbicides subsequently were applied on 2 occasions to reduce competition to spruce (Table 1). Water yields had remained at elevated levels on both watersheds 6 and 7, with slightly higher values on watershed 6 (Fig. 2). In recent years, however, the spruce canopy on watershed 6 has begun to close, and water yield is showing strong indications of returning to and probably dropping below pretreatment levels (Fig. 2). This would not be unexpected for a hardwood to conifer conversion. Swank and others (1988) pointed out that transpiration and interception losses are greater from young conifers than mature hardwoods, particularly during the dormant season.

On Fernow watershed 7, a final herbicide application to kill back all regrowth took place 6 years after the initial cutting. The substantial increases in water yield ($>250 \text{ mm yr}^{-1}$) declined over a 6-year period in relation to increasing dry-matter production of regrowth (Kochenderfer and Wendel 1983) to between 50 and 100 mm, where they persisted for 14 years (Fig. 2). Comparisons with Fernow watershed 3 suggest a possible explanation for this extended period of increases of 50 to 100 mm. After a series of selection and patch cuttings, watershed 3 was clearcut but not herbicided. Increases in water yield declined much more rapidly than on watershed 7 (Fig. 2). Species composition of regrowth is similar on both watersheds, but regrowth on watershed 3 consisted almost exclusively of sprouts. By contrast, herbicide applications on watershed 7 eliminated sprouts, and regrowth originated from seeds. By utilizing the rooting network from the previous forest, the regrowth composed of sprouts may have better access to soil moisture, and transpiration may be greater, at least during the first 15 to 20 years of stand establishment, than for regrowth originating from seeds. The final 2 years of water yield data from watershed 7 suggest a shift more in line with watershed 3, but additional data are needed to draw conclusions.

The long-term trends at Hubbard Brook are different from those at the other three study locations. Decreases in water yield were evident early in the regrowth phase on watersheds 2 and 4, and persist through the remaining 13 years of record on both watersheds (Fig. 2). The explanation may lie with a posttreatment change in species composition. Before treatment, basal area was distributed about evenly among beech, birch, and maple species. During regrowth, nearly 80% of the basal area has been in birch and pin cherry (a common pioneer species in northern hardwood forests) with the remainder divided between beech and maple. Federer (1977) showed that birch and pin cherry have significantly lower leaf resistances (3.2 s cm^{-1}) than beech and maple species (4.0 to 4.5 s cm^{-1}). Thus, transpiration may be greater from the regrowing stand dominated by birch and pin cherry than from the mature, undisturbed forest, the end result being less water available for streamflow.

DISCUSSION

Surface Water Supplies

Results from the four study sites indicate the potential to increase water yield from forested watersheds in the northeastern United States. Based on experiments at Hubbard Brook, Fernow, and Leading Ridge, in which watersheds were clearcut and then herbicided, the maximum possible increase is in the range of 250 to 300 mm yr^{-1} . However, in light of controversy over the use of herbicides, it is likely that attempts to increase water yield will be confined to cutting. Even then, the studies indicate that various sizes of clearcuts, without control of regrowth, can

provide immediate increases in annual yields ranging from about 110 mm (at Marcell) to 150 mm (at Hubbard Brook and Leading Ridge) to 250 mm (at Fernow). However, such increases diminish fairly rapidly, more so in some areas (Hubbard Brook and Leading Ridge) than others (Fernow and Marcell).

When cutting forests with an objective of increasing water yields, one must consider the possible impacts of a change in species during regrowth. The long-term results from Fernow and Hubbard Brook show that desired increases in water yield occurring immediately after cutting may be compensated in later years if hardwoods are converted to softwoods, or if there is a major shift in composition of hardwood species.

It is clear that the prolonged increases in water yield that occur after cutting in other regions of United States, such as from deeper soils of the southeast (Swank and others 1988) or from slowly regenerating forests of the west (Troendle and King 1985), cannot be expected in the Northeast. Shallow soils and rooting depths, shorter growing seasons, rapid root occupancy and leaf-area development by natural regeneration, lower evapotranspiration, and complete recharge of soil moisture during every dormant season all act to limit the magnitude and duration of increases in water yield in the Northeast.

Global Climate Change

The potential for a gradual change in species composition of forests is a major concern related to global climate change (Roberts 1989). The Hubbard Brook findings have implications regarding this concern. If one or two species were to drop out of the current hardwood forest, there could be detectable impacts on water yield. For example, the replacement of beech and maple at Hubbard Brook with birch and cherry resulted in decreases in water yield that averaged about 50 mm yr⁻¹. Although these decreases are small, they could become important if global climate change included a decrease in precipitation or conditions that favor increased evapotranspiration.

Nutrient Cycling

Forest cutting affects many processes involved in nutrient cycles and can lead to mobilization and increased leaching of nutrients (Hornbeck and others 1987). The mobilization and leaching of nutrients usually coincide with maximum increases in water yield. Thus, the larger the increases in water yield, the greater the potential to transport an additional mass of nutrients from cutover watersheds.

Forest cutting had negligible effects on nutrient leaching to streams at Marcell (Verry 1972), Fernow (Aubertin and Patric 1974), and Leading Ridge (Lynch and Corbett 1990), but caused significant increases at Hubbard Brook (Bormann and others 1968, Hornbeck and others 1987). In the 7 years after the clearfelling and herbicide experiment on watershed 2 at Hubbard Brook, increased leaching losses of nitrogen in streams represented a loss of nearly one-fourth of the total nitrogen capital of the watershed. A significant portion of this nitrogen loss was transported by the increased water yields that occurred in response to cutting and herbicide applications. By contrast, leaching losses of nitrogen after the less drastic strip cutting of watershed 4 represented <1% of total capital (Hornbeck and others 1987). Part of the explanation for this reduced loss lies with the much smaller increases in water yield, and less opportunity for nitrogen to be transported from the watersheds. Before recommendations are made to increase water yields from forests where nutrient leaching may be a problem, the potential impacts of added nutrient losses on site productivity and water quality must be considered.

Hydrologic Modeling

A primary objective of watershed studies is to provide data for developing and testing hydrologic models. The variety of responses to treatments in the northeastern United States suggests why it has been difficult to obtain good simulations of changes in water yield, especially those that are long term and more subtle.

The role of changes in species composition may have to be simulated more carefully. At present, some forest hydrology models use leaf area as the primary parameter for governing transpiration rates and water yield responses

after treatment. As leaf area increases to an established level (e.g., 4 ha ha⁻¹), water yields gradually are returned to pretreatment levels. However, as suggested by long-term results at Fernow and Hubbard Brook, the changes in water yield might be more appropriately modeled with parameters such as leaf resistance, sapwood area, or indicators of leaf and needle geometry. Such parameters might allow better simulation of the processes that eventually resulted in long-term decreases in water yield at Fernow and Hubbard Brook.

Long-Term Research.

The knowledge summarized in this paper was obtained as a result of a continuing commitment to long-term research. Counting calibration periods, the studies have spanned at least 3 decades at Marcell, Leading Ridge, and Hubbard Brook, and 4 decades at Fernow. The reward for this long-term commitment is a more complete understanding of the impacts of forests and associated treatments on the hydrologic cycle. Watershed studies have taken on an added dimension over the past 2 decades as they have been expanded into ecosystem studies (Hornbeck and Swank 1992). The merging of forest hydrology with ecosystem studies ensures that watershed studies will continue as a primary source of knowledge about the role of forests in the hydrologic cycle.

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SEASONAL ISOTOPE HYDROLOGY OF APPALACHIAN FOREST CATCHMENTS

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Abstract: Seasonal hydrologic behavior of small forested catchments in the Appalachians was studied using oxygen-18 as a tracer. Oxygen-18 in samples of precipitation and streamflow were used to determine seasonal variations of subsurface water recharge and movement within two 30-40 ha forest catchments (Watershed 3 and 4) at the Fernow Experimental Forest in northcentral West Virginia and a 1,100-ha forested catchment in northcentral Pennsylvania for the period March 1989-March 1990. Precipitation or throughfall in both regions showed expected seasonal sine-wave variations in oxygen-18 with minima occurring in winter and maxima occurring in summer. Baseflow stream samples for both small watersheds at Fernow showed similar seasonal sine-wave variations in oxygen-18 with amplitudes damped by about 90% and time lags to peak oxygen-18 of about 110 days relative to precipitation variations. Damping of amplitudes on the Fernow basins was equivalent to a mean transit time for subsurface baseflow water of about 1.5 years. Baseflow oxygen-18 on the larger Pennsylvania basin showed no discernible seasonal pattern in oxygen-18, which indicated mean transit time of subsurface water was at least 3-5 years. These results imply that both small Fernow basins exhibit relatively shallow and rapid recycling of subsurface water and that both basins would respond quickly and similarly to changes in watershed condition. On the larger Pennsylvania basin, a much larger, more slowly-cycling groundwater reservoir exists and baseflow would respond much more slowly to changes in watershed conditions.

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SPATIAL CHARACTERISTICS OF TOPOGRAPHY, ENERGY EXCHANGE, AND
FOREST COVER IN A CENTRAL APPALACHIAN WATERSHED

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Abstract: Spatial variation of topography, net radiation, evapotranspiration, and forest stand in the central Appalachian watershed is described. The study area is the control watershed 4 (39° 20'N, 79° 49'W) located in the Fernow Experimental Forest at Parsons, West Virginia. The watershed encompasses an area of 39.2 ha, it has a south-east orientation, and the average slope inclination is 14°. The forest cover is ca. 85 years old and consists of upland oak and cove hardwoods. Topographic analysis was based on data for 432 triangular segments with an average area of 360 m², covering the whole watershed. Partial areas for defined slope and azimuth ranges and the distribution of both parameters are illustrated. Half of the watershed area has an azimuth between 90 and 150° (east facing slopes), and 65% of the area has slope inclination ranging from 10 to 20°. Net radiation (Rn) was computed for all terrain segments. Its distribution in the watershed is illustrated, and its average yearly sum for the whole watershed was 2.2 GJ m². Yearly sum of Rn of southwest facing slopes was 55% (lower sites) to 60% (upper sites) greater than that of east facing slopes. The average yearly precipitation (P) and evapotranspiration (Et) of the watershed are 145.5 cm and 81.7 cm, respectively. A regression formula defines yearly sum of Et as a function of P and Rn of the watershed. Using this formula, average yearly sums of Et of all terrain segments were calculated. The distribution of the yearly average sum of Et in the watershed is illustrated; yearly Et of partial areas varied from ca. 60 to 85 cm. The average air-dry above ground biomass for 112 plots was 320.3 t ha⁻¹. East facing slopes had the highest air-dry biomass (354 t ha⁻¹) and the southwest facing slopes the lowest (224 t ha⁻¹). Thirty-five species were recorded on the plots surveyed. The most frequent species were sugar maple (32.1% of the total number of trees, DBH > 5 cm), red maple (19.3%), American beech (9.7%), northern red oak (7.6%), black cherry (4.1%), sweet birch (3.6%), and chestnut oak (2.4%). Red oak had the highest total biomass (30.2% of the total for all species), followed by sugar maple (13.8%), black cherry (13.0%), red maple (9.9%), chestnut oak (6.9%), yellow-poplar (5.7%), American beech (4.7%), and white oak (4.5%).

INTRODUCTION

On a broad scale, the major plant associations of the central Appalachian region are oak forests and northern hardwoods. The relationship between forest and climate of the region is well established. Regional energy-water relations for a horizontal surface - are defined by Hare [1972 (in Miller, 1977)]. However, on smaller scales, there is a wide variety of vegetation types that, according to Rumney, (1968) is a natural consequence of variations in topography, weather patterns and underlying bedrock. There are numerous descriptions of forests in the region (e.g., Hack and Goodlett, 1960; Trimble, 1973; Burns, 1983). However, for most forest sites, quantitative information on topography related variation in meteorologic, hydrologic, and other parameters is missing. Foresters correlate forest growth in the region with such parameters as slope aspect and inclination, soil depth and fertility, precipitation, and stone content (Trimble and Weitzman, 1956; Yawney, 1964; Yawney and Trimble, 1968; Auchmoody and Smith, 1979). However, Carmean (1975) remarked that "correlations cannot be accepted as evidence of cause and effect relations" and that "features of soil, topography, and climate found to be correlated with site index are indirect indices

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of more basic growth controlling factors and conditions, such as available moisture and nutrients, and microclimatic factors that affect evapotranspiration and tree physiological processes". This calls for the understanding of ecological processes at specific forest sites and is compatible with geophysics of landscapes and with landscape ecology (Armand, 1964; Forman, 1983; Swanson et al. 1988).

Among many processes that take place in the forest, cycles of water and energy play a key role. Hydrologic studies at the watershed level yield information on average values of the water balance components. The number of such studies is limited, and in addition the water balance components so obtained cannot be related to specific forest sites with varying topography and location in the watershed. Net radiation of the forest is regarded as the main source of energy needed for the processes of growth, etc. But, studies dealing with the distribution of net radiation in forested watersheds are infrequent (Tajchman et al. 1988; Fu et al. 1995).

For this particular study, we have selected a forested watershed (watershed 4) in the Fernow Experimental Forest at Parsons, West Virginia, which has been the subject of hydrologic and meteorologic observations for more than 40 years (Adams et al., 1993). The objectives of the study were to obtain a detailed analysis of a) topography, b) energy and water exchange, and c) forest cover.

STUDY SITE

The study area, the control watershed 4, is shown Fig. 1. The watershed area is 39.2 ha, the average watershed elevation is 804 m with the maximum of 869 m and minimum of 739 m. The watershed has a southeast orientation and ca. 65% of its area has the azimuth ranging from 90° (east facing) to 180° (south facing). Slope inclination ranges from 2 to 29° and the average value is 14°. The predominant soil is Calvin silt loam with considerable stone content. Soil depth to bedrock averages 0.8 m, ranging from 0.56 to 1.2 m. About 95% of the tree roots were found in the upper 0.90 m layer of the soil (Patric, 1973; Kochenderfer et al. 1987).

The area was heavily logged between 1905 and 1910; no surface disturbance has been permitted since that time, except for a road constructed adjacent to its upper boundary in the 1930's. The major forest types in the watershed are upland oaks and cove hardwoods. The upland oak type occurs on drier areas and consists primarily of red oak (*Quercus rubra*), chestnut oak (*Quercus prinus*), and white oak (*Quercus alba*). Cove hardwood type occupies moist sites along the streams and consists mainly of sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*), frequently including yellow-poplar (*Liriodendron tulipifera*) and scattered American beech (*Fagus grandifolia*).

The growing season is May through September, and average frost-free season is 145 days (Patric, 1973). Precipitation is evenly distributed throughout the year, and the yearly average is 145.5 cm. About 44% (64.1 cm) of total precipitation occurs during the growing season. The months of June and July have the greatest average precipitation, 14.4 and 13.6 cm, respectively. September and October are the driest months, with average precipitation of 10.3 cm and 9.7 cm, respectively. The yearly average temperature in the study area is 8.8°C. July and August have the highest average monthly temperatures of 19.3 and 18.7°C, respectively. January has the lowest monthly average temperature of -3.1°C.

METHODS

Topography

For spatial analysis of the watershed, its photogrammetric map (Greenhorne and O'Mara, Inc.) in scale 1:2,500 was considered in the three dimensional coordinate system with x-axis directed toward east, y-axis directed toward north, and z-axis directed toward zenith. The watershed area was divided into 432 triangular segments with an average area of 360 m². Using the Summagraphics Microgrid II digitizer, the x and y coordinates of the corners of all triangles

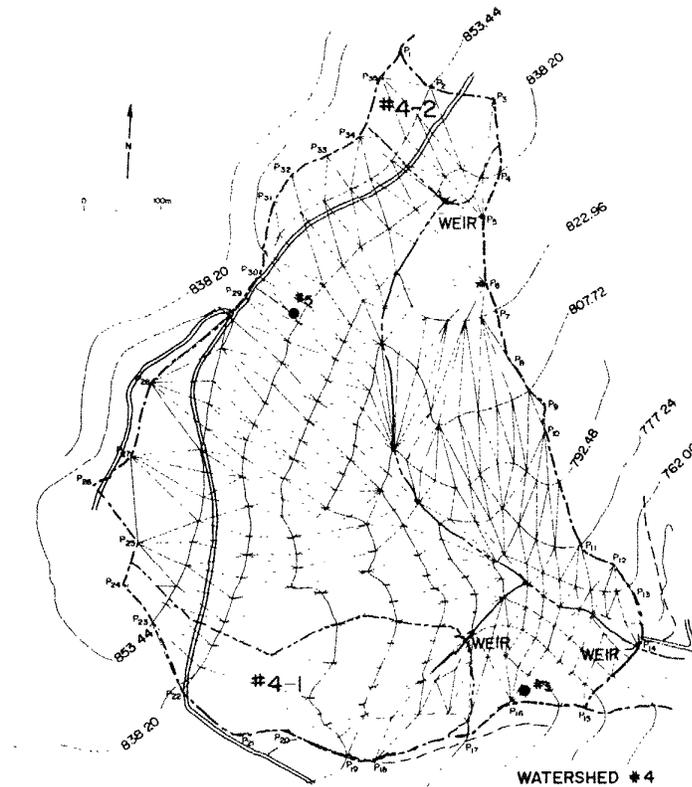


Figure 1. Topographic map and triangulated network of Watershed 4 (Fu et al., 1995).

were determined; the elevation marked on contour lines was accepted for the z-coordinate. The x,y,z coordinates of the corners of triangles were used to compute their azimuth, inclination, and area (Tajchman, 1975).

Water and Energy Balances

The following formula defines the water balance of a watershed

$$P = Et + R + \Delta W, \quad (1)$$

where P is precipitation of the watershed averaged over its area, Et is evapotranspiration of the watershed, R is runoff, and ΔW represents the change of the soil water content in the watershed during the period of observation. For periods starting and ending with the same soil water content $\Delta W = 0$ and the water balance of the watershed is given by

$$P = Et + R. \quad (2)$$

The parameters P and R are known from observation and Et can be obtained from Eq. (2).

The energy balance of the watershed, after neglecting the relatively small amounts of energy used in photosynthesis and energy stored in the soil, is given by

$$R_n = L E_t + H, \quad (3)$$

where R_n is net radiation of the watershed, L is the latent heat of evaporation of water, and H is the heat exchange between the watershed and the atmosphere. In calculating the yearly energy balance of the watershed, the latent heat of E_t obtained from Eq. (2) can be applied. Calculations were carried out for 39 hydrologic years (1951-1990) which start on May 1 of a calendar year and ends on April 30 of the next calendar year.

The net radiation of the watershed is given by

$$R_n = G (1 - r) + R_l, \quad (4)$$

where G is global radiation, r is the reflectivity of the forest for solar radiation and R_l is the longwave radiation balance. The average r values of 0.17 and 0.20 were accepted for the growing season and for the dormant season, respectively (DeWalle and McGuire, 1973; Lee and Sypolt, 1974). The term $G (1 - r)$ represents the amount of solar radiation absorbed by the forest. Net radiation data for the watershed are not available from direct observation. However, they can be calculated for all terrain segments and then for the whole watershed area if the following parameters are known:

- a) Monthly sums of global radiation at a horizontal surface in the study area,
- b) Climatological data on air temperature, humidity, and sky cover,
- c) Topographic parameters of terrain segments including azimuth, inclination, and the view factor,
- d) The times of sunrise and sunset of all terrain segments.

Using monthly sums of global radiation (horizontal surface) for Parsons (1965-1977) and the monthly average sky cover data for Elkins, ca. 24 km south-east of Parsons, the following regression formula was obtained

$$G = G_0 (0.82 - \alpha C), R^2 = 0.87, \quad (5)$$

where G_0 is the monthly sum of extraterrestrial radiation, and C is average monthly sky cover in fractions of unity. Monthly values of the coefficient α are listed in Table 1. Eq. (5) was used to calculate the missing data on global radiation at Parsons during the period 1951-1990.

Table 1. Monthly values of α (Eq. 5) at Parsons, W.Va.

Month	α	Month	α
January	0.598	July	0.514
February	0.562	August	0.516
March	0.546	September	0.534
April	0.576	October	0.613
May	0.537	November	0.639
June	0.500	December	0.622

The following regression formula describes yearly sums of Et as functions of the corresponding P and Rn.

$$Et = 0.2052 P + 5841 (Rn/L), R^2 = 0.82, \quad (6)$$

where Et and P are in cm, Rn in kJ m^{-2} , and L is the latent heat of evaporation of water. Assuming that the same relationship exists between long term average monthly sums of Et, P, and Rn, Eq. (6) was used to calculate 39 years average monthly values of Et of all terrain segments. Then, yearly sums of Et were obtained. The standard deviation of the difference between measured and calculated yearly sums of Et was 1.85 cm, and the relative error ranged from 0 to 7.8% (average = 2.8%). For more details see Fu (1992).

Above Ground Biomass and Species Composition

Data on DBH and species composition were collected during the summer of 1993 on eighty seven 804 m^2 ($93 \times 93 \text{ ft.}$) plots randomly distributed in the watershed. All trees with DBH > 5 cm were recorded. Additional data on DBH and species composition in the watershed, collected in 1990 at $25\,809 \text{ m}^2$ (0.2 acre) plots randomly distributed in the watershed, were included in the study.

The location of the plots is seen in Fig. 2. The above ground air-dry biomass of single trees at each plot was obtained using the relationships reported by Brenneman et al. (1978).

RESULTS AND DISCUSSION

Topographic parameters were computed for all terrain segments and were used to obtain a) partial areas of the watershed with definite ranges of inclination and azimuth, and b) maps showing the distribution of inclination and azimuth in the watershed.

Figures 3 and 4 show partial areas of the watershed in percent of its total area within different intervals of inclination and azimuth. As shown in Fig. 3, slopes with the inclination ranging from 10 to 15° occupy 42% and those with inclination ranging from 25 to 30° occupy only 3% of the total watershed area. Fig. 4 shows, e.g., that, east and south-east facing slopes with the azimuth ranging from 90 to 150° occupy about 50% of the watershed area, and the north facing slopes with the azimuth ranging from 330 to 30° occupy about 7% of the total watershed area. Since site quality is related to aspect, knowing of the relative amount of area in each aspect can be useful in the preliminary evaluation of forest land in the study area.

The distribution of slope inclination and azimuth in the watershed is seen in Figs. 5 and 6, respectively. The western half of the watershed contains more or less topographically uniform areas with inclination ranging from 8 to 12° (Fig. 5), and with azimuth ranging from 100 to 140° (Fig. 6). The eastern half of the watershed is characterized by a more complex topography with inclination of partial areas ranging from 6° in the north-eastern part of the watershed to 26° in the south-eastern part of the watershed. The prevailing aspect in this part of the watershed is south and south-west.

Topography affects the radiation exchange in complex terrain. This is seen in Fig. 7 where the distribution of the average yearly sums of net radiation in the watershed is marked by isolines. In the western half of the watershed the net radiation is more or less uniformly distributed, and in the eastern half a variation is substantial. In the western half of the watershed the yearly sum of net radiation amounts to approximately 2.20 GJ m^{-2} , and in the eastern part it varies from approximately 1.60 GJ m^{-2} to 2.20 GJ m^{-2} . The yearly average net radiation of the whole watershed is 2.20 GJ m^{-2} .

The evapotranspiration of the watershed is a component of its water and energy balances (Eqs. 1 and 3). Its average value for the period 1951-1990 was 81.7 cm, and the equivalent latent heat amounted to 2.02 GJ m^{-2} . One can determine from Eq. (3), that the yearly average sum of the sensible heat transferred from the watershed to the atmosphere amounted to 0.18 GJ m^{-2} or 8.2% of Rn.

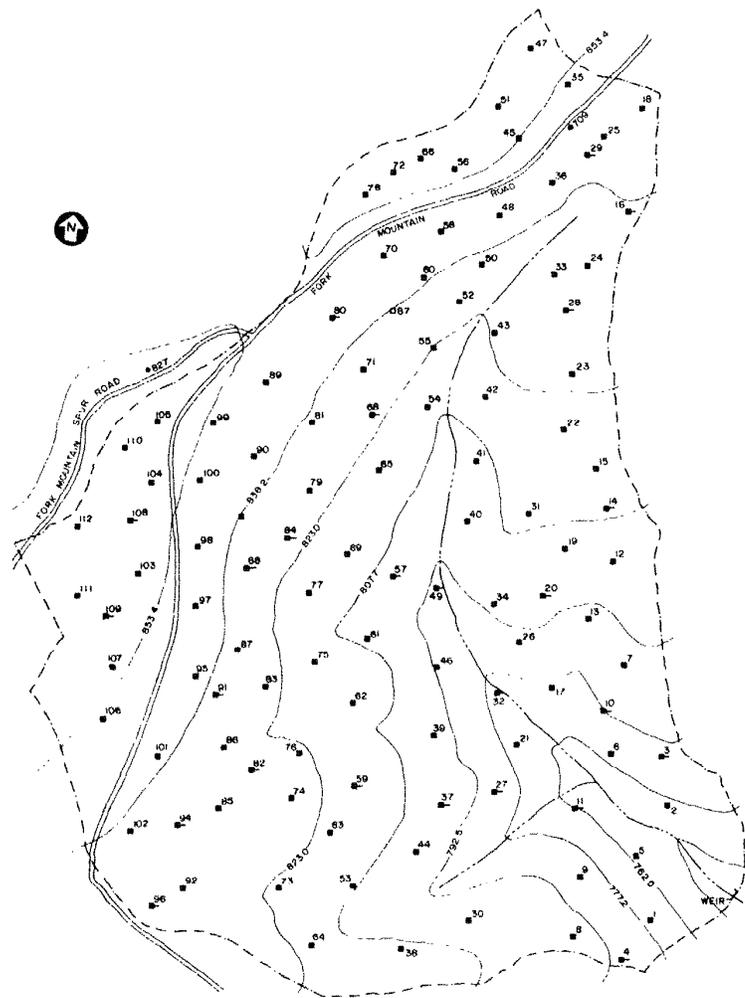


Figure 2. Location of sampling plots. Squares with a dash represent permanent plots of the U.S. Forest Service.

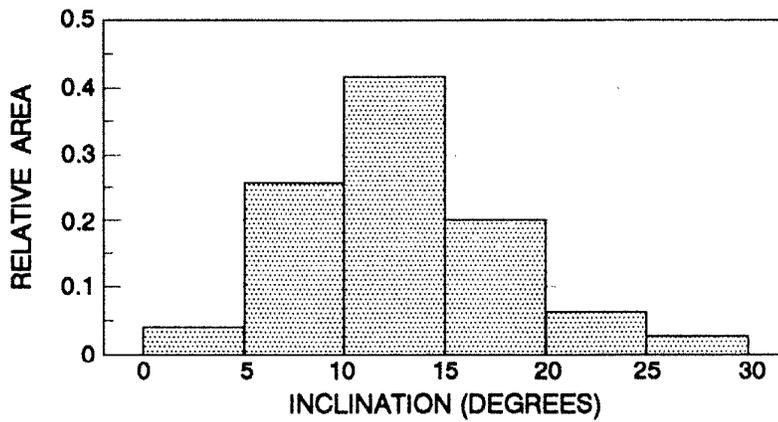


Figure 3. Ranges of slope inclination and the corresponding partial areas (%) of the watershed.

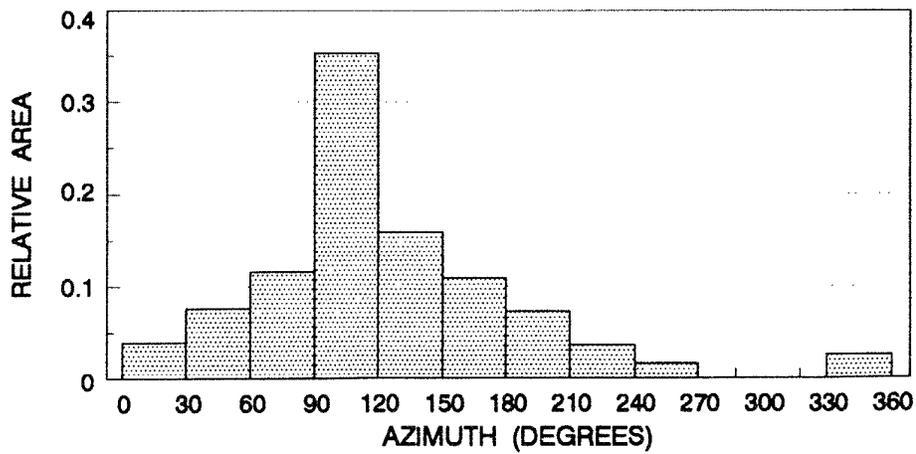


Figure 4. Ranges of slope azimuth and the corresponding partial areas (%) of the watershed.

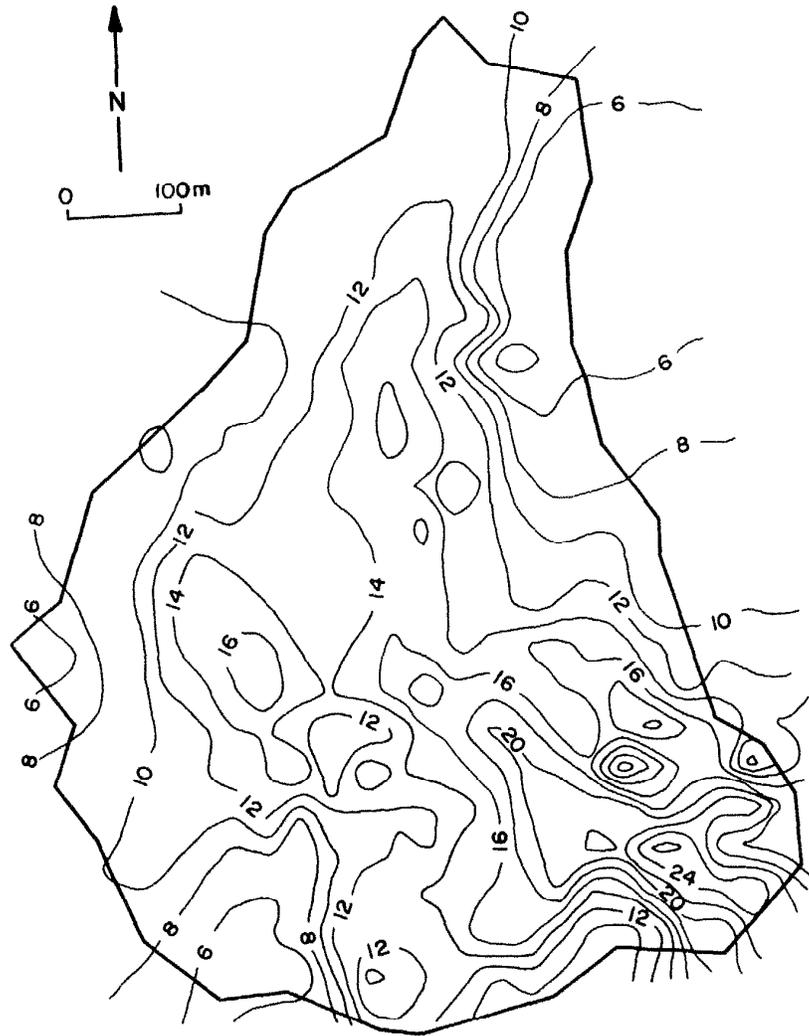


Figure 5. Distribution of slope inclination (degrees) in Watershed 4 (Fu et al., 1995).

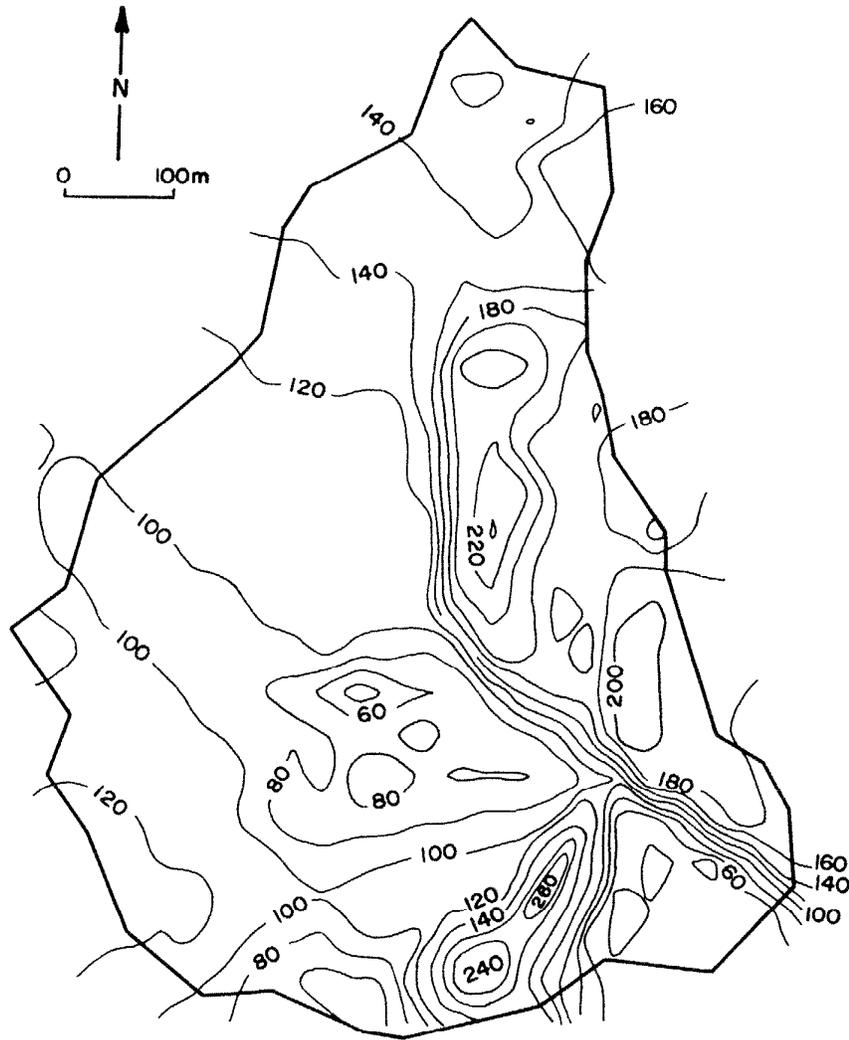


Figure 6. Distribution of slope azimuth (degrees) in Watershed 4 (Fu et al., 1995).

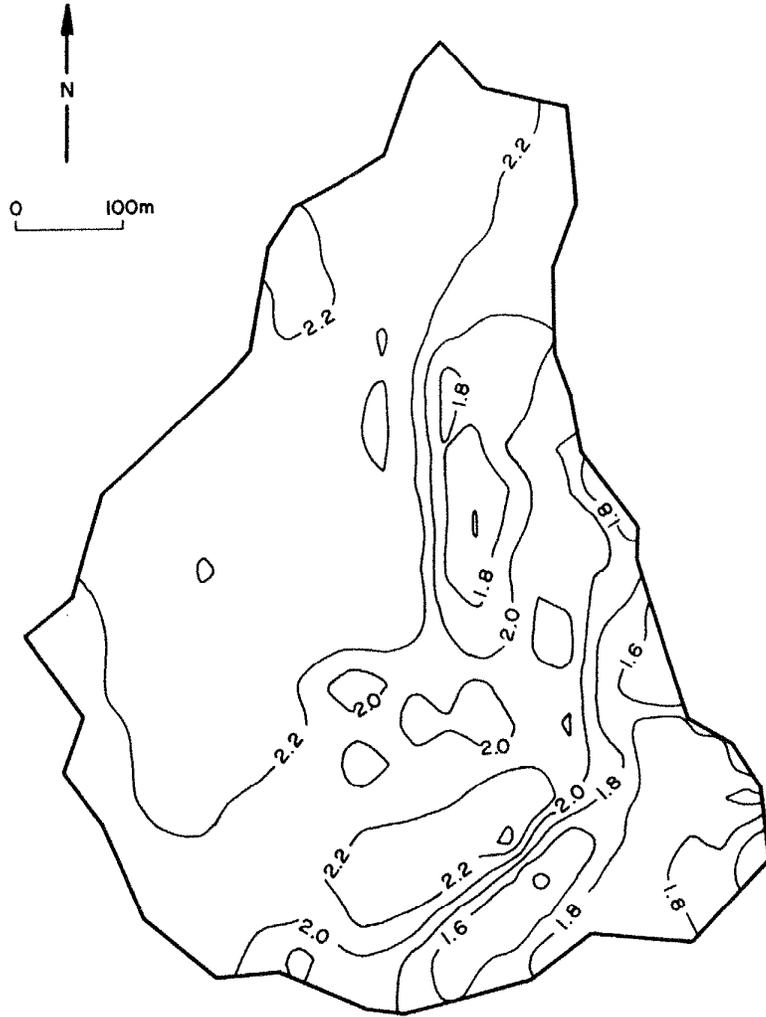


Figure 7. Distribution of the yearly sums of net radiation ($G J m^{-2}$) (Fu et al., 1995).

Applying Eq. (6) to all terrain segments, their Et values were obtained. A linear interpolation was applied to obtain the distribution of Et values in the watershed, represented by isolines on the map of the watershed (Fig. 8). In the western half of the watershed, Et varies from 82 to 85 cm per year and is uniformly distributed. In the eastern half of the watershed, the yearly average sum of Et varies from 60 to 82 cm, and its distribution is complex.

Figure 9 shows the location of plots where trees were sampled, and the numbers at each plot express the above ground air dry biomass in tons per hectare. A total of 35 species were found on the plots (Table 2). The average biomass for 112 plots is 320.3 t ha^{-1} . The difference between the maximum and minimum biomass of single plots is equivalent to 152% of the average value. The coefficient of variation of single plot biomass decreases when the number of plots (n) increases, and reaches a more or less steady value when $n \geq 20$.

Plot biomass values were compared to those of Rn and Et, and the possible relationship between the biomass and two other parameters was examined. In the eastern part of the watershed with a more complex topography, the coefficient of variation of the plot biomass is 29.9%; the corresponding coefficients of variation for Rn and Et are 8.9% and 6.4%, respectively. In the western part of the watershed, with more uniform topography, the coefficient of variation for plot biomass is 25.3%, and those for Rn and Et are 3.1 and 2.4%, respectively. The correlation between the above ground biomass and Rn and Et is illustrated in Table 3.

The above data (Table 3) show a poor correlation between biomass and the two other parameters for single plots. However, the correlation coefficient increases with number of plots averaged, and it exceeds 0.8 for $n \geq 15$.

The average biomass for different ranges of azimuth is given in Table 4.

For the azimuth ranges 0 - 30°, 210 - 240°, and 240 - 270° only 3, 5, and 2 plots are available, respectively. Data for these azimuth ranges should not be regarded as representative. Sites with azimuth ranging from 90 to 120° have the highest average above ground biomass. For the azimuth values decreasing or increasing from this azimuth range the average above ground biomass decreases (Table 4).

Species found on the plots surveyed are listed in Table 5 together with the number of trees and air dry biomass for each species and the corresponding percentages of the totals. According to Table V, the most prevalent species in the watershed based on number of trees are Sugar maple (32.1%), Red maple (19.3%), American beech (9.7%), Northern red oak (7.6%), Black cherry (4.1%), Sweet birch (3.6%), Chestnut oak (2.4%), Downy serviceberry (2.4%), and Yellow-poplar (1.8%). Each of the remaining species accounts for less than 1.5% of the total. The following eight species account for 88.7% of the total biomass: northern red oak (30.2%), sugar maple (13.8%), black cherry (13.0%), red maple (9.9%), chestnut oak (6.9%), yellow-poplar (5.7%), American beech (4.7%), and white oak (4.5%).

Species frequency and stand composition vary with site azimuth. Some typical examples are listed in Table 6.

CONCLUSIONS

Future improvement in ecological forest management will depend on progress in understanding processes and interactions which take place in the forest. This particular study shows results of a three-dimensional analysis of topography, radiation exchange, and evapotranspiration in a forested watershed. This is probably the first attempt to calculate the distribution of evapotranspiration in a forested watershed. However, our results on Et should be verified in independent research, e.g., on isolated plots in the watershed. The distribution of the 39-year average yearly sum of Et was obtained under the assumption that for an "average year" Eq. (6) applies to all terrain segments, and that soil conditions and forest cover are uniform. Data on spatial distribution of soil horizon thicknesses, stoniness, organic matter content, and stand density (which could be described in the x, y, z - coordinate system) would allow modifications to Eq. (6) for specific terrain segments.

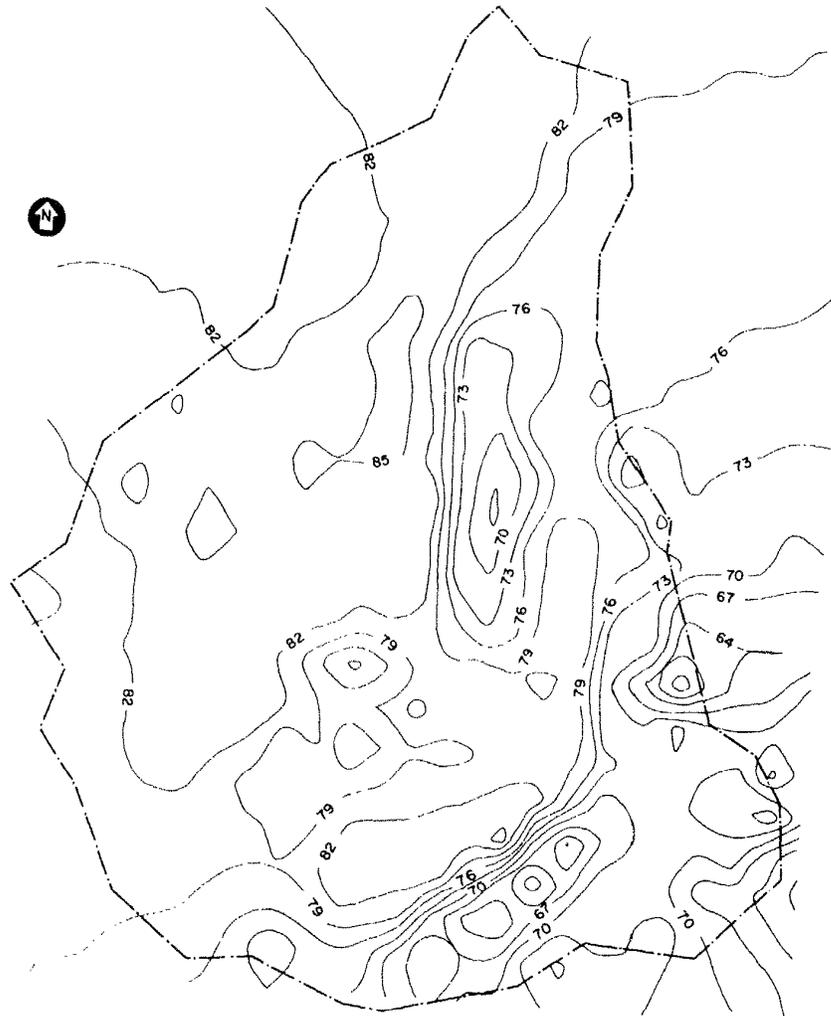


Figure 8. Distribution of the yearly sums of evapotranspiration (cm) (Fu, 1992).

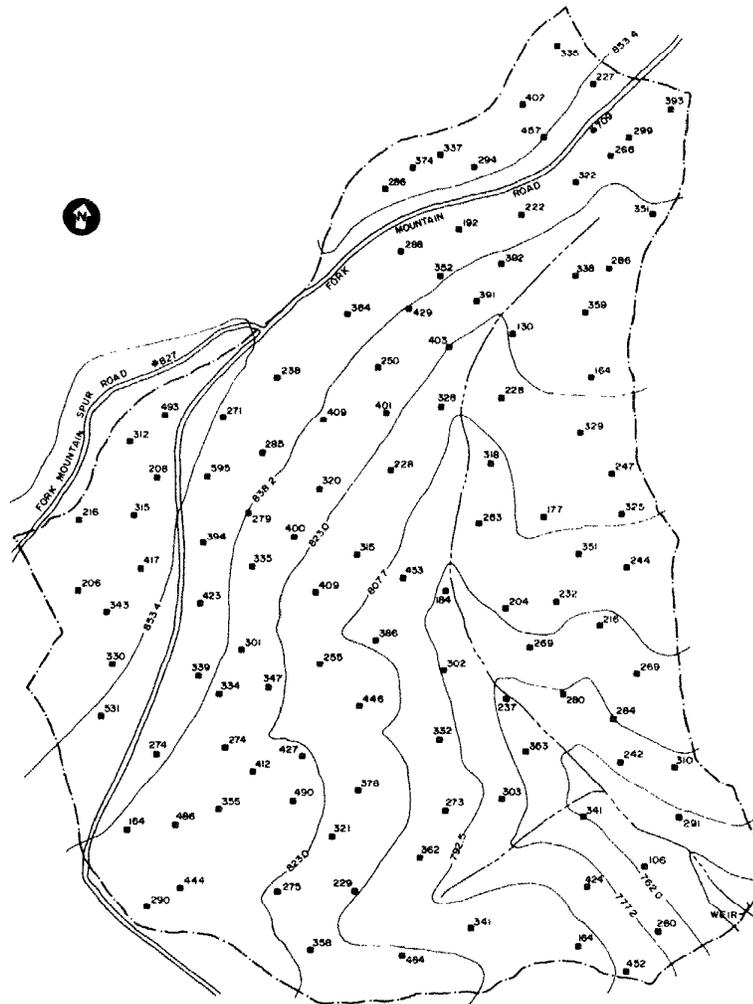


Figure 9. Above ground air-dry biomass at sampling plots.

Table 2. Species found in Watershed 4.

Common Name	Scientific Name
Ailanthus	<i>Ailanthus Altissima</i> (Mill.) Swingle
American basswood	<i>Tilia Americana</i> L.
American beech	<i>Fagus grandifolia</i> Ehrh.
American chestnut	<i>Castanea dentata</i> (Marsh.) Borkh.
Bigtooth aspen	<i>Populus gradidentata</i> Michx.
Blackgum	<i>Nyssa sylvatica</i> Marsh.
Black locust	<i>Robinia Pseudoacacia</i> L.
Cherry	
Black	<i>Prunus serotina</i> Ehrh.
Pin	<i>Prunus pensylvanica</i> L.f.
Cucumber tree	<i>Magnolia acuminata</i> L.
Deciduous holly	<i>Ilex decidua</i> Walt.
Downy serviceberry	<i>Amelanchier arborea</i> (Michx. f.) Fern.
Flowering dogwood	<i>Cornus florida</i> L.
Fraser magnolia	<i>Magnolia fraseri</i> Walt.
Grapevine	<i>Vitis</i> L.
Hawthorn	<i>Crataegus</i> L.
Hickory	
Bitternut	<i>Carya cordiformis</i> (Wangenh.) K. Koch
Shagbark	<i>Carya ovata</i> (Mill.) K. Koch
Eastern hophornbeam	<i>Ostrya virginiana</i> (Mill.) K. Koch
Maple	
Mountain	<i>Acer spicatum</i> Lam.
Red	<i>Acer rubrum</i> L.
Striped	<i>Acer pensylvanicum</i> L.
Sugar	<i>Acer saccharum</i> Marsh.
Oak	
Black	<i>Quercus velutina</i> Lam.
Chestnut	<i>Quercus prinus</i> L.
Northern red	<i>Quercus rubra</i> L.
Scarlet	<i>Quercus coccinea</i> Muenchh.
White	<i>Quercus Alba</i> L.
Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees.
Sourwood	<i>Oxydendron arboreum</i> (L.) DC.
Sweet birch	<i>Betula lenta</i> L.
White ash	<i>Fraxinus americana</i> L.
Witch hazel	<i>Hamamelis virginiana</i> L.
Yellow-poplar	<i>Liriodendron tulipifera</i> L.

Table 3. The correlation coefficient for above ground biomass, net radiation (Rn) and evapotranspiration (Et) for single plots and for different numbers of plots averaged.

		Biomass					
		Single plots	Number of plots averaged (n)				
			5	10	15	18	28
Rn	0.21	0.54	0.78	0.86	0.89	0.92	
EIT	0.18	0.57	0.75	0.83	0.82	0.89	

Table 4. Average above ground biomass in watershed 4 for azimuth ranges.

Azimuth (degrees)	Number of plots	Average biomass (t ha)
0 - 30	3	263.0
30 - 60	10	312.3
60 - 90	14	335.8
90 - 120	33	353.7
120 - 150	22	327.4
150 - 180	14	294.3
180 - 210	9	285.1
210 - 240	5	223.9
240 - 270	2	290.6

Table 6. Azimuth of maximum frequency for different species in watershed 4.

Northeast facing	East facing	South facing	Southwest facing
American beech	American basswood	Black gum	
Striped maple	Black cherry	Chestnut oak	
	Black locust	Downy serviceberry	
	Eastern hophornbean		
	Mountain maple		
	N. red oak		
	Sugar maple		Cucumber tree
	Sweet birch		Fraser magnolia
	White ash		White oak
	Witch hazel		
	Yellow-poplar		

Red maple has a relatively high frequency within the azimuth range of 80 - 200° .

Table 5. Species, number of trees with DBH > 5 cm, and the above ground air-dry biomass for 112 plots in watershed 4.

Species	Number of trees	Percent of total number of trees	Biomass t	Percent of total biomass
Bigtooth aspen	1	0.01	0.22	0.01
Bitternut hick.	6	0.09	2.44	0.08
Shagbark hick.	22	0.32	14.58	0.51
American hornbeam	5	0.07	0.05	0.00
East. hophornbeam	46	0.67	1.48	0.05
Sweet birch	246	3.59	72.56	2.50
American beech	662	9.67	135.73	4.67
American chestnut	11	0.16	0.76	0.03
White oak	70	1.02	131.96	4.54
Chestnut oak	165	2.41	200.40	6.90
North. red oak	518	7.56	876.92	30.19
Scarlet oak	10	0.15	13.18	0.45
Black oak	10	0.15	10.51	0.36
Cucumbertree	90	1.31	17.62	0.61
Fraser magolia	51	0.74	2.45	0.08
Yellow poplar	122	1.78	165.13	5.68
Sassafras	22	0.32	3.45	0.12
Downy serviceberry	164	2.39	4.22	0.14
Fire of pin cherry	2	0.03	0.58	0.02
Black cherry	283	4.13	376.77	12.97
Black locust	46	0.67	28.66	0.99
Ailanthus	1	0.01	0.03	0.00
Sugar maple	2200	32.13	399.62	13.76
Striped maple	231	3.37	1.39	0.05
Red maple	1319	19.26	287.31	9.89
Mountain maple	87	1.27	0.76	0.03
American basswood	79	1.15	18.85	0.65
Blackgum	98	1.43	33.41	1.15
Flowering dogwood	16	0.23	0.13	0.01
Sourwood	53	0.77	8.79	0.30
White ash	108	1.58	94.10	3.24
Grapevine	26	0.38	Not counted	
Hawthorn	1	0.01	0.01	0.00
Deciduous holly	8	0.12	0.01	0.00
Witch hazel	68	0.99	0.32	0.01
Total (All plots)	6848	100	2904	100

Results of this study suggest that at least 20 800 m² sampling plots are needed to obtain the average above ground biomass, representative for a large partial area of the watershed. The correlation between the above ground biomass, and Rn and Et is poor ($r \approx 0.2$) for single plots, increasing with the number of plots averaged, and for 18 plots it amounts to 0.89 for Rn and 0.82 for Et. Better correlations with the averaged plots area may be related to plot to plot variation in soil parameters (stoniness, thickness of A- and B-horizon) and in stand density (leaf area index).

The list of species identified in watershed 4 is similar to that for the Fernow Experimental Forest reported by Trimble (1973). Topography related variations of species frequency and above ground biomass in watershed 4 correspond more or less to those found in the Little Laurel Run catchment, West Virginia University Forest, near Coopers Rock, and elsewhere (Knight, 1980; Tajchman and Wiant, 1983; unpublished data). Because of the differences in sampling and reporting procedures and lack of information on stand development, a quantitative comparison of results from different reports would be difficult and would exceed the objectives of our study.

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DROUGHT TOLERANCE OF SUGAR MAPLE ECOTYPES

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Abstract: Sugar maple declines periodically occur in rural and urban areas. These declines usually follow periods of below-average precipitation leading to the speculation that moisture deficiency is a primary cause of the decline. Sugar maple ecotypes with greater tolerance to drought should have greater longevity and vitality as a result of this tolerance. Sugar maple and black maple trees from the western and southern range of these species purportedly have greater drought tolerance. However, the quantification of physiological, morphological, and anatomical characteristics to explain and substantiate this purported tolerance is lacking. We present results on the response of greenhouse grown seedlings of five ecotypes from Oklahoma, Missouri, Iowa, Tennessee, and Ontario to experimental drought. Plant water relations (net photosynthesis, stomatal conductance, and water use efficiency) and tissue water relations (modulus of elasticity, osmotic potential at 0 and 100 percent turgor, and relative water content at 0 turgor) were used to test for variation in drought tolerance. Xylem anatomy, leaf structure and biomass partitioning further differentiated ecotypic variation.

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