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Proceedings of a Meeting

Held at

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University Park, PA

March 3-6, 1991

Edited by

Larry H. McCormick and Kurt W. Gottschalk

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FOREWORD

This conference is the eighth 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, and University of Tennessee. The purpose of these conferences has remained the same: to provide a forum for the exchange of information concerning the central hardwoods and to engender coordination among forest scientists in the central hardwood region. This purpose is evidently well-served: the last several conferences have each attracted some 45 to 65 program contributions, and the audiences have been correspondingly large.

Previous organizers have refrained from drawing precise boundaries around the "central hardwood region." We prefer to continue that policy on the grounds that to do otherwise might preclude some very worthwhile participation. Thus, while the principal focus has remained on the oak resource for reasons that are obvious, the ecological scope has broadened from oak-hickory (in the early meetings) to Appalachian oak (Knoxville and State College) and mesophytic forests. With a few exceptions, the commercially significant species are similar for all these forest types, and advancements in knowledge are of general interest.

But the central hardwood region is not merely a collection of similar forest types. It also has historical, demographic, political, and economic characteristics that tend to distinguish it from other forest regions of the United States. For example, the population is heavily rural and agricultural, primary wood markets tend to be diffuse and unorganized, wilderness values and endangered species have generally not been overriding issues, and a relatively minor proportion of the forest land is controlled by public agencies or corporate ownerships. These and related conditions play critical roles in the practice of forestry in this region, and in the aggregate they emphasize its distinction from other regions; but no single one is necessarily unique to the central hardwoods. For these reasons, the characteristics of nonindustrial private forest land owners in Massachusetts might be just as relevant to the central hardwood region as regeneration methods for white oak in Indiana.

Since these proceedings are being published in advance, we have no way of judging the ultimate success of the upcoming Eighth Conference. Of course, our earnest hope is that this meeting shall sustain the excellent reputation of the series. We believe this hope is encouraged by the quality of the papers in these proceedings.

REVIEW PROCEDURES

Each manuscript published in these proceedings was critically reviewed by at least two 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 style of their papers.

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EFFECTS OF DROUGHT AND SHADE ON GROWTH AND WATER USE OF
QUERCUS ALBA, *Q. BICOLOR*, *Q. IMBRICARIA* AND *Q. PALUSTRIS* SEEDLINGS

Joseph J. McCarthy and Jeffrey O. Dawson¹

Abstract: Growth and water use efficiency were determined for 2-year-old white oak (*Quercus alba*), swamp white oak (*Q. bicolor*), shingle oak (*Q. imbricaria*) and pin oak (*Q. palustris*) seedlings grown under three shade treatments (30, 55 and 73%) and two irrigation regimes (container capacity and mild drought). With species and water regimes combined, the dry weight increment, root, stem, leaf, shoot dry weight and water use efficiency of the oaks decreased significantly as shade level increased from 30 to 73%. Shade had no effect on height increment, while shoot/root dry weight ratio increased with increasing shade. White oak and swamp white oak closely followed this overall pattern, but the only response shingle oak and pin oak exhibited to increasing shade levels was an increase in shoot/root ratio of 24 and 26%, respectively.

With species and shade levels combined, experimentally imposed drought reduced the oak seedling dry weight increment, root, leaf, and shoot dry weights, caliper increment and water use efficiency. The drought treatment had no effect on seedling height increment, but increased the shoot/root dry weight ratio. Under the drought regime, white oak and shingle oak had the highest water use efficiency values (1.65 and 1.73 mg cm⁻³) compared with values of 1.46 mg cm⁻³ for pin oak and 1.01 mg cm⁻³ for swamp white oak. White oak and shingle oak also had the lowest shoot/root ratios (0.60 and 0.87) when compared with pin oak (0.96) and swamp white oak (1.08).

Upland white oak and shingle oak seedlings had the lowest specific leaf areas (158.7 and 157.7 cm²/g) while the bottomland pin oak (176.1 cm²/g) and swamp white oak (174.8 cm²/g) had the highest. Pin oak and shingle oak seedlings flushed more times (2.5 and 1.9) during the growing season than swamp white oak (1.6) and white oak (1.0). Drought reduced the number of flushes of all the tested oak species with the exception of white oak, while shade had no detectable effect on oak seedling flushing.

INTRODUCTION

The effects of shade on growth and development of oak seedlings have been examined in numerous studies by growing seedlings under shade cloth or similarly altering radiation levels

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(Shirley 1929, McGee 1968, Loach 1969, Musselman and Gatherum 1969, Phares 1971, Farmer 1975, Johnson 1984, Gottschalk 1985). The results of these studies have sometimes been inconsistent with one another. For example, in some cases height growth increased with increasing shade (Shirley 1929, Musselman and Gatherum 1969), in other cases it decreased with shade (McGee 1968, Johnson 1984). Others studies indicated that shade had no effect on oak height growth (Farmer 1975) or that peak growth occurred at intermediate irradiance levels with height decreases in both directions (Phares 1971, Shirley 1929). One reason for such inconsistencies may be the use of first year seedlings in most of these studies. Early survival and growth of oak seedlings is strongly influenced by the stored carbon and nutrient reserves of the hypocotyledons (Crow 1988). However, once seedlings establish root systems adequate for supplying water and nutrients to the plant, increased irradiance levels will usually result in increased growth rates. Another factor not considered in many of these studies is the possibility of interaction between irradiance and soil moisture. Together with shade, competition for water and nutrients in the understory of forest stands with an abundance of dominant tree roots in surficial soil can reduce seedling growth (Carvell and Tryon 1961, Ferrell 1953). Oak seedlings will benefit from light shade because it moderates temperatures and water use (Kramer and Kozlowski 1979). Exposure to full solar irradiance can induce severe water stress in plants, especially during times of drought. Root growth of northern red oak (*Quercus rubra* L.) is particularly sensitive to even moderate drought. Red oak seedlings subject to various degrees of drought did not regenerate new roots at -0.6 MPa (-6 bars) (Larson and Whitmore 1970). However, white oak roots have been reported to be able to continue growth when the surrounding soil water potential was -1.2 MPa (Teskey *et al.* 1978). Farmer (1980) found that white oak seedlings have lower shoot/root ratios than northern red oak and it has been reported that white oak also has a deeper root system than northern red oak (Stout 1968, Hinckley *et al.* 1980).

Few studies of any oak species have examined the combined effects of shading and drought on growth and water use of seedlings (Gatherum *et al.* 1963, Musselman and Gatherum 1969). Consequently growth and water use of four oak species under varying shade and soil moisture conditions were examined in this study. Two of the oak species studied belong to the subgenus *Leucobalanus*, the white oaks [swamp white oak (*Quercus bicolor* Willd.) and white oak (*Q. alba* L.)] and two belong to the subgenus *Erythrobalanus*, the red oaks [pin oak (*Q. palustris* Muenchh.) and shingle oak (*Q. imbricaria* Michx.)] (Harlow *et al.* 1979). Within each subgenus a bottomland species (swamp white oak and pin oak) and an upland species (white oak and shingle oak) were included in this study. Shingle oak and swamp white oak were selected because they have been little studied to date.

Because various silvicultural methods call for the reduction of overstory canopy to stimulate oak reproduction, there is a need to more precisely determine which irradiance levels provide the best survival and growth conditions for seedlings of a given oak species. Since competition by roots for soil moisture is often severe in the understory of forest stands, and since this competition also limits the ability of plants to tolerate understory conditions, this study was designed to determine the combined effects of reduced irradiance and soil moisture on growth and development of oak seedlings. The objectives of this study were to determine if there are differences in growth and water use efficiency (mg/cm^3) within each oak species

among three shade levels and two soil water regimes and to determine if differences were associated with oak species, oak subgenus, or ecological niche of a species.

METHODS

The study was conducted during the summer of 1989, in a greenhouse constructed with iron-free glass located at the University of Illinois in Urbana-Champaign. Iron-free glass allows penetration of solar radiation of a spectral quality more similar to natural radiation in comparison with the glass normally used in greenhouses. Temperatures in the greenhouse ranged from 23-26°C during the day and 20-23°C during the night. The seedlings were grown under natural light and photoperiod between May 22 and October 16. One hundred 2-0 bare-root dormant seedlings each of white oak, swamp white oak, pin oak, and shingle oak were obtained from commercial nurseries in the midwestern U. S.. All seedlings were in the 15-30 cm shoot height class, with the exception of white oaks which ranged from 30-46 cm in shoot height. The seedlings were measured for initial stem height and caliper (diameter) at 1 cm above the root collar and then planted in a steam pasteurized 1:1:1 fertile loamy soil: perlite: sphagnum peat moss mixture (pH of 5.5) in 60 cm tall by 10 cm diameter cylindrical pots. The pH did not change appreciably during the course of this study. No fertilizers were added to the soil mixture. The initial fresh weights of all seedlings and pot weights were determined. In each pot, a seedling was planted in 2.6 kg of the air dry soil mixture. The seedlings then were watered daily with tap water and allowed to break bud and grow for five weeks. After five weeks, 30 seedlings of white oak, 25 seedlings of swamp white oak, and 20 seedlings of pin oak and shingle oak (unequal replicates due to mortality) were placed under each of three shade tents with advertised shade values of 30%, 55%, and 73% of incident light. The advertised shade percentages of these tents were found to correspond exactly with the percentage reductions in PAR ($\pm 1\%$) measured with a Li-Cor Integrating Photometer at noon and 4 p.m. (Model LI-188B with quantum sensor, Li Cor Inc., Lincoln, Nebraska). The shade tents were 1.33 m wide x 1.67 m long and had 1.33 m walls on each of four sides. An additional three seedlings per species were destructively measured to obtain an estimate of total, root, stem, leaf and shoot (sum of leaf and stem) fresh and dry mass. These ratios of initial dry weight to fresh weight measurements were used to obtain a value of seedling dry weight at this stage of the study. Dry weight increments were estimated by difference from the dry seedling weights at the end of the study. The proportions of dry to fresh weight obtained for the three seedlings per species were highly consistent, differing by no more than 5% in any case. The estimated initial dry weight means and standard deviations were 33.34 ± 9.76 g for white oak, 8.13 ± 2.20 g for swamp white oak, 7.48 ± 3.33 g for shingle oak, and 7.51 ± 1.82 g for pin oak seedlings.

The seedlings were grown for 2-3 weeks with regular watering to allow them to acclimate to the shade. Then all pots were watered to the drip point, allowed to drain for 24 h, and weighed to determine container water capacity, (the difference between total pot weight 24 h after watering and the sum of container, dry soil mixture, and initial plant fresh weights). Half of the seedlings of each species under each shade treatment were maintained at 90-95%

of container water capacity while the remaining seedlings had drought imposed by withholding watering.

Three pots with seedlings maintained at container water capacity for each shade and species combination were sampled randomly every 2-5 days and weighed to monitor the water lost from the pots. All pots were then watered accordingly to restore container-capacity weight and the amount of water added at each watering was recorded. Three pots without seedlings for each shade treatment and watering regime were mixed in with the other seedling pots, weighed, and watered periodically in the same manner as the respective pots containing seedlings in order to estimate pot evaporation. Water use for each plant between bimonthly weighings was calculated as the change from initial weight of watered pots containing seedlings plus the amount of water added during the interval minus the water loss of the corresponding check pots lacking seedlings. The water in the system due to increasing seedling weight was not considered because it constituted an insignificant proportion of transpired water.

The dry weights of seedlings at the beginning of the treatment period were estimated by destructively sampling a second set of three seedlings of each species just prior to treatment initiation. Initial estimated dry weights of seedlings were increased according to mean proportionate increase in dry weight calculated for the samples of the respective oak species. The proportionate increase in dry weight for a species did not vary by more than 4% from the mean proportion. A change in whole plant dry weight for the final two-month treatment period was estimated by subtracting the estimated dry weights of seedlings at the beginning of the treatment period from the final dry weights. A water use efficiency value was calculated from the estimated change in whole plant dry weight divided by the estimated water use over the final 2 month treatment period.

The pots that were allowed to dry for the drought regime were weighed every 2-3 weeks after the initial 2-week acclimation period and watered with measured amounts of tap water when needed to maintain 25-30% relative water capacity (RWC), which was found to be at or just above that which caused partial stomatal closure in red, white and bur oak seedlings grown under the same conditions (unpublished data). This range also corresponds to predawn leaf water potentials of the same red, white, and bur oak seedlings, of -1.0 ± 0.3 MPa determined with the use of a pressure bomb (Soilmoisture Plant Water Status Console Model 3005, Santa Barbara, California).

The artificially imposed drought regime lasted for two months. Approximately 1 month was necessary to reach 25-30% RWC and seedlings were maintained for an additional month under mild drought conditions of -1.0 ± 0.3 MPa predawn seedling water potentials. The final seedling heights and calipers were also measured at this time. Then all seedlings were harvested by gently washing the soil mixture from the roots in water and root, shoot, and foliage fresh and oven-dry (70°C for 24 h) weights were determined.

Analysis of variance was used to determine variation due to species, shade and irrigation regimes in a 4x3x2 factorial treatment design with the use of the General Linear Models procedure of SAS (SAS Institute 1982). The experimental design was a systematic split-split

plot with shade as main plots and species and irrigation as subunits and sub-subunits respectively. Individual seedlings were randomly assigned to sub-subunits and rerandomized twice during the treatment period. Interactions between these three variables were also included in the model. Scheffe's multiple-comparison procedure was used to determine differences of all main effects (Steel and Torrie 1980).

The number of flushes (foliar growth and expansion between periods of bud set) per tree were also tabulated throughout the study. Specific leaf area was determined at the end of this study by cutting a total of 60 leaf discs 1-cm in diameter (from fully expanded leaves randomly selected from seedlings in each of six shade x drought treatments) for each species and determining the oven-dry weights. The total area of the leaf discs were then divided by the total dry weight to obtain the specific leaf area (cm²/g).

RESULTS

Irradiance

Growth of oak seedlings of all species combined varied significantly with irradiance levels (Tables 1 and 2). Mean dry weight increment, caliper increment, root and shoot dry weights, and water use efficiency decreased significantly as shade levels increased from 30% to 73%. The shoot/root ratio increased as shade levels increased from 55% to 73%. The caliper increments were similar for the 55% and 73% shade levels, which were 20 percent less than those at the 30% shade level. The mean dry weight increment at the 73% shade level was 56 and 42 percent less than at the 30% and 55% shade levels respectively. The water use efficiency declined 42 percent between the 30% and 73% shade levels. Shading had no significant effect on leaf dry weight or height increment.

The effect of irradiance, or shade levels, on white oak followed the same trends as for the regression model with species and irrigation levels pooled, except that shading did not affect the shoot/root ratio (Table 3). The dry weight increment for white oak was 83% less at the 73% shade level compared with the 30% shade level. There were consistent increases at the 55% shade level for shoot, root and stem dry weight. The increases were not statistically significant, however, but may have been due to an intermediate-shade reduction of evapotranspiration.

The effect of irradiance on the growth and water use of swamp white oak differed from the overall pattern for all oak species combined in that only mean dry weight increment, root dry weight and shoot dry weight were affected. The mean dry weight increment declined 52 percent from the 30% to the 73% shade level. The root and shoot dry weights were least, though not significantly so, at the intermediate (55%) shade level (Table 4).

Table 1.--Analysis of variance for growth and water use variables of four oak species grown under wet and dry irrigation regimes and three shade levels.

Source of variation	Degrees of freedom	Mean squares for						
		Dry Wt. Increment	Water Use Efficiency	Root Dry Wt.	Stem Dry Wt.	Leaf Dry Wt.	Top Dry Wt.	
Oak Species	3	87.76*	27.90**	6144.32**	583.94**	108.56**	1176.32**	
Shade Regime	2	288.67**	25.25**	358.49**	30.40**	15.57	70.52*	
Spec. x Shade.	6	70.95*	7.12	214.96**	24.60*	10.79	62.90**	
Irrigation Regime	1	1331.51**	78.48**	1131.52**	9.78	43.29**	94.21*	
Spec. x Irr.	3	26.61	14.43**	75.55	0.64	1.50	3.20	
Shade x Irr.	2	149.76**	4.52	45.40	5.20	4.81	18.53	
Spec. x Shd. x Irr.	6	21.73	0.90	24.27	2.73	2.63	9.87	
Error	256	29.77	3.68	44.65	4.46	5.51	16.66	

Source of variation	Mean squares for		
	Shoot/Root Ratio	Caliper Increment (x1000)	Height Increment
Oak Species	1.91**	18.54**	79.01
Shade Regime	0.23*	1.73**	60.89
Spec. x Shade.	0.17*	1.36**	79.65
Irrigation Regime	2.66**	7.81**	16.78
Spec. x Irr.	0.20*	1.10	77.60
Shade x Irr.	0.05	0.19	89.49
Spec. x Shd. x Irr.	0.06	0.28	54.47
Error	0.06	0.32	55.61

* Significant at the 0.05 level

** Significant at the 0.01 level

Table 2.--Mean growth and water use values for oak seedlings grown at three shadelevels, with four oak species and two soil moisture levels pooled.

GROWTH VARIABLE	PERCENT SHADE		
	30	55	77
Observations (n=)	95	92	93
Dry Weight Increment (g)	6.23 a*	4.66 a	2.72 b
Water Use Efficiency (mg cm ⁻³)	2.45 a	2.11 a	1.42 b
Root Dry Weight (g)	12.80 a	13.30 a	9.42 b
Stem Dry Weight (g)	3.79 a	4.02 a	2.86 b
Leaf Dry Weight (g)	4.47 ns	3.91	3.64
Shoot Dry Weight (g)	8.26 a	7.94 ab	6.51 b
Shoot/Root Ratio (dry weight)	0.75 ab	0.72 b	0.82 a
Caliper Increment (mm)	0.34 a	0.27 b	0.26 b
Height Increment (cm)	15.02 ns	13.72	13.57

* Means within a row followed by the same letter are not significantly different at 0.05 level according to Scheffe's test.

The shoot/root ratio was the only growth variable significantly affected by shading in pin oak and shingle oak seedlings. The shoot/root ratio increased 25 percent from the 55 to 73% shade level for both pin and shingle oak (Tables 5 and 6).

Table 3.--The effects of shade on growth and water use variable means of white oak.

<u>WHITE OAK</u>											
Percent Shade	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC [#]	15	2.78	28.91	7.89	7.12	15.02				
	DR	15	2.27	20.61	6.82	5.41	12.23				
	Mean ⁺	30	2.53a*	24.76a	7.36a	6.27ns	13.62a				
55	CC	14	2.51	33.92	9.74	6.99	16.74				
	DR	15	2.34	24.64	8.41	5.31	13.72				
	Mean	29	2.42a*	29.28a	9.08a	6.15	15.23a				
73	CC	13	0.60	18.82	4.83	4.34	9.17				
	DR	15	0.34	16.64	5.71	4.32	10.03				
	Mean	28	0.47b	17.73b	5.27b	4.33	9.60b				
Percent Shade	Irrigation Level	N	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)					
30	CC	15	13.43	0.52	0.38	13.73					
	DR	15	4.17	0.63	0.038	15.20					
	Mean	30	8.80a	0.57ns	0.38a	14.47ns					
55	CC	14	10.64	0.50	0.24	13.79					
	DR	15	4.09	0.57	0.17	13.63					
	Mean	29	7.36a	0.54	0.20 b	13.71					
73	CC	13	2.32	0.53	0.15	10.74					
	DR	15	0.75	0.60	0.09	10.20					
	Mean	28	1.53 b	0.57	0.12 b	10.47					

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

+ Mean is for the pooled irrigation values at the given shade level.

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

ns Not significant.

Table 4.--The effects of shade on growth and water use variable means of swamp white oak.

SWAMP WHITE OAK									
Shade Level	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)		
30	CC [#]	12	2.55	9.23	2.61	4.54	7.15		
	DR	13	0.98	5.42	2.28	3.12	5.40		
	Mean ⁺	25	1.76 ^{ns}	7.33 ^{a*}	2.44 ^{ns}	3.83 ^{ns}	6.28 ^{ns}		
55	CC	11	1.43	6.55	2.12	2.77	4.89		
	DR	12	0.93	4.07	1.81	2.78	4.59		
	Mean	23	1.18	5.31 ^b	1.97	2.78	4.74		
73	CC	14	1.44	7.06	2.06	3.21	5.27		
	DR	11	1.14	4.86	2.76	2.76	4.94		
	Mean	25	1.29	5.96 ^{ab}	2.12	2.98	5.10		

Shade Level	Irrigation Level	N	Dry WL increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC	12	8.81	0.79	0.27	19.29
	DR	13	1.63	1.01	0.03	16.65
	Mean	25	5.22 ^a	0.90 ^{ns}	0.15 ^{ns}	17.97 ^{ns}
55	CC	11	3.89	0.75	0.14	9.86
	DR	12	1.70	1.16	0.05	17.12
	Mean	23	2.79 ^{ab}	0.96	0.10	13.49
73	CC	14	3.05	0.75	0.24	13.78
	DR	11	1.93	1.08	0.01	14.95
	Mean	25	2.49 ^b	0.91	0.12	14.37

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

+ Mean is for the pooled irrigation values at the given shade level.

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

ns Not significant.

Table 5.-The effects of shade on growth and water use variable means of pin oak.

PIN OAK										
Percent Shade	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)			
30	CC ^a	10	2.88	9.67	2.99	3.52	6.52			
	DR	10	1.57	5.05	1.76	2.42	4.18			
	Mean ^b	20	2.22 ^{ns}	7.36 ^{ns}	2.38 ^{ns}	2.98 ^{ns}	5.35 ^{ns}			
55	CC	10	2.47	8.12	2.07	3.28	5.36			
	DR	10	1.14	5.02	1.67	2.62	4.29			
	Mean	20	1.81	6.57	1.87	2.95	4.82			
73	CC	10	2.14	6.66	1.84	3.28	5.12			
	DR	10	1.67	4.35	1.88	3.36	5.24			
	Mean	20	1.91	5.50	1.86	3.32	5.18			

Percent Shade	Irrigation Level	N	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC	10	8.42	0.68	0.56	15.85
	DR	10	2.11	0.82	0.51	10.25
	Mean	20	5.26 ^{ns}	0.75 ^{b*}	0.54 ^{ns}	13.05 ^{ns}
55	CC	10	6.23	0.66	0.60	14.60
	DR	10	1.70	0.82	0.36	13.05
	Mean	20	3.96	0.74 ^b	0.42	13.82
73	CC	10	4.40	0.77	0.63	14.40
	DR	10	2.55	1.22	0.44	16.30
	Mean	20	3.48	1.00 ^a	0.54	15.35

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

+ Mean is for the pooled irrigation values at the given shade level.

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

ns Not significant.

Table 6.--The effects of shade on growth and water use variable means of shingle oak.

SHINGLE OAK											
Shade Level	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)	Dry Wt. Increment (g)	Shoot/Root Ratio	Caliper Increment (mm)	Height Increment (cm)
30	CC [#]	10	5.08	8.33	1.53	4.39	5.92	7.17	0.74	0.33	17.05
	DR	10	1.79	6.14	1.54	3.82	5.35	2.70	0.89	0.32	11.35
	Mean ⁺	20	3.44 ^{ns}	7.24 ^{ns}	1.54 ^{ns}	4.10 ^{ns}	5.63 ^{ns}	4.94 ^{ns}	0.81 ^{ab*}	0.33 ^{ns}	14.20 ^{ns}
55	CC	10	3.91	7.22	1.31	3.09	4.40	4.26	0.62	0.40	14.40
	DR	10	2.09	5.44	1.21	2.86	4.07	3.00	0.74	0.34	13.00
	Mean	20	3.00	6.33	1.26	2.98	4.24	3.63	0.68 ^b	0.37	13.70
73	CC	10	3.61	7.42	1.70	4.38	6.08	6.03	0.81	0.38	16.35
	DR	10	1.29	4.48	1.10	3.23	4.33	1.86	0.99	0.34	14.15
	Mean	20	2.45	5.98	1.40	3.80	5.20	3.93	0.90 ^a	0.36	15.25

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

+ Mean is for the pooled irrigation values at the given shade level.

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

ns Not significant.

Irrigation

Mean growth values for all oak seedlings combined (Table 1) and individual oak species (Table 7) varied significantly with irrigation regimes. Experimentally-imposed drought reduced the mean dry weight increment, root, leaf and shoot dry weights, caliper increment and water use efficiency, while it increased the shoot/root ratio. There were reductions of 65 percent in mean dry weight increment, 42 percent in water use efficiency and 31 percent in caliper increment for all oak species combined over the course of this study. The combined shoot/root ratio mean increased by 22 percent in the drought stressed oak seedlings compared with those at container capacity. Oak height increment was not significantly affected by drought in this study.

Drought decreased the mean dry weight increment of white oak by 67 percent and the dry root weight 25 percent, while it increased the shoot/root ratio by 17 percent relative to seedlings grown with an adequate water supply (Table 7). Drought had no statistically significant effect on water use efficiency, caliper increment, stem, leaf and shoot dry weight, although the values for these variables decreased due to drought at each shade level (Table 3).

The effect of drought on swamp white oak (Table 7) followed the pattern for all oak species combined with the exception that drought did not significantly affect the stem, leaf, and shoot dry weights. Declines were 66 percent in mean dry weight increment, 43 percent in water use efficiency and 87 percent in caliper increment. The root dry weight declined 37 percent and the shoot/root ratio increased 42 percent relative to well-watered swamp white oak seedlings. Growth and water use values declined with drought, while shoot/ratio increased with drought for all shade levels and stem dry weight increased with drought at the 73% shade level (Table 4). Under the drought regime, water use efficiency increased with shade, but this interaction was not significant.

For pin oak, drought had no detectable effect on stem, leaf, and shoot dry weights (Table 7). Reductions of 67 percent in mean dry weight increment, 42 percent in water use efficiency, 27 percent in caliper increment and 41 percent in root dry weight occurred relative to well watered pin oak seedlings. The mean shoot/root ratio increased 30 percent overall due to drought.

The effect of drought on shingle oak (Table 7) was to decrease the mean dry weight increment by 57 percent and water use efficiency by 59 percent. The dry root weight declined 30 percent and the shoot/root ratio increased 21 percent with drought. Decreases in all variables except shoot/root ratio were found due to drought at all shade levels (Table 6). Shoot/root ratio increased due to drought at each shade level.

A shade x irrigation interaction occurred for the mean dry weight increment of swamp white oak. The mean dry weight increment decreased with shade at container pot capacity, but increased (non-significant) with shade under the drought regime (Table 8).

Table 7.--The effects of drought on the growth and water use of white (WO), swamp white oak (SWO), pin oak (PO) and shingle oak (SO).

Species	Irrigation Level	N	Water Use Efficiency	Root Dry Weight (g)	Stem Dry Weight (g)	Leaf Dry Weight (g)	Shoot Dry Weight (g)
WO	CC#	42	1.96ns	27.45*	7.56ns	6.22ns	13.78ns
	DR	45	1.65	20.63	6.98	5.01	11.99
SWO	CC	37	1.79*	7.61*	2.26ns	3.51ns	5.77ns
	DR	36	1.01	4.80	2.09	2.90	4.99
PO	CC	30	2.50*	8.15*	2.30ns	3.36ns	5.66ns
	DR	30	1.46	4.81	1.77	2.80	4.57
SO	CC	30	4.20*	7.68*	1.51ns	3.95ns	5.46ns
	DR	30	1.73	5.35	1.28	3.30	4.58
MEAN	CC	139	2.53*	13.74*	3.71ns	4.39*	8.10*
	DR	141	1.46	9.97	3.41	3.64	7.05

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

* Means within the column pair for an oak species are significantly different at 0.05 level according to the F-test.

ns Not significant.

Table 7 (Cont'd).--The effects of drought on the growth and water use of white (WO), swamp white oak (SWO), pin oak (PO) and shingle oak (SO).

Species	Irrigation Level	N	Dry Wt. Increment (g)	Shoot Root Ratio	Caliper Increment (mm)	Height Increment
WO	CC#	42	9.06*	0.52*	0.30ns	12.82ns
	DR	45	3.00	0.60	0.21	13.01
SWO	CC	37	5.17*	0.76*	0.22*	14.40ns
	DR	36	1.74	1.08	0.03	16.29
PO	CC	30	6.35*	0.70*	0.59*	14.95ns
	DR	30	2.12	0.96	0.44	13.20
SO	CC	30	5.82*	0.72*	0.37ns	15.93ns
	DR	30	2.52	0.87	0.33	12.83
MEAN	CC	139	6.74*	0.67*	0.35*	14.37ns
	DR	141	2.39	0.87	0.24	13.85

CC is the 90-95% container capacity regime, DR is the drought regime (20-25% container capacity).

* Means within the column pair for an oak species are significantly different at 0.05 level according to the F-test.
ns Not significant.

Table 8.--Interaction of shade and drought on the dry weight increment (g) of swamp white oak.

<u>Irrigation</u>	<u>Shade Percentage</u>			
	<u>30</u>	<u>55</u>	<u>73</u>	<u>Mean</u>
Container Capacity	8.81 n=12	3.89 n=11	3.05 n=14	5.17**
Drought Regime	1.63 n=13	1.70 n=12	1.93 n=11	1.74
Mean	5.22 a	2.79 ab	2.49 b*	

* Means within a row followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

** Means in the column are significantly different at 0.05 level according to the F test.

There is a possibility that size and shoot/root ratio may be correlated and that treatments influencing seedling size influenced this ratio. However, the slopes and intercepts of linear regressions of final dry weight and shoot/root ratio were different for irrigation compared with shade treatments. This indicates that the treatments influenced shoot/root ratios independently from any total plant dry weight relationship.

Other variables measured were number of flushes and specific leaf area. Pin oak flushed the most with an average of 2.5, followed by shingle oak (1.9), swamp white oak (1.6), and white oak (1.0) (Table 9). The specific leaf area was greatest in bottomland pin oak (176.1 cm²/g) and swamp white oak (174.8 cm²/g) and lowest for the upland shingle oak (157.7 cm²/g) and white oak (158.7 cm²/g).

DISCUSSION

The results of this study are consistent, for the most part, with the findings of Musselman and Gatherum (1969), who found that stem, leaf, shoot, and root dry weight decreased with shade and with reductions in available soil moisture for northern red oak seedlings. In contrast with the Musselman and Gatherum results, we did not find any significant increase in height of four oak species with increased shade. Increases in shoot/root ratio with decreases in soil moisture were also reported by Gatherum *et al.* (1963) for species of two hardwood and three coniferous seedlings. Norby and O'Neill (1989) reported a greater water use efficiency for white oak (6.3 mg cm⁻³) than our overall mean (1.81 mg cm⁻³). However, this discrepancy may be due to their use of first year seedlings rather than third year seedlings from bare-root nursery stock as employed in this study.

Table 9.--The effect of irrigation regime on the observed number of flushes of four oak species.

Species	Container Capacity	Observed Flushes		Range
		Drought Regime	Mean	
White oak	1.00	1.01	1.00	1-2
Swamp white oak	1.68	1.61	1.64	1-3
Pin oak	2.70	2.30	2.50	1-4
Shingle oak	2.00	1.77	1.90	1-3

White oak is generally considered intermediate in shade tolerance and is more tolerant than the red oaks (Fowells 1965). Swamp white oak, a member of the white oak group, is also considered intermediate in shade tolerance (Fowells 1965). Pin oak, in the red oak group, is a common associate of swamp white oak. However, pin oak is considered to be intolerant of shade and it is recommended that pin oak receive at least 2/3 of full solar irradiance for successful regeneration (Fowells 1965). Shingle oak, another member of the red oak group, occurs on a variety of sites, from dry upland ridges to rich and moist river bank soils (Iles 1988). Although there is little published research on the biology of shingle oak, it is considered to be somewhat intolerant of shade (Elias 1980).

In this study (Tables 3 and 4), 55% shade did not markedly reduce growth or water use efficiency of the white oaks relative to 30% shade. However, reduction in irradiance caused by the 73% shading did reduce growth and water use efficiency significantly in comparison with lower shade levels. Hence, increases in solar irradiance above 45% will probably not benefit growth as markedly as decreases in solar irradiance below 45% will inhibit growth. This study revealed few differences among shade levels between 30 and 73% on growth and water use efficiency of shingle and pin oak (Tables 5 and 6) in comparison to the white oaks.

Although shingle oak and pin oak are considered shade intolerant, the only response these species exhibited to the tested shade levels was to increase shoot/root ratio with shade (Tables 5 and 6). This response is indicative of shade intolerant trees such as jack pine (*Pinus banksiana*) (Kimmins 1987) and yellow poplar (*Liriodendron tulipifera*) (Loach 1970). Shade intolerant trees show a greater increase in shoot/root ratio as shade increases than do more tolerant species. Newhouse and Madgewick (1968) have found that rapid shoot growth in tree species is associated with intolerance of shade. Other authors have noted that the more tolerant tree species are characterized by the maintenance of a uniform pattern of growth over a wide range of shade (Baker 1945, Loach 1967 and Loach 1970). Consistent with these patterns, shingle oak and pin oak (Tables 5 and 6) showed an increase in shoot/root ratio with increasing shade while the more tolerant white oak and swamp white oak did not (Tables 3

and 4). Additionally, shade intolerant and faster growing shingle oak and pin oak flushed more times than the more tolerant white oak and swamp white oak seedlings. Reich et al. (1980) stated that multiple flushes occur in white, bur and post oak seedlings during the spring under conditions of favorable light and moisture, while single flushes occur when unfavorable conditions are present. Shingle oak and pin oak seem to be able to flush repeatedly, and more times than the white oaks, even when conditions are only marginally favorable for growth.

White oak and shingle oak seedlings seem to be more drought tolerant than pin oak and swamp white oak seedlings. Four important characteristics that can be used to help indicate drought tolerance in a tree species are higher water use efficiency, lower shoot/root ratio, lower specific leaf area, and less stem diameter inhibition than drought intolerant species (Gottschalk 1985, Larcher 1980). White oak alone exhibited an ability to maintain similar water use efficiency values under either irrigation regime (Table 7). Under the drought regime, rankings for water use efficiency from highest to lowest were: shingle oak (1.73 mg cm^{-3}), white oak (1.65 mg cm^{-3}), pin oak (1.46 mg cm^{-3}) and swamp white oak (1.01 mg cm^{-3}). The rankings for shoot/root ratio under drought from lowest (most advantageous) to highest were: white oak (0.60), shingle oak (0.87), pin oak (0.96), and swamp white oak (1.08). With moisture and shade treatments combined (no significant differences among them in area to weight ratio), the upland white oak and shingle oak had the lowest specific leaf areas. Such low specific leaf areas are characteristic of drought avoiders (Larcher 1980). Caliper increment or radial stem growth of oaks is much more sensitive to stress and limiting factors than other variables such as height growth (Gottschalk 1985). The bottomland species, pin oak and swamp white oak, were the only species that showed a significant decrease in caliper increment due to drought. Swamp white oak was the most sensitive of the two as its caliper increment declined 86 percent, while pin oak's declined only 35 percent relative to the radial stem growth increments of well watered seedlings.

Under drought conditions, species that maintain a low shoot/root ratio are able to maximize water uptake by having a greater root surface to exploit scarce soil water and minimize evapotranspiration through reduced foliage quantity. Plants with a high water use efficiency under dry soil conditions can more efficiently use available water in producing phytomass (Larcher 1980). The two upland species, white oak and shingle oak, differed in their physiological responses to drought. Overall, white oak had a much lower shoot/root ratio (0.56) than shingle oak (0.80), while shingle oak had a much greater water use efficiency than white oak (Table 10). These differences may reflect different adaptive strategies to drought of these two upland oak species. The more shade intolerant shingle oak, with its high water use efficiency and high shoot/root ratio, is better equipped to compete both on droughty soils and on fertile sites where both soil moisture and irradiance may be limited due to competition from fast growing plants.

The two white oak species in this experiment exhibited higher shade tolerance and lower water use efficiencies than the two red oak species studied.

Pin oak and shingle oak are species which inhabit sites that may experience flooding and drought during the same growing season. Thus high water use efficiencies may be a

Table 10.--Sources of variation among species, with shade and irrigation levels pooled.

Species	Water Use Efficiency (mg cm ⁻³)	Shoot/Root Ratio	Caliper Increment (mm)
White oak	1.81 b*	0.56 c	0.24 c
Swamp white oak	1.41 b	0.92a	0.12 d
Pin oak	1.98ab	0.83ab	0.52a
Shingle oak	2.96a	0.80 b	0.35 b

* Means within a column followed by the same letter were not significantly different at 0.05 level according to Scheffe's test.

physiological adaptation allowing pin and shingle oaks to grow on sites with alternating wet and dry periods. High water use efficiencies and high shoot/root ratios together allow a tree to compete well for solar radiation while at the same time efficiently using limited soil water resources on good sites where vegetative competition is great. Our results indicate that shingle oak is better able to maintain a high water use efficiency under drought conditions in comparison with pin oak. Furthermore, shingle oak does not drastically increase its shoot/root ratio in response to drought as does pin oak. This may be due in part to the coarse root system of shingle oak which is more sensitive to stress than the highly fibrous root system of pin oak (Struve and Moser 1984). Shingle oak is found more on dry upland sites than is pin oak, perhaps owing to the noted differences in functional and structural response to drought between these two species.

Of the white oaks, swamp white oak seems to be the most site specific. It had the lowest water use efficiency and highest shoot/root ratio for any of the oak species in this study (Table 10). This is consistent with its natural occurrence on poorly drained-upland depressions, swamp margins, stream banks and moist, peaty flats (Fowells 1965), sites which rarely undergo drought. Swamp white oak exhibited an irradiance x drought interaction (Table 8) in that at container water capacity the dry weight increment decreased with shade, but increased with shade under drought conditions. This interaction is probably due to a reduction in evapotranspiration of this midtolerant oak species caused by shade under drought conditions.

The extension of these data to ecological behavior of these oak species requires caution. In a forest not only is the quantity of light changed, but also the quality of light as the overstory canopy differentially absorbs and transmits various wavelengths of PAR and other solar radiation. Also, frequent dieback or browsing of advance oak regeneration will influence shoot/root ratios in the field. Hence the results of this study relate more to early establishment and growth of oak seedlings in forest understories than to the longer-term

patterns of growth and development of advance oak regeneration, and should be extrapolated to field conditions with caution until confirmed by field studies.

SUMMARY

This study has shown that both increasing shade and drought decrease the growth and water use efficiency of four oak species of the central United States. Overall, the red oaks (shingle and pin oak) had the highest water use efficiencies and flushed more than white oak and swamp white oak, consistent with the generally faster juvenile growth rates of intolerant species. Shingle and pin oak also increased markedly in shoot/root ratio in response to shade, which is a characteristic of shade intolerant trees. Swamp white oak and white oak have the characteristics of midtolerant species, maintaining similar shoot/root ratios under a range of intermediate shade levels, exhibiting fewer flushes and smaller caliper increments overall in comparison with the two red oaks.

Under drought conditions, white oak and shingle oak had the lowest shoot/root ratios, highest water use efficiencies and smallest specific leaf areas, appropriate to their observed ability to grow on dry sites. However, both white and shingle oaks seem to have broad ecological amplitudes with respect to soil water availability, growing on mesic sites and, in the case of shingle oak, also on moist soils and on poorly drained flats with pin oak and post oak. Pin oak, which was between white oak and swamp white oak in shoot/root ratio and water use efficiency values under drought conditions, and similar to swamp white oak in specific leaf area, occurs in bottomland areas subject to flooding and in pin oak-post oak flats with a fragipan creating alternating wet and dry conditions. Swamp white oak and pin oak, the bottomland species, were the only ones to exhibit a significant decrease in caliper increment with drought. Swamp white oak was the most sensitive of the four oak species to drought, consistent with its ecologically narrow niche of moist sites.

This study examined two of the most important factors influencing forest regeneration, irradiance and soil moisture. The results indicate that the two white oaks were more shade tolerant than the two red oaks and will, therefore, more successfully survive in smaller openings and under denser canopies than pin and shingle oak. The data show a tendency suggesting that on sites where soil moisture may be limiting part of the season, shade levels from 55-73% may reduce evapotranspiration and increase growth of swamp white oak seedlings compared with more open conditions on the same site. Shingle oak may be a suitable native tree for minespoil reclamation and urban planting due to its drought tolerance and high water use efficiency described in this study combined with its moderately fast growth rate, mast production for wildlife and tolerance of wide pH ranges (Iles 1968).

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HEIGHT AND DIAMETER VARIATION IN TWELVE WHITE ASH PROVENANCE/PROGENY TESTS IN EASTERN UNITED STATES

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Abstract: Results from 12- and 13-year-old rangewide provenance/progeny tests of white ash (*Fraxinus americana* L.) planted at 12 locations throughout the eastern United States are reported. Although heritability of white ash tree height and dbh is high at both the provenance and family levels, the trend in variance components is for increasing provenance and declining family components. Tree height is negatively correlated with latitude in southern outplantings and positively correlated with latitude in the north. Plantations with the tallest trees were those that had been clean cultivated for several years after establishment.

INTRODUCTION

Rangewide provenance/progeny tests of white ash (*Fraxinus americana* L.) were established in 1976 and 1977 with plantings at more than 20 locations throughout the eastern United States and Canada. The study was initiated because of the increased importance and value of the white ash. Several papers have reported early growth and survival results from that study, including preliminary white ash seed source recommendations for planting in different parts of the geographic species range (Bey et al. 1977, Clausen 1982, Clausen 1984, Clausen et al. 1981). Summarizing those early recommendations, at age 5 northward movement of seed or seedlings not exceeding 322 km (200 miles) generally resulted in some growth increases over local plant material, except in the northernmost parts of the species range where only local seed sources should be used. This paper reports growth results through age 13.

MATERIALS AND METHODS

Open-pollinated seeds were collected from up to 10 native parent trees at each of 59 locations throughout the natural range of white ash in 1973 and 1974 and then sown in a southern Illinois nursery (Bey et al. 1977, Clausen et al. 1981). Resulting 1-0 seedlings were used to establish 22 plantations throughout the eastern United States and Canada in 1976. By the 1988-1989 dormant season, when these data were collected, many personnel changes, budget

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constraints, and shifts in program emphasis among cooperating agencies had resulted in abandonment of test sites in northern Alabama, Tennessee, New York, and Ontario, Canada. In other cases, high tree mortality and poor growth precipitated abandonment of plantings in Minnesota, northern Wisconsin, and Missouri, as well as plantings in Ontario and New Brunswick, Canada. As a result, 13-year measurements were only available from 10 plantations; this paper is based on height and dbh data from trees 13 years after outplanting in those 10 plantations in addition to two plantings that were established 1 year later (Nebraska and Michigan) and from which measurements reflected growth 12 years after outplanting. The latter two provenance outplantings were established in 1977 with surplus stock after seedling distribution to the 1976 planting sites. Unfortunately, there were not enough seedlings of different open-pollinated families for a progeny test, and family identity of seedlings at the Michigan and Nebraska sites was not retained.

The number of provenances in each plantation ranged from 16 in Alabama to 35 in the Michigan plantation, and the number of families per plantation ranged from 39 to 52 (table 1). The geographic origins of the families also varied from plantation to plantation. Most plantations contained families from portions of the range near their particular geographic location in order to minimize mortality of more distant, nonadapted trees. Three plantations (OH, AL, and IL) were designed to have 45 families from 19 widely separated provenances in common so provenance x environment interactions could be evaluated. All plantations were established in a randomized complete block design with five-tree row plots and five replications at a spacing of 3.7 m except in OH where a completely random design (no blocks) was used.

Table 1.--Location of plantations and number of white ash provenances and families in each¹

Plantation (state)	County	Latitude °N	Longitude °W	Number of provenances	Number of families
Ohio (OH)	Muskingum	40.0	82.0	21	49
Alabama (AL)	Macon	32.4	85.6	16	42
Illinois (IL)	Union	37.5	89.3	26	52
Kentucky (KY)	Rowan	38.2	83.4	23	43
West Virginia (WV)	Tucker	39.0	79.7	22	45
Kansas (KS)	Jefferson	39.0	95.2	27	44
Louisiana (LA)	St. Landry	30.4	92.0	19	45
Indiana (IN)	Crawford	38.2	86.3	22	39
Arkansas (AR)	Montgomery	34.6	93.6	18	42
Wisconsin (WI)	Iowa	43.0	90.1	24	40
Michigan (MI)	Kalamazoo	42.3	85.3	35	--
Nebraska (NE)	Adams	40.5	98.3	27	--

¹Family identity of seedlings was not retained at the Michigan and Nebraska outplantings.

Differences in performance among provenances and families in each plantation were tested by the General Linear Model analysis of variance technique based on plot means to accommodate missing data. Variance components were calculated for between- and within-provenance comparisons. When appropriate, correlation and regression analyses were used to estimate the relationship between tree height and provenance latitude, longitude, and elevation. Data were analyzed using programs of the Statistical Analysis System (SAS Institute 1982).

Table 2.--Plantation averages for height, dbh¹, survival, standard deviations, and ratios of tallest to shortest trees²

Plantation	Height (m)	Standard deviation (m)	Ratio of tallest: shortest	Dbh (cm)	Standard deviation (cm)	Survival (%)	Number of surviving trees
OH	7.7	1.7	2.6	9.4	3.0	62	710
AL	7.0	0.9	1.5	7.9	1.1	97	1025
IL	6.8	1.1	1.7	7.7	2.7	92	1192
KY	4.0	0.7	2.0	4.9	1.2	63	676
WV	3.5	0.7	1.9	3.8	1.2	52	581
KS	3.2	0.6	2.0	3.2	0.9	93	1031
LA	3.0	1.3	5.0	2.7	1.5	74	829
IN	3.0	1.0	7.2	---	---	69	670
AR	2.9	0.8	3.2	3.3	1.4	50	525
WI	2.5	0.5	2.0	2.5	0.7	57	570
MI	5.7	0.6	2.0	5.8	0.9	83	726
NE	3.3	0.5	1.9	4.5	0.8	56	375

¹ Dbh data for the Indiana outplanting were not available.

² Michigan and Nebraska data reflect age 12 measurements. Data for all other plantations reflect age 13 measurements.

RESULTS AND DISCUSSION

After 13 years in the field, survival ranged between 97% and 50% (table 2). Average height of white ash trees ranged from 2.5 m at the southern Wisconsin site to 7.7 m in Ohio (table 2), a threefold difference in height growth between outplantings with the slowest and fastest growth, respectively. As observed earlier by Clausen (1984), the three plantations with the fastest growth (OH, AL, and IL) were all clean cultivated during the first 2 to 3 years after outplanting. The implication is that white ash is extremely sensitive to competition from weeds and brush during the early establishment phase and that the effects of plantation maintenance persist for a long time thereafter.

The trend in diameters at breast height (dbh) closely mirrors the pattern in tree height; as expected, on the average the tallest trees tend to have the greatest diameters (table 2). The overall correlation of height with dbh was 0.78. The height-to-height ratios for the of tallest to shortest provenances ranged from 1.5 at the Alabama plantation to 7.2 at the Indiana plantation (table 2).

Analysis of variance for height and dbh indicates a predominance of statistical significance, as indicated by probabilities of greater F-values (table 3). The provenance effect was statistically significant at all outplanting sites for both height and dbh at age 13 (table 3). In an earlier report on this study, the provenance effect for height was nonsignificant at the Indiana, Kansas, and Wisconsin locations at age 5 (Clausen 1984). By age 13 this effect had become significant at all sites, including the latter three. However, statistical significance for the family effect was less common than for the provenance effect.

Table 3.--Probabilities of greater F-values in analyses of variance of white ash height and dbh.

Plantation	Block		Provenance		Family/provenance	
	Height	Dbh	Height	Dbh	Height	Dbh
OH	----	----	0.0001	0.0001	0.0003	0.0001
AL	0.0015	0.0015	0.0001	0.0001	0.0001	0.0001
IL	0.0001	0.0001	0.0001	0.0001	0.0016	0.0001
KY	0.0341	0.0154	0.0001	0.0001	0.0472	0.0069
WV	0.0675	0.2821	0.0001	0.0001	0.1143	0.0664
KS	0.0160	0.0581	0.0001	0.0001	0.0001	0.0001
LA	0.6123	0.9030	0.0001	0.0001	0.0066	0.0007
IN	0.3288	----	0.0002	----	0.3273	----
AR	0.0001	0.0001	0.0001	0.0008	0.9708	0.4687
WI	0.0002	0.0002	0.0001	0.0001	0.8768	0.9363
MI	0.0001	0.0001	0.0001	0.0001	----	----
NE	0.0001	0.0002	0.0001	0.0057	----	----

Provenance variance components for height (table 4) appear to be increasing; the overall mean provenance component averaged over all locations increased from 28.6% at age 3 to 38.5% at age 13, although this trend was not consistent at all sites. For example, at the Kentucky site the provenance component decreased from 30% at age 3 to 14% at ages 5 and 13. In Kansas, this component increased from 4% at age 3 to 18% at age 5 and dropped to 10% by age 13.

At the latest measurement the provenance component was greater than the family component at all but two locations for height and at all but one location for dbh. For both height and dbh the mean provenance component was more than three times greater than the family component at age 13. In contrast to the trend for increasing provenance components, family

variance components for height appear to be declining in magnitude; the mean family component decreased from 11.9% of total variance at age 3 to 7.5% at age 13 (table 4).

Table 4.--Provenance and family-within-provenance variance components as a percent of total variation and heritabilities for age 13 height and dbh¹

Plantation	Height						Dbh		Heritability			
	Provenance			Family			Prov.	Fam.	Height		DBH	
	Age (yrs)			Age (yrs)			Age (yrs)		Prov.	Fam.	Prov.	Fam.
	3	5	13	3	5	13	13	13	Prov.	Fam.	Prov.	Fam.
	----- % -----			----- % -----			----- % -----					
OH	24	43	17	5	1	5	22	4	0.82	0.56	0.85	0.60
AL	51	65	68	12	9	0	46	9	0.96	0.75	0.91	0.77
IL	64	60	46	6	12	4	68	3	0.91	0.54	0.96	0.61
KY	30	14	14	6	2	16	15	20	0.77	0.38	0.80	0.51
WV	17	28	47	17	4	0	40	5	0.90	0.29	0.88	0.34
KS	4	18	10	17	26	31	10	37	0.79	0.74	0.80	0.81
LA	57	67	75	8	7	3	64	8	0.97	0.48	0.96	0.57
IN	0	0	28	30	10	16	--	--	0.87	0.12	--	--
AR	30	21	25	18	20	0	27	0	0.73	0	0.63	0
WI	9	6	57	0	13	0	47	0	0.87	0	0.80	0
mean	28.6	32.2	38.7	11.9	10.4	7.5	37.6	10.8	0.86	0.39	0.84	0.47

¹ Variance components for ages 3 and 5 previously published by Clausen (1984).

Heritabilities for height and dbh (table 4) indicate that a great deal of variation in these plantations is heritable. The mean provenance heritability of 0.81 to 0.85 is the same order of magnitude observed for loblolly pine (*Pinus taeda*) of this age and indicates that most of the variation among provenances can be utilized for growth improvement (Kung 1989). Similarly, the mean family-within-provenance heritability of 0.39 to 0.47 is consistent with heritability values for height in black walnut (Rink 1984, Rink and Clausen 1989).

Combined location analyses of variance across all planting sites indicated significant provenance x plantation location interactions for both height and diameter. These interactions imply that provenance selection for optimum growth at different geographic localities and perhaps for specific sites within localities may be important for artificial regeneration of white ash. Because these combined location ANOVA's were so highly imbalanced, variance component extraction from them would produce variance components less precise than would be possible from a completely balanced design. To aid in interpreting the interaction, we used an individual location response surface model with linear and quadratic provenance latitude and longitude and their crossproducts as independent variables; response surface regressions are commonly used to model genotypic response to environment. Results of these

CONCLUSIONS

Clausen (1984) pointed out the beneficial effects of plantation maintenance during the plantation establishment phase of this study. Present results confirm those observations. Perhaps fewer test plantings would have been abandoned if more plantation maintenance had been available.

Present 13-year data indicate that height growth improvements of 25 to 30% on sites with good growth and more than 50% on sites with poor growth may be obtained through proper provenance selection. Seed source recommendations made by Clausen (1984) are still applicable. This is further emphasized by significant provenance x site interactions.

The predominance of statistical significance for provenance effects for height and diameter and the magnitude of provenance variance components indicate the importance of proper provenance selection in artificial regeneration programs for white ash. High heritabilities, based on open-pollinated half-sib family variance components, indicate that individual tree selection is also effective in white ash. However, the latter variance components are relatively low and seem to be declining in magnitude with age. Because variance components follow fluctuating patterns that are probably species specific, we will have to track these patterns to determine how effective individual tree selection is at different ages.

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STOMATAL CONDUCTANCE OF SEEDLINGS OF THREE OAK SPECIES
SUBJECTED TO NITROGEN FERTILIZATION AND DROUGHT TREATMENTS

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Abstract: Both nitrogen-fertilized and unfertilized white oak, bur oak, and red oak seedlings were subjected to progressive drought in a greenhouse study. Stomatal conductance was measured before and during drought treatment. When water was not limiting to seedling growth and function, N-fertilized white oak showed greater maximum stomatal conductance ($200 \text{ mmol m}^{-2} \text{ s}^{-1}$) compared to N-deficient white oak ($74 \text{ mmol m}^{-2} \text{ s}^{-1}$). Neither bur oak nor red oak showed any discernible differences in stomatal conductance between fertilization treatments before imposition of drought. During drought, N-limited red oak maintained greater stomatal conductance at a lower soil relative water content compared to N-fertilized red oak. N-fertilized bur oak decreased stomatal conductance partially during moderate drought and ceased conductance completely during extreme drought, whereas N-deficient bur oak maintained high levels of conductance during moderate drought and halted conductance precipitously during severe drought. No discernible difference between N-fertilization treatments was found for white oak stomatal conductance during drought. Red oak and white oak seedlings exhibited lower stomatal conductance values less readily and under drier soil conditions than did bur oak, suggesting superior drought adaptability of bur oak.

INTRODUCTION

Stomatal conductance represents a compromise between carbon assimilation and excessive water loss by transpiration (Ludlow 1980). Mineral nutrient status may directly affect rates of photosynthesis by altering the content and function of key metabolites and enzymes and may also have indirect effects by altering stomatal responses. Nutrient deficiency may increase or decrease stomatal sensitivity to soil moisture availability (Radin *et al.* 1982; Lahiri 1980; Wang *et al.* 1988). Thus, the stomatal and photosynthetic response to drought for a given species may be altered by nutrient status.

White oak (*Quercus alba* L.), red oak (*Q. rubra* L.), and bur oak (*Q. macrocarpa* Michx.) are oaks of the central hardwood region. Bur oak traditionally has been characterized as drought-tolerant and the most xeric of the three species, though it is bimodal in distribution

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occurring on both mesic and xeric sites (Abrams 1986), while white and especially red oak are regarded as more exclusively mesic (Fowells 1965).

We examined the effects of two nitrogen regimes on stomatal conductance of bur, red, and white oak seedlings during the progressive soil drying of an artificially imposed drought.

METHODS

Fifty 2-0 bare-root dormant seedlings of each of red oak, white oak, and bur oak were planted in a steam-sterilized 1:1:1 loamy soil:vermiculite:peat moss mix in 60 cm tall by 10 cm wide cylindrical pots. Half of the plants of each species were given 200 ml of N-free 1/4 strength modified Hoagland's solution weekly and the other half were given the same plus 5 ppm N as NH_4NO_3 . Plants were watered daily. After sixteen weeks in the greenhouse (26° day, 18° night, photoperiod extended to 16 h by sodium vapor lamps) drought was imposed by withholding water.

The results of a preliminary study indicated that the plants reached their daily maximum level of stomatal conductance between 1000 and 1100 local standard time; therefore all stomatal conductance measurements were made between those hours. Plants were sampled randomly. Stomatal conductance was measured on the abaxial leaf surface with a steady state diffusion porometer (LI-1600 Li-Cor, Lincoln, NE); relative humidity varied between 15 and 30% on the days when measurements were taken. Predawn leaf water potential was measured on a subsample of fully-expanded leaves with a pressure chamber (# 3000 Soil Moisture Corp., Santa Barbara, CA) at 0300-0400 the morning following stomatal conductance measurements. This allowed us to determine the relationship between soil relative water content and soil water potential estimated as predawn leaf water potential (Nobel 1983). Soil relative water content was determined by weighing the pots during the afternoon of each measurement day and comparing the soil mass of each pot with the saturated (12 h after final watering) soil mass and the dry (constant weight at 70°) soil mass. The formula used to calculate relative water content (RWC) was:

$$\text{RWC} = (\text{fresh mass} - \text{dry mass}) / (\text{saturated mass} - \text{dry mass}).$$

Leaf relative water content was determined but it was not found to differ by species or treatment.

RESULTS AND DISCUSSION

Stomatal response was interpreted by boundary line analysis (Webb 1972) where a line is drawn at the boundary of the maximum stomatal conductance values and all points below are assumed to be limited by some factor other than that of the independent variable (Hinckley et al. 1978). This technique is useful owing to the fact that stomata respond to the complex

interaction of a number of environmental and endogenous factors that could not be controlled during this experiment (e.g. daily variation in solar radiation). Conductance measurements $>10 \text{ mmol m}^{-2}\text{s}^{-1}$ were considered to signify at least partially opened stomates based on our measurements of leaves with completely closed stomates indicating that cuticular conductance for all species was about $3\text{-}8 \text{ mmol m}^{-2}\text{s}^{-1}$.

Stomatal Response with High Soil Moisture

White oak increased its maximum rate of stomatal conductance from 74 to 200 $\text{mmol m}^{-2}\text{s}^{-1}$ when supplied with N fertilizer and water was not limiting (Figures 1*a,b*). This is consistent with the results of Minshall (1975) who found that urea or nitrate stimulated transpiration of tomato, Mingeau and Robelin (1972) who found that N-deficiency decreased transpiration of sunflower, and Nagarajah (1981) who found that N-deficiency of tea caused a decrease in stomatal conductance and transpiration. A general correlation between foliar N and net photosynthesis and stomatal conductance has been reported in an extensive survey of native C_3 plants (Field and Mooney 1986). Neither red oak (Figures 1*c,d*) nor bur oak (Figures 1*e,f*) showed any response to N fertilization treatment when soil moisture levels were high.

Stomatal Response during Drought

White oak +N and -N showed similar responses during drought (Figures 1*a,b*): both N-fertilized and N-deficient plants decreased stomatal conductance suddenly at 22% RWC (-1.8 MPa soil water potential). Red oak stomatal conductance ceased at about 22% RWC (-1.8 MPa) when supplied with N (Figure 1*c*), but continued until 19% RWC (-2.5 MPa) during N-deficiency (Figure 1*d*). This resembles the response of N-deficient beans as described by Shimshi (1970). The response of bur oak is the most distinctive. N-fertilized bur oak accomplished a partial decrease of stomatal conductance at about 33% RWC (-0.5 MPa) and maintained moderately low stomatal conductance to below 20% RWC (-2.1 MPa) (Figure 1*e*). The response of N-deficient bur oak differs; its stomates halted conductance suddenly at about 23% RWC (-1.5 MPa) (Figure 1*f*).

These data suggest a drought adaptation of bur oak seedlings. Under conditions of soil nitrogen availability, bur oak seems to employ a drought avoidance tactic (Jones 1980); the seedlings avoid excessive plant water loss and rapid depletion of limited soil water reserves by closing stomates partially as soil water potential decreases below -0.5 MPa, allowing only a limited level of gas exchange and water loss. These results are similar to those obtained with bur oak under drought conditions in Kansas forests (Abrams and Knapp 1986). This apparent anticipation of extreme drought reflects the ecological performance of bur oak which occurs on droughty sites and soils as well as on more mesic sites which support red and white oak (Fowells 1965).

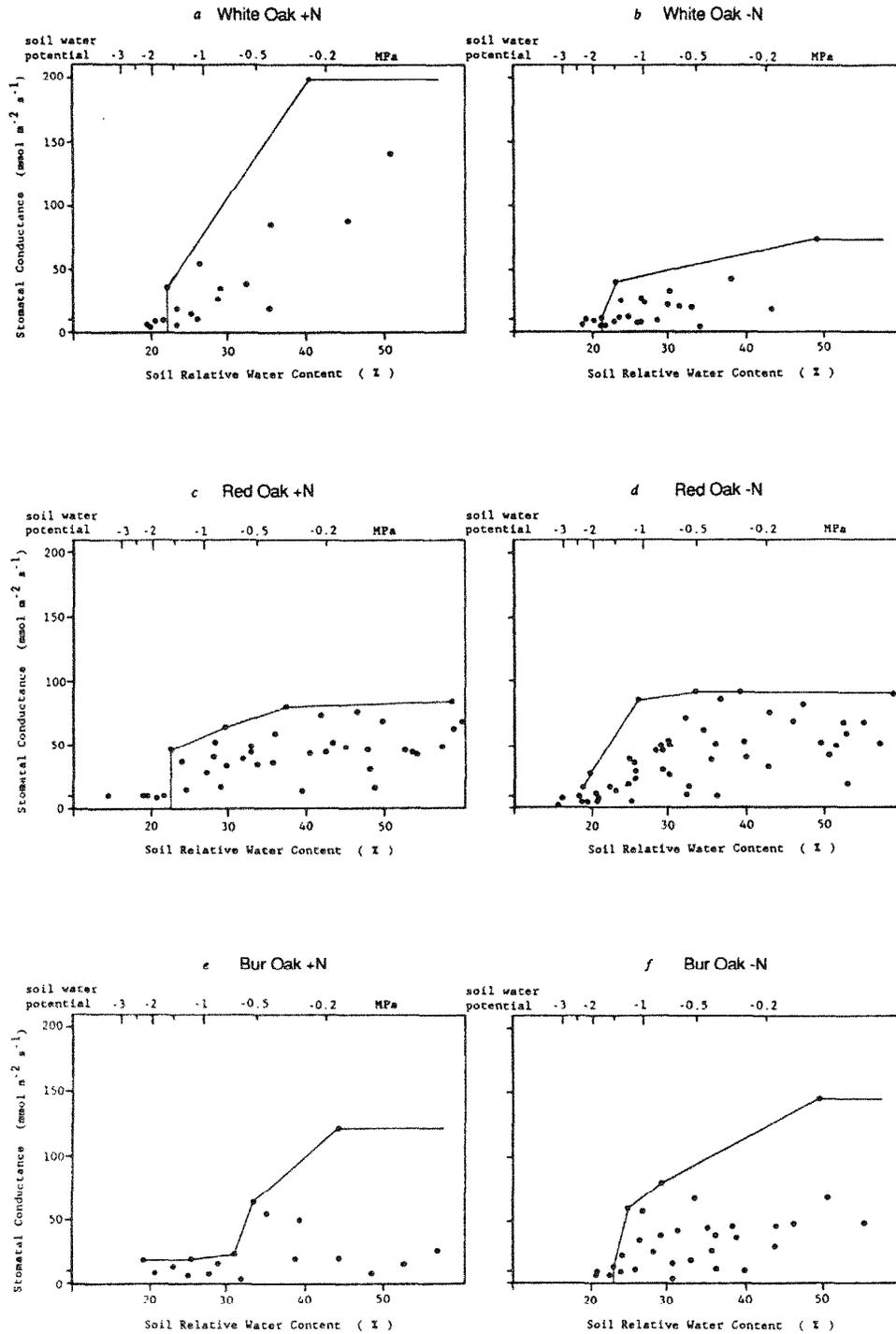


Figure 1. Stomatal conductance of N-fertilized and unfertilized white oak (a,b), red oak (c,d), and bur oak (e,f) seedlings during a progressive drought.

The stomatal conductance data may reflect the fact that white and red oak thrive naturally on more mesic sites than bur oak; on mesic sites stomatal sensitivity to increasing drought is less critical for survival. Bur oak on a mesic site would incur all the disadvantages of an anticipatory response to moderate drought (less capability for photosynthetic gas exchange, slower growth) in exchange for only marginal benefits (water conservation during relatively rare extreme droughts). The tendency of N-deficient red oak to maintain stomatal conductance during extreme drought conditions may indicate that red oak requires N to conserve water. The absence of the drought-adaptive stomatal response in N-deficient bur oak may reflect a nitrogen requirement for the expression of the drought-adaptive response. This suggests a mechanism to explain the seemingly anomalous findings of Abrams (1985) that the growth rate of bur oak trees in Kansas stands was greatest when available soil NH_4 and NO_3 were lowest. Perhaps anticipatory stomatal closing of bur oak with the onset of drought was sufficiently enhanced on soils of greater N fertility in Kansas' dry climate to reduce net photosynthesis and growth of the trees.

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STAND DENSITY, STAND STRUCTURE, AND SPECIES COMPOSITION
IN TRANSITION OAK STANDS OF NORTHWESTERN PENNSYLVANIA

Susan L. Stout¹

ABSTRACT: Transition stands, those containing species associated with both the northern hardwood and oak-hickory forest types, are important to forest diversity in northwestern Pennsylvania. These stands have high value for a variety of forest uses, including timber production, wildlife habitat, and aesthetics. Diameter distributions are characteristically stratified by species, with the most valuable oak species among the largest trees in the stand. Understories typically consist of a mixture of northern hardwood species with those often found in the understory of true oak-hickory stands, such as dogwood, blackgum, and cucumbertree. In this paper, I characterize diameter distributions for transition stands in northwestern Pennsylvania, and discuss their silvicultural implications. Traditional measures of density tend to overestimate the density of such stands. Three alternatives, one based on tree-area ratio and two based on Reineke's stand-density index, are reported.

INTRODUCTION

The forests of the Allegheny Plateau region of northwestern Pennsylvania are dominated by Allegheny hardwood and northern hardwood forest types. Thus stands of the oak-hickory or oak transition forest types are important for diversity to the wood-using industry, to many wildlife species, and to recreationists and conservationists. Stands of the oak transition forest type represent a challenge to managers because they contain a mix of species somewhat different from the classic central hardwood stand. Often, the oak species are among the largest trees in the stand, dominating one or more subordinate canopy layers composed of a mix of traditional oak associates, such as red maple (*Acer rubrum* L.), dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* L.), and hemlock (*Tsuga canadensis* (L.) Carr), and species less often associated with the oaks, such as sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.). These species cover a wide range of growth rates and tolerance to shade, and, in mixture with the oaks, achieve levels of density (numbers of trees or basal area per acre) not usually associated with the oaks. Because these stands are highly stratified by species and the oak species are difficult to regenerate, the consequences of management actions in these stands are quite important.

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The United States Forest Service estimates that 20 percent of the land area of the Allegheny National Forest, or about 100,000 acres, is covered by stands in which oak is an important component (Allegheny National Forest 1986). When stands that had experienced severe mortality as a result of the combination of gypsy moth defoliation and drought were sampled in the late summer and early fall of 1988, approximately one-third of the area sampled was typed as oak transition, while the remainder was typed as oak-hickory (Allegheny National Forest 1989). These determinations were made by analyzing the sample data with the SILVAH computer program.² In SILVAH, oak-hickory stands are defined as those having at least 50 percent of their basal area in oak and hickory species and at least 65 percent of their basal area in oak, hickory, or commonly associated species. Transition hardwoods are those in which at least 25 percent of the basal area is in each of oak and northern hardwood species, and at least 65 percent of the basal area is in these species plus common associates of either. In these stands, it is not uncommon for northern red oak (*Quercus rubra* L.) to be the sole oak species.

The origin of stands of the oak-hickory and oak transition types on the Allegheny Plateau is not as well documented as is the origin of stands of the Allegheny hardwood forest type. The northwestern Pennsylvania Allegheny Plateau region was virtually completely harvested during turn-of-the century logging, resulting in an even-aged forest. Records from logging companies active during the railroad logging era from 1890 through about 1930 show that most of the stands included in this paper probably originated from a sequence of cuttings. The first was for hemlock and desirable hardwood sawtimber during the period from 1894-1912, and the second for smaller and poorer quality trees between 1913-1930 (Casler 1976). This combination of cuttings was usually quite complete, and similar to a shelterwood sequence. Thus these stands are essentially even-aged and about 70 years old.

In the Allegheny Plateau region, oak-hickory and oak transition stands tend to occur near the river basins, where humans have been in residence, and using fire, for many hundreds of years. The influence of humans and fire is believed to have favored the establishment of oak along waterways, due to the tolerance of oak seedlings for fire. Many of these stands still contain old chestnut (*Castanea dentata* (Marsh.) Borkh.) stumps, suggesting that the chestnut blight may have played a role in releasing oak to greater dominance. Transition stands often are on high-quality sites, where the regeneration of oak species suffers from the competition of fast-growing associates like red maple and black cherry (*Prunus serotina* Ehrh.).

In this paper, I report on the diameter distribution and species composition of 21 research plots representative of the mixed oak-northern hardwood stands of northwestern Pennsylvania, and on the changes that occur as a result of various silvicultural strategies. I also report on efforts to assess relative stand density in these stands.

² Marquis, David A., and Richard L. Ernst. in preparation. User's guide to SILVAH: A stand analysis, prescription, and management simulator program for hardwood stands of the Alleghenies.

METHODS

Twenty-one research plots currently under study by staff of the Northeastern Forest Experiment Station's Forestry Sciences Laboratory at Warren in northwestern Pennsylvania were selected for this study on the basis of species composition. These plots were used in a variety of studies focusing on the management of developing stands for timber and aesthetic objectives, but the data reported in this paper are from pretreatment tallies. Plot size ranged from 0.6 to 4.9 acres. Data collected in each stand included a complete tally of all trees 1.0 inches d.b.h. and larger on each plot by species and 1-inch diameter class. All plots had been free of human disturbance but many showed evidence of natural disturbance, especially chestnut stumps. Northern red oak is the principal oak species on these plots; white oak (*Quercus alba* L.) is the other major oak species. All stands met the criteria for stands at average maximum density (Ernst and Knapp 1985), as they showed no evidence of past cutting, little understory development, and mortality was readily observed among the smallest trees.

Data from each plot were summarized into per acre values of numbers of trees, basal area, and sum of diameters and diameters squared. For each plot, both the quadratic mean diameter (QMD, or diameter of the tree of average basal area) and the medial diameter (MD, or diameter of the tree at the mid-point of the basal area distribution), were also calculated. MD is calculated as a weighted average diameter. Each 1-inch diameter is multiplied by the basal area in that diameter class, and the sum divided by the stand basal area. Composite diameter distributions were calculated by averaging per acre values of numbers of trees per diameter class. Statistical analyses were conducted with SYSTAT statistical analysis software (Wilkinson 1988), and a 5% significance level was accepted in all tests.

DIAMETER DISTRIBUTIONS

The characteristics of the individual stands are summarized in Table 1. MD in these stands ranged from 10.3 to 17.0 inches, and the percent of basal area in oak species ranged from 25 to 75.

The frequency distribution of diameters for all of these stands has a roughly inverse J shape. Figure 1 shows the averaged frequency distributions of diameter for each of three groups of these stands, using medial diameter as the grouping variable. Figure 1d is the frequency distribution of diameter from Schnur's (1937) representative stand table for an age 60 oak stand on a site index 60 site, shown here for contrast. Frequently, the inverse J-shaped diameter distribution is associated with uneven-aged stands, but in the even-aged forests of the Allegheny plateau region, many stands have inverse J-shaped diameter distributions because of the persistence of a dense lower canopy layer of shade-tolerant species. In species composition and diameter distribution, the sapling class in these transition oak stands is similar to the shade tolerant understory layer in even-aged Allegheny and northern hardwood stands.

Table 1. Selected characteristics of sample Pennsylvania oak transition stands.

	Minimum	Maximum	Mean +/- Std. Dev.
No. trees/acre	265	920	449 +/- 163
Basal area/acre (ft. ²)	122.3	200.4	154.0 +/- 18.7
Medial Diameter	10.3	17.0	13.5 +/- 1.8
Quadratic Mean Diameter	5.4	11.0	8.2 +/- 1.4
% northern red oak (in basal area)	0	75	40 +/- 18
% oaks (in basal area)	25	75	48 +/- 14

In the smallest diameter stands (Fig. 1a), 46 percent of the sapling (one-inch through five-inch diameter classes) basal area consists of American beech trees, 40 percent of red maple trees, and the remainder consists of birch (*Betula* L.), cucumbertrees (*Magnolia acuminata* L.), sugar maple, and noncommercial species. Average sapling basal area is 17 square feet. The smallest oaks in these stands are 7 inches in diameter, but the pole class (6-inch through 11-inch) is dominated by red maple, which averages 48 percent of the 53 square feet of poletimber. No other species represents more than 11 percent of the poletimber basal area. Among the sawtimber classes (those 12 inches and larger), the oaks dominate, with northern red oak representing 64 percent of the sawtimber basal area.

The pattern for the other two groups is similar. In the medium-diameter stands (Fig. 1b), beech and red maple dominate the sapling class, red maple dominates the pole-size class, and northern red oak dominates the sawtimber-size classes. In the largest diameter stands (Fig. 1c), eastern hemlock dominates the sapling class. Red maple and eastern hemlock are important in the pole-size classes, and northern red oak, red maple, and white oak dominate the sawtimber sizes.

If we look closely at these inverse J curves, we can see them as the curves of three species groups superimposed. The tail of the curve is formed by the inverse J shape of the diameter distribution of shade-tolerant species, while the red maple/intermediate-tolerance species and oak groups each have bellshaped distributions with different means.

If we contrast these patterns with the diameter distribution of Schnur's classic oak stand (Fig. 1d), we see that the overall form as well as the distribution by species is different. This frequency distribution of diameters has a bell shape rather than an inverse J shape, and the distribution for each species group is bellshaped as well. In particular, the shade-tolerant understory species are not as numerous as in northwestern Pennsylvania oak stands, nor does their distribution in the small size classes have an inverse J shape.

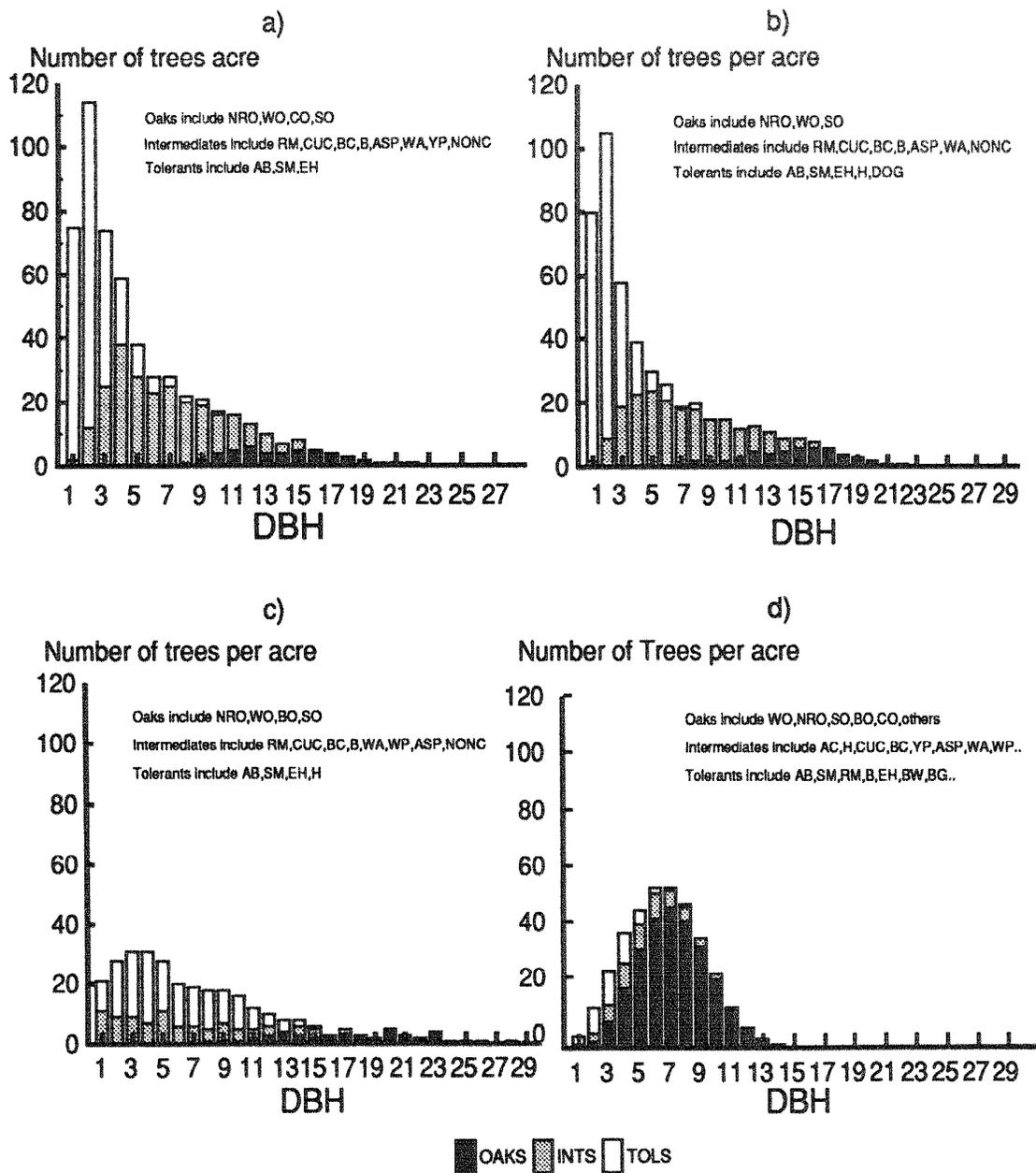


Figure 1. Diameter distributions of composites of the study plots, grouped by medial diameter, and showing species composition. a) Medial diameters from 10. - 12.5 inches. b) Medial diameters from 12.5 - 14.5 inches. c) Medial diameters from 14.5 - 17.0 inches. d) Schnur's (1937) SI 60, age 60 oak stand.

SILVICULTURAL IMPLICATIONS

In the face of serious difficulties in obtaining natural regeneration of oak species, the stratification by species described represents a serious challenge to forest managers who wish to preserve oak. Partial cuttings are desirable to increase the rate of growth of the best trees for the management objective. For wood products, thinnings provide faster diameter growth of the residual trees, capture some potential mortality, and shorten rotation lengths. For wildlife-habitat management, partial cuttings stimulate the growth of tree crowns and increase mast production. But to achieve multiresource objectives in these stands, managers must remain sensitive to a variety of special concerns. Guidelines to minimize gypsy moth impacts (Gansner and others 1987) are important, as is an understanding of the likely impact of common silvicultural practices on species composition. Figure 2 shows residual diameter frequency distributions of the composite, medium diameter class stand shown in Figure 1b after 2 common partial cuts.

Uneven-age management practices like single-tree selection have been shown to favor regeneration of species more shade tolerant than the oaks (Schlesinger 1976). In northwestern Pennsylvania oak stands, however, application of uneven-age practices may reduce the proportion of oak by the cutting alone. The theory of uneven-age silvicultural systems is the creation and preservation of a balanced inverse J diameter distribution in which the largest diameter trees are the oldest and the smaller diameter trees are the youngest. The inverse J shape of diameter distributions in northwestern Pennsylvania oak stands and the shade tolerance of the northern hardwood species in the smaller age classes will ease the transition to uneven-age management in these even-aged stands. At each cutting cycle, the oldest or largest trees are removed, the younger or smaller trees are thinned, and space is created for regeneration. If density is reduced to the levels recommended to obtain a good growth response in the residual trees (Marquis and others 1984, Roach and Gingrich 1968),³ and no cutting is done in the sapling class, the effect will be to reduce the proportion of oak. The higher the minimum cutting diameter employed, the more pronounced this effect will be. But even if cutting is uniform throughout the retained diameter classes, removing trees from the large end of the diameter distribution, above the selected maximum diameter, will reduce the proportion of oaks over time. Figure 2a shows the species composition of the residual stand after hypothetical selection cutting of the stand in Figure 1b to a Q of 1.5 and a residual density 65 percent that of the original stand, with a maximum retained tree size of 23 inches. No trees smaller than 5.5 inches d.b.h. were cut. The cutting removed 55 square feet of basal area in 73 trees per acre. In this stand, with an original maximum tree diameter of 23 inches, the proportion of oak was unchanged at 47 percent. Little or no replacement of the oaks can be expected to occur under this silvicultural system.

Management guidelines for even-age silviculture in many eastern hardwood stands recommend intermediate thinnings that concentrate removals in the smaller merchantable

³ Stout, Susan L. *in preparation*. Uneven-age management. *In*: Quantitative silviculture for hardwood stands of the Alleghenies. Available from the author.

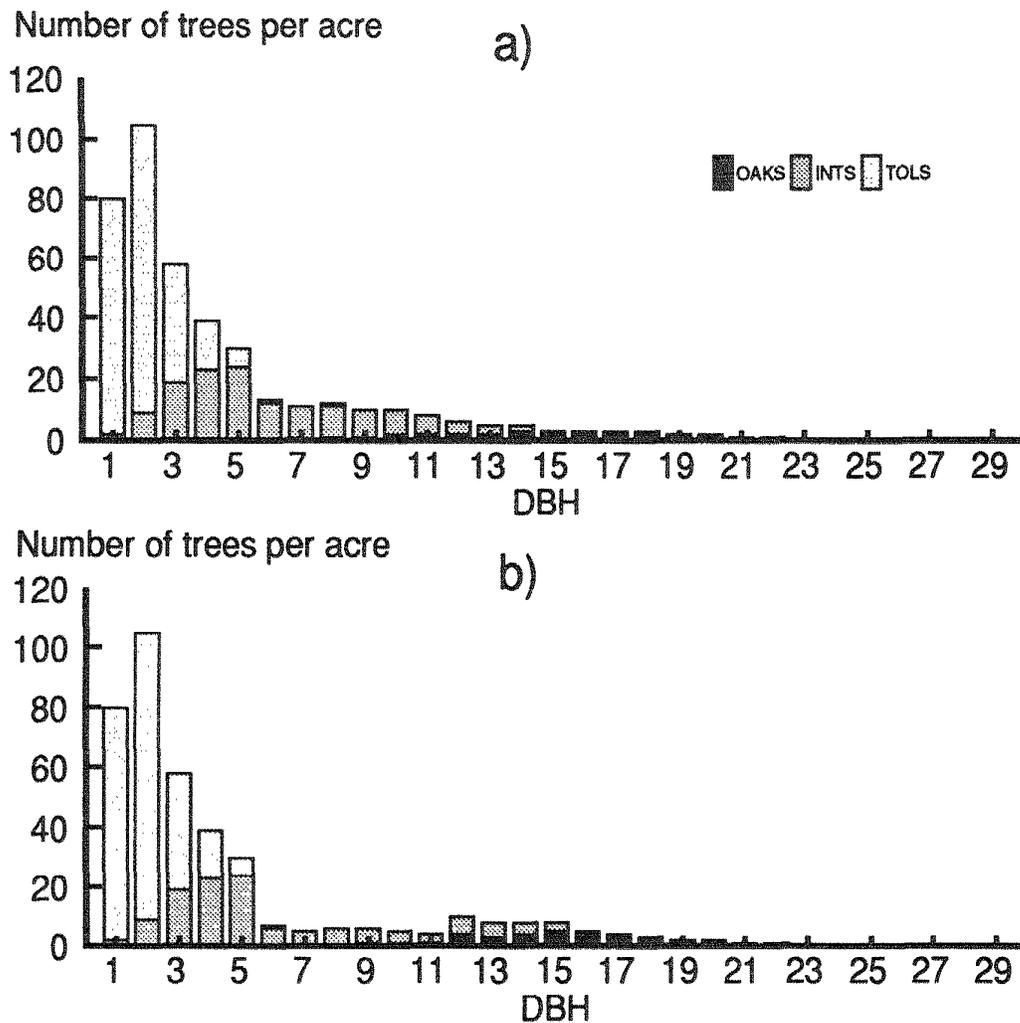


Figure 2. Changes in diameter distribution in the composite stand from Figure 1b. a) after a selection system partial cut. b) after an even-age commercial thinning.

stems, with only enough removals in the largest diameter and tallest trees to free some room in the main canopy (Marquis and others 1984, Roach and Gingrich 1968). Because such treatments concentrate removals in the size classes dominated by non-oak species, they tend to increase the proportion of oak (Figure 2b). In the composite stand shown in Figure 2, the commercial thinning to 65 percent of the original density, primarily from below, increased the proportion of oak from 47 percent to 54 percent of the basal area. This cutting removed 51 square feet in 92 trees per acre. Control of density in these treatments may be difficult,

however, as none of the currently available measures of relative density gives desirable results in northwestern Pennsylvania transition oak stands.

ASSESSING RELATIVE DENSITY

Measures of relative stand density allow foresters to assess the crowding in forest stands as a function of average tree size and, in some cases, species composition. Relative density is expressed as a percent of the average maximum density observed in undisturbed stands of similar average tree size and species composition (Ernst and Knapp 1985). In theory, most undisturbed stands should have relative density values close to 100 percent; in years of optimum growing conditions, tree growth and survival may be high, and relative-density estimates may exceed 100 percent by small amounts, while episodes of poor growing conditions will result in mortality and lower relative-density estimates.

Correct assessment of relative density is key to understanding and managing mixed-species stands. In stands of the same average tree size, but different species composition, absolute measures of density, such as numbers of trees or basal area per acre, vary with species composition, sometimes by as much as 50 percent. Basal-area values that are unrealistically high in one species mix may be average in another. Managers who underestimate the relative density of these complex stands may miss opportunities to increase individual tree growth and crown development, while managers who overestimate relative density risk loss of productivity or encouragement of undesirable plants. Yet assessment of relative density can be particularly difficult in stratified mixed stands. The stands included in this study were specifically chosen to represent the conditions of average maximum density. Thus, one criteria for choosing a density measure for use in these stands is the nearness of the mean estimate of density to 100 percent, as well as the proportion of these stands whose density is estimated as close to 100 percent. Table 2 shows the density of these northwestern Pennsylvania oak stands as assessed by five different measures.

The oak stocking chart in Roach and Gingrich (1968) expressed average maximum density as a curve that showed the average maximum basal area and numbers of trees per acre in upland central hardwood stands as their QMD increased. This chart was extended and used to determine percent oak stocking shown in the first row of Table 2. The oak stocking chart was developed partly with the stand tables in Schnur (1937), and was intended for use in these typical, white oak dominated stands with bellshaped diameter distributions. When applied to northwestern Pennsylvania stands such as those studied here, the charts yield estimates of density well above 100 percent. The mean value is 140 percent, and the estimates range from 111 to 169 percent. Densities this high suggest stagnation and severe mortality among the smallest trees in these stands, which is inconsistent with observation in these stands.

Table 2.--Relative density of study plots as calculated by five density measures.

	Minimum	Maximum	Mean +/- Std. Dev.
Oak Stocking Chart ¹	111	169	140 +/- 14
SILVAH Relative Density ²	85	143	105 +/- 14
NE-TWIGS Generalized Stocking Percent ³	60	97	83 +/- 8
PA Oak tree-area ratio ⁴	79	125	105 +/- 11
PA Oak Stand Density Index ⁴	74	121	96 +/- 11

¹ Roach and Gingrich (1968)

² Marquis, David A., and Richard L. Ernst. in preparation. User's guide to SILVAH: a stand analysis, prescription, and management simulator program for hardwood stands of the Alleghenies. Available from the author.

³ Gribko and others (in press).

⁴ Determined using measures developed for this study.

The SILVAH computer programs calculate the density of forest stands using a variant of the measure developed by Roach (1977) and Stout and Nyland (1987). With this procedure, the density contribution of individual trees is estimated as a function of their species and diameter. Species are assigned to one of three groups, based predominantly on their growth rates and tolerance to shade. These include a fast-growing, shade-intolerant group consisting of black cherry, white ash (*Fraxinus americana* L.), and yellow-poplar (*Liriodendron tulipifera* L.); a slow-growing, shade-tolerant group consisting of sugar maple, American beech, and striped maple (*Acer pennsylvanicum* L.); and an intermediate group whose main constituent was red maple, but to which most species were assigned for application purposes. Northwestern Pennsylvania transition hardwood stands were not in the data base used to develop the tree-area coefficients for Allegheny hardwoods. In the SILVAH programs, the density coefficients for the intermediate group are used for northern red oak. The coefficients for the slow-growing shade-tolerant group were so similar to those reported by Gingrich (1968) for the white oaks and hickory that these species were assigned to that group. The densities reported in the second row of Table 2 are the result of calculations made with the SILVAH computer programs. The mean value of relative density calculated by SILVAH is 105 percent, only slightly higher than the value we would prefer in unmanaged stands. But the range of values observed in this small group of stands, from 79 to 125 percent, suggests that this measure does not discriminate well between understocked, fully stocked, and overstocked stands.

A different approach to estimating density in mixed stands was taken by the developers of NE-TWIGS, the northeastern regional variant of the TWIGS forest growth projection system (Teck 1990). NE-TWIGS calculates a generalized stocking percent (GSP) for all stands. This measure is a weighted average relative stand density, calculated using Stand Density Index (Reineke 1933) values for seven different forest types. GSP is influenced by the species composition of the stand, and is a summation of weighted relative stand densities, where each species can only represent a single forest type (personal communication, Richard

Teck). The NE-TWIGS GSP values for these stands are reported in the fourth row of Table 2. The mean value of relative density calculated by NE-TWIGS is 83%, quite low for undisturbed stands. But the range of estimates is the narrowest of any of the measures reported, from 60 to 97 percent.

The values from the 21 undisturbed stands studied here were used to estimate the coefficients for two new measures of relative density for undisturbed stands. The fifth and sixth rows of Table 2 show the density of these stands by two measures developed during this study. Column 5 shows the results of applying a tree-area ratio measure developed from these data. The mean value is close to 105 percent. The range of values calculated for these stands is from 79 percent to 125 percent.

The tree-area ratio equation calculated for these transition stands is:

$$Tree\ area = -0.0068718 * N + 0.0167869 * \sum_{i=1}^N D_i + 0.0019797 * \sum_{i=1}^N D_i^2 \quad (1)$$

where N is number of trees per acre and D_i is the diameter of the i th tree.

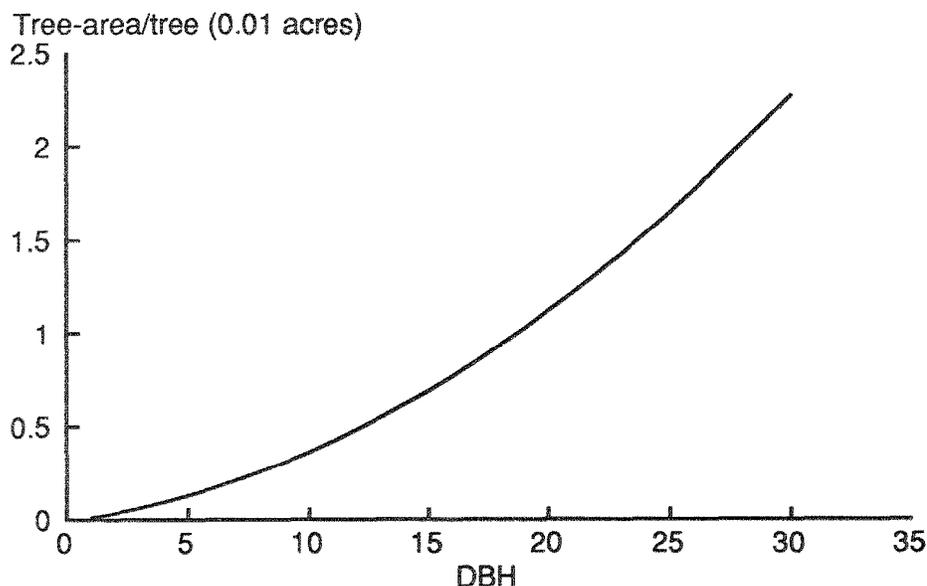


Figure 3. Tree area per tree (in centacres) as estimated by the tree-area ratio equation developed for this data set.

This tree-area curve is shown in Figure 3 as it would be used to estimate the density contribution of an individual tree. With 21 stands in the data used to estimate the coefficients for this equation, separation into species groups did not significantly improve the fit of the equation.

Row 6 of Table 2 contains an estimate of stand density based on the relationship between the number of trees and the quadratic stand diameter, as suggested by Reineke (1933). For the 21 undisturbed stands studied here:

$$\log_{10} N = 4.393 - 1.962 * \log_{10} QMD \quad (2)$$

where N is number of trees per acre and QMD is the quadratic mean diameter.

This equation has an r^2 of .88. The values in row 6 are ratios of the number of trees per acre in each of these stands to the number predicted by equation (2), expressed as a percent. This measure has a mean value of 96 percent in these stands, with a range from 74 percent to 121 percent.

DISCUSSION

The research reported here is part of a larger effort to develop regional tools to assess relative density in mixed hardwood stands. Managers must be able to discriminate between stands whose density is close to the average maximum for a type and those whose density is well below the average maximum, regardless of their management objective. Such discrimination is key to identifying opportunities and projecting changes (Stout and Larson 1987). The work reported here highlights the difficulties of assessing density in complex, stratified mixtures. The structure of these stands, with bellshaped oak distributions in the larger diameters and inverse J distributions of shade-tolerant northern hardwoods in the smaller diameters, contributes to their consistently overstocked ratings by traditional measures.

As our understanding of the interactions of these structures with site, management, and stand development improves, we will develop new and more efficient methods of assessing density in such stands. Differences among density measures reported here may help managers choose which of the existing measures of density they prefer, as well as point directions for future research. The new measures developed using this data provide the mean relative-density estimates closest to 100 percent for these 21 undisturbed stands, but their ranges are quite large, and they are untested outside this data set. The NE-TWIGS measure has the narrowest range, but underestimates the density of these stands, heightening the risk of missed treatment opportunities. Estimates made using the oak stocking guide or SILVAH tend to be high and have wide ranges, but may be acceptable as they minimize the risk of missed treatment opportunities.

CONCLUSIONS

Oak stands in northwestern Pennsylvania are usually stratified mixtures of central and northern hardwood species. In many such stands, northern red oaks are the largest trees in the stand, with red maple, the other oak species, cucumbertree, eastern hemlock, birch, and others in the middle of the diameter distribution, and American beech, sugar maple, and eastern hemlock forming a dense, sapling understory. Managers of such stands must be sensitive to the effects of silvicultural treatments on species composition by cutting alone; uneven-age cuts will tend to decrease the proportion of oak species or leave it unchanged, and even-age cuts will tend to increase it. Traditional measures of relative density are often poor at discriminating among these stratified oak stands with respect to stocking for any management objective. Both tree-area ratio and stand density index procedures offer some promise for assessing density in these stands.

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COMPOSITION AND STRUCTURE OF AN OLD-GROWTH VERSUS

A SECOND-GROWTH WHITE OAK FOREST IN SOUTHWESTERN PENNSYLVANIA

Julie A. Downs and Marc D. Abrams¹

Abstract: A relatively undisturbed, old-growth *Quercus alba* remnant and a second-growth example of the forest type were surveyed in 1988-89 to investigate the successional status of *Q. alba* in the region. Oaks (*Q. alba*, *Q. rubra*, and *Q. velutina*) totalled 18% importance in the old-growth stand and 30% importance in the second-growth stand. The overstory of the old-growth stand was mainly comprised of *L. tulipifera*, *F. grandifolia*, *Q. alba* and *Nyssa sylvatica*, whereas the overstory of the second-growth stand was mainly *Q. alba* with a relatively minor component of *F. grandifolia*, *A. saccharum*, and *L. tulipifera*. *Acer rubrum*, *A. saccharum*, and *Prunus serotina* were the dominant seedlings in both stands. The younger stand had greater sapling density. Both stands had few *Quercus* individuals in the understory. The oldest and largest trees in both stands were *Q. alba* with ages of 310 years and 148 years in the old-growth and second-growth stand, respectively. However, over 90% of all trees in the old-growth stand were < 120 years-old. Logging of several trees in the 1930's and 40's appears to have accelerated the dominance of the mixed-mesophytic species in the old-growth forest. The radial growth patterns of trees varied with species and canopy position. However, the oldest oak trees had average growth rates of < 0.75 mm/yr and > 1.5-2.0 mm/yr in the old-growth and second-growth stands, respectively. Many of the understory trees had average growth rates of > 1.5-2.0 mm/yr in both stands. We believe these stands represent an early versus late stage of oak replacement by mixed-mesophytic species, a process that seems inevitable in many eastern oak forests.

INTRODUCTION

Oak (*Quercus*) forests dominate much of the eastern deciduous forest biome and have been considered a climax type by early ecologists (Braun 1950, Clements 1936). Indeed, oak presence and dominance was recorded in presettlement forests of the northeast and mid-Atlantic regions (Bromley 1935, Loeb 1987, Russell 1980, Secor 1975, Spurr 1951). Oak dominance prior to European settlement in these regions may be explained, in part, by periodic fire set by early Native Americans and by lightning (Buell et al. 1954, Lorimer 1985). Following European settlement, cutting and slash fires further perpetuated or even

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RESULTS

In Sophia's Woods, the old-growth stand, *Fagus grandifolia* (Ehrh.) (beech), *Acer rubrum* (L.) (red maple) and *Liriodendron tulipifera* (L.) (tulip poplar) represented 63% of the importance value total (Table 1). White oak, *Quercus rubra* (L.) (northern red oak), and *Q. velutina* (Lam.) (black oak) totalled only 18% importance. The importance of white oak in Sophia's Woods was mainly due to its high basal area from a few large diameter individuals. Bear Run, the second-growth stand, was dominated by white oak, *Acer saccharum* (Marsh.) (sugar maple), red maple and tulip poplar which represented 76% of the importance value.

Table 1.--Relative importance values for trees (> 10 cm dbh) surveyed during 1988 and 1989 in an old-growth (Sophia's Woods) and a second-growth (Bear Run) stand on mesic sites in southwest Pennsylvania. Relative importance value is the sum of the relative dominance, frequency, and density divided by three for each species.

Species	Importance Value	
	Sophia's Woods	Bear Run
<i>Quercus alba</i>	11	27
<i>Quercus velutina</i>	3	1
<i>Quercus rubra</i>	4	1
<i>Acer rubrum</i>	20	12
<i>Acer saccharum</i>	5	25
<i>Liriodendron tulipifera</i>	18	11
<i>Fagus grandifolia</i>	25	7
<i>Betula lenta</i>	4	4
<i>Nyssa sylvatica</i>	4	1
<i>Prunus serotina</i>	2	1
<i>Tilia americana</i>	2	--
<i>Cornus florida</i>	1	4
<i>Carya</i> spp.	1	2
<i>Ulmus</i> spp.	--	4

Prunus serotina (Ehrh.) (black cherry), red maple and sugar maple were the dominant seedlings surveyed in Sophia's Woods and Bear Run, despite the low importance of black cherry trees on both sites (Table 2). Sugar maple and red maple had similar seedling densities at Bear Run, while the density of red maple seedlings was 400% greater than that of sugar maple in Sophia's Woods. Sophia's Woods had greater total seedling density than

Table 2.--Seedling and sapling data (no./ha \pm se) from the 1988 and 1989 survey of an old-growth forest (Sophia's Woods, SW) and a second-growth forest (Bear Run, BR) on mesic sites in southwest Pennsylvania.

Species	Seedlings		Saplings	
	SW	BR	SW	BR
<i>Acer rubrum</i>	23400 \pm 300	7600 \pm 153	50 \pm 2	900 \pm 3
<i>Acer saccharum</i>	5100 \pm 61	7100 \pm 119	100 \pm 3	50 \pm 2
<i>Prunus serotina</i>	11000 \pm 138	14300 \pm 123	50 \pm 2	500 \pm 15
<i>Nyssa sylvatica</i>	4900 \pm 160	600 \pm 18	50 \pm 2	450 \pm 10
<i>Quercus alba</i>	3000 \pm 82	500 \pm 10	0 \pm 0	300 \pm 8
<i>Quercus rubra</i>	2500 \pm 58	800 \pm 22	0 \pm 0	0 \pm 0
<i>Quercus velutina</i>	100 \pm 5	0 \pm 0	0 \pm 0	0 \pm 0
<i>Fraxinus</i> spp.	1500 \pm 27	700 \pm 17	100 \pm 3	150 \pm 5
<i>Fagus grandifolia</i>	1100 \pm 15	300 \pm 8	100 \pm 5	700 \pm 14
<i>Carya</i> spp.	500 \pm 18	900 \pm 25	0 \pm 0	100 \pm 3
<i>Cornus florida</i>	100 \pm 5	900 \pm 25	0 \pm 0	100 \pm 3
<i>Hamamelis virginiana</i>	0 \pm 0	4900 \pm 159	0 \pm 0	600 \pm 16
<i>Crataegus</i> spp.	0 \pm 0	700 \pm 3	0 \pm 0	50 \pm 2
<i>Sassafras albidum</i>	0 \pm 0	600 \pm 15	0 \pm 0	0 \pm 0
<i>Ulmus</i> spp.	0 \pm 0	500 \pm 25	0 \pm 0	50 \pm 2
<i>Asimina triloba</i>	0 \pm 0	400 \pm 12	0 \pm 0	100 \pm 3
<i>Betula lenta</i>	0 \pm 0	100 \pm 5	0 \pm 0	50 \pm 2
<i>Liriodendron tulipifera</i>	0 \pm 0	100 \pm 5	0 \pm 0	50 \pm 2
Total	53300 \pm 874	41000 \pm 744	450 \pm 17	4150 \pm 90

Bear Run and twice the number of species with seedling density > 1000/ha. However, these species (which included *Nyssa sylvatica* (Marsh.) (blackgum), northern red oak, white oak, *Fraxinus* spp. (ash) and beech) had few if any saplings (from 0-100/ha) in Sophia's Woods. At Bear Run these same species had saplings with densities in the range of 150-900/ha (with the exception of northern red oak). Seedlings and saplings of tulip poplar were absent in the sample plots at both sites, but were observed under canopy gaps.

Diameter class distribution in both stands approximated a reverse-J curve typical of an uneven-aged condition (Figure 1) (cf. Smith 1986). In Sophia's Woods the large diameter classes (> 60 cm) were dominated by white oak and beech, whereas the medium classes (35-60 cm) were dominated by tulip poplar and beech with some blackgum. The small diameter classes (< 35 cm) at Sophia's Woods were dominated by red maple, with some sugar maple, beech and tulip poplar also present. White oak and beech dominated the larger and medium diameter classes and sugar maple followed by red maple dominated the smaller diameter classes at Bear Run. Relatively few oak trees were surveyed in the smaller diameter classes at either site. Diameter distribution and tree size was similar in both stands despite the great difference in stand ages.

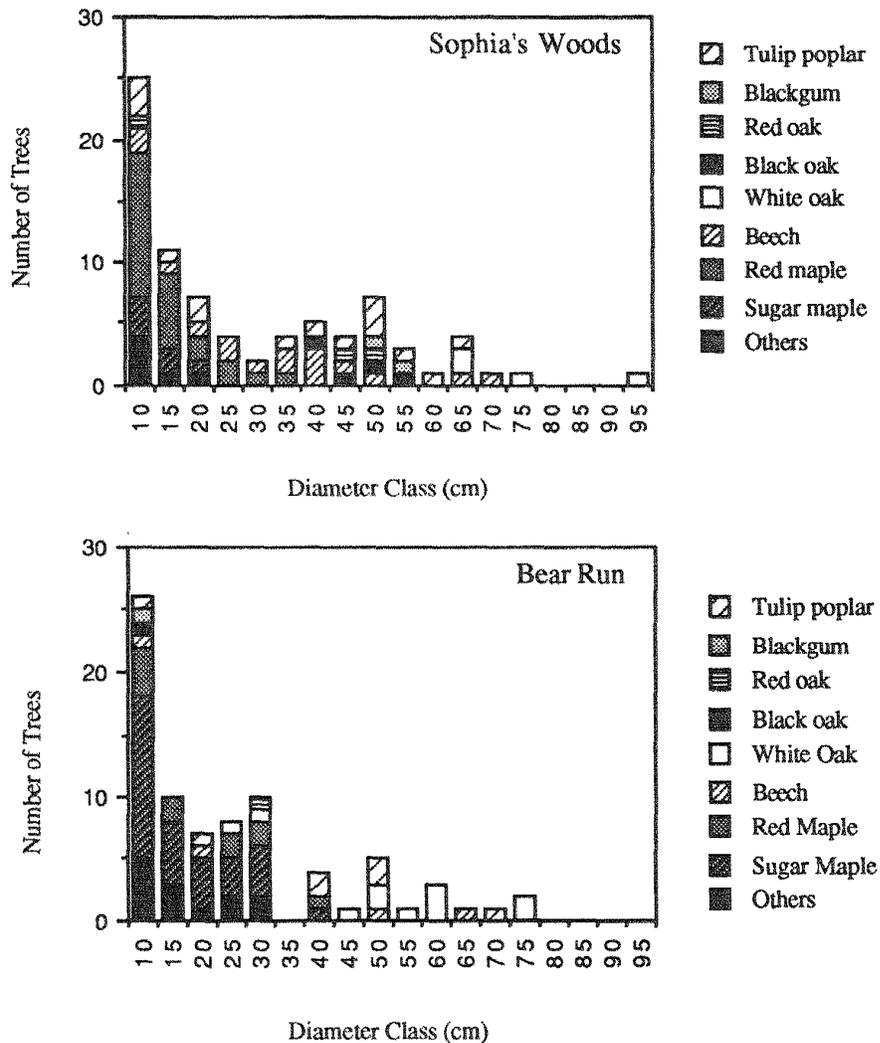


Figure 1. Diameter distribution of tree species in an old-growth oak forest (Sophia's Woods) and a second-growth oak forest (Bear Run) in southwestern Pennsylvania. Other species include *Betula lenta*, *Prunus serotina*, *Tilia americana*, *Cornus florida* and *Aesculus* spp. in Sophia's Woods and *Betula lenta*, *Prunus serotina*, *Cornus florida*, *Carya* sp. and *Ulmus* spp. in Bear Run. The Bear Run distribution excludes a white oak tree surveyed in the 125 cm class.

Table 3.--Canopy and diameter class distributions among the surveyed trees at Sophia's Woods (SW) and Bear Run (BR), old-growth and second-growth stands, respectively, in southwest Pennsylvania, surveyed in 1988 and 1989. N=number of individuals. Large, medium and small diameter classes are dbh >60, 35-60 and <35 cm, respectively.

Canopy Class	Species	N		Diameter Class	
		SW	BR	SW	BR
Dominant:	<i>Liriodendron tulipifera</i>	5	1	Medium	Large
	<i>Fagus grandifolia</i>	4	1	Large	Large
	<i>Quercus alba</i>	3	3	Large	Large
	<i>Quercus velutina</i>	1	0	Medium	-----
	<i>Nyssa sylvatica</i>	1	0	Large	-----
	<i>Tilia americana</i>	1	0	Medium	-----
Codominant:	<i>Liriodendron tulipifera</i>	2	3	Medium	Medium
	<i>Fagus grandifolia</i>	2	1	Medium	Medium
	<i>Nyssa sylvatica</i>	1	0	Medium	-----
	<i>Betula lenta</i>	1	0	Medium	-----
	<i>Quercus alba</i>	0	8	-----	Medium
	<i>Acer saccharum</i>	0	2	-----	Medium
	<i>Acer rubrum</i>	0	1	-----	Medium
Intermediate:	<i>Fagus grandifolia</i>	6	0	Medium	-----
	<i>Liriodendron tulipifera</i>	4	1	Small	Medium
	<i>Acer rubrum</i>	2	3	Small	Small
	<i>Acer saccharum</i>	0	9	-----	Small
	<i>Quercus rubra</i>	2	0	Medium	-----
	<i>Quercus velutina</i>	1	0	Medium	-----
	<i>Carya</i> spp.	0	2	-----	Small
	<i>Ulmus</i> spp.	0	2	-----	Small
	<i>Prunus serotina</i>	0	1	-----	Small
	Overtopped:	<i>Acer rubrum</i>	22	8	Small
<i>Acer saccharum</i>		6	18	Small	Small
<i>Fagus grandifolia</i>		7	2	Small	Small
<i>Liriodendron tulipifera</i>		2	2	Small	Small
<i>Betula lenta</i>		2	3	Small	Small
<i>Carya</i> spp.		1	0	Small	-----
<i>Prunus serotina</i>		2	0	Small	-----
<i>Quercus rubra</i>		1	1	Small	Small
<i>Quercus alba</i>		0	1	-----	Small
<i>Quercus velutina</i>		0	1	-----	Small
<i>Cornus florida</i>		1	4	Small	Small
<i>Ulmus</i> spp.		0	1	-----	Small
<i>Nyssa sylvatica</i>		0	1	-----	Small

Canopy position of trees in Sophia's Woods and Bear Run was closely related to their respective diameter class (Table 3). However, species composition within canopy classes differed between the old-growth and second growth stands. More dominant beech and tulip poplar were surveyed at Sophia's Woods versus Bear Run. Eight codominant white oaks were surveyed at Bear Run compared to none at Sophia's Woods. Sugar maple and red maple were overstory codominants at Bear Run but not at Sophia's Woods. Sophia's Woods had a greater number of dominant overstory species, which included blackgum, black oak, and *Betula lenta* (L.) (black birch), not present at Bear Run. Overtopped trees in Sophia's Woods were primarily red maple, beech and sugar maple, while at Bear Run more overtopped sugar maple and less beech and red maple were present.

Two white oaks were estimated to be > 300 years-old at Sophia's Woods (Figure 2). However, greater than 90% of all sampled trees were less than 120 years-old, including many beech, tulip poplar and red maple, but few oaks. Several beech and tulip poplar were in the canopy despite their relatively young ages (Table 3). At Bear Run, white oak, with a maximum age of 148 years, and to a lesser extent beech, dominated the higher age classes. A greater number of 90-148 year-old white oaks were surveyed at Bear Run compared to Sophia's Woods. Sugar maple was much more dominant in the younger age classes at Bear Run compared to Sophia's Woods. Relatively few individuals in the 20-year class were observed at either site.

Radial growth patterns of the surveyed trees varied with species and canopy position in both stands (Figures 3 and 4). Several cores of Sophia's Woods showed release in the 1930's and 40's which coincided with reported logging activities (Figure 3D, E, F, G, and H). Many trees in Bear Run also exhibited periodic release, such as intermediate white oak, red maple and sugar maple, presumably in response to natural gaps (Figure 4B, D, G). A codominant sugar maple in Bear Run had high but decreasing growth with age, suggesting it had originated in a gap and had no accelerated growth after reaching the canopy (Figure 4C) (cf. Lorimer et al. 1988). A dominant white oak in Sophia's Woods exhibited this same pattern (Figure 3C). An understory northern red oak at Bear Run had early growth of 5.0 mm/yr and a decrease to < 1.0 mm/yr probably as a result of gap closure (Figure 4H). A codominant beech at Bear Run (Figure 4E) displayed moderate, low, then high radial growth, suggesting that it grew during the opening and closing of a gap and then was released upon reaching the canopy. Tulip poplar exhibited the highest average growth rate of any species in both stands (3.0 mm/yr), with no extended periods of suppression.

Differences in radial growth between stands were apparent when comparing the oldest oaks. At Sophia's Woods a 310 year-old white oak and a 240 year old black oak averaged < 0.60-0.75 mm/yr radial growth (Figure 3A, B). In contrast, the oldest white oaks of Bear Run averaged > 1.5-2.0 mm/yr radial growth (Figure 4A, B). Younger trees of all species at both sites, in general, had average growth rates exceeding 1.5-2.0 mm/yr.

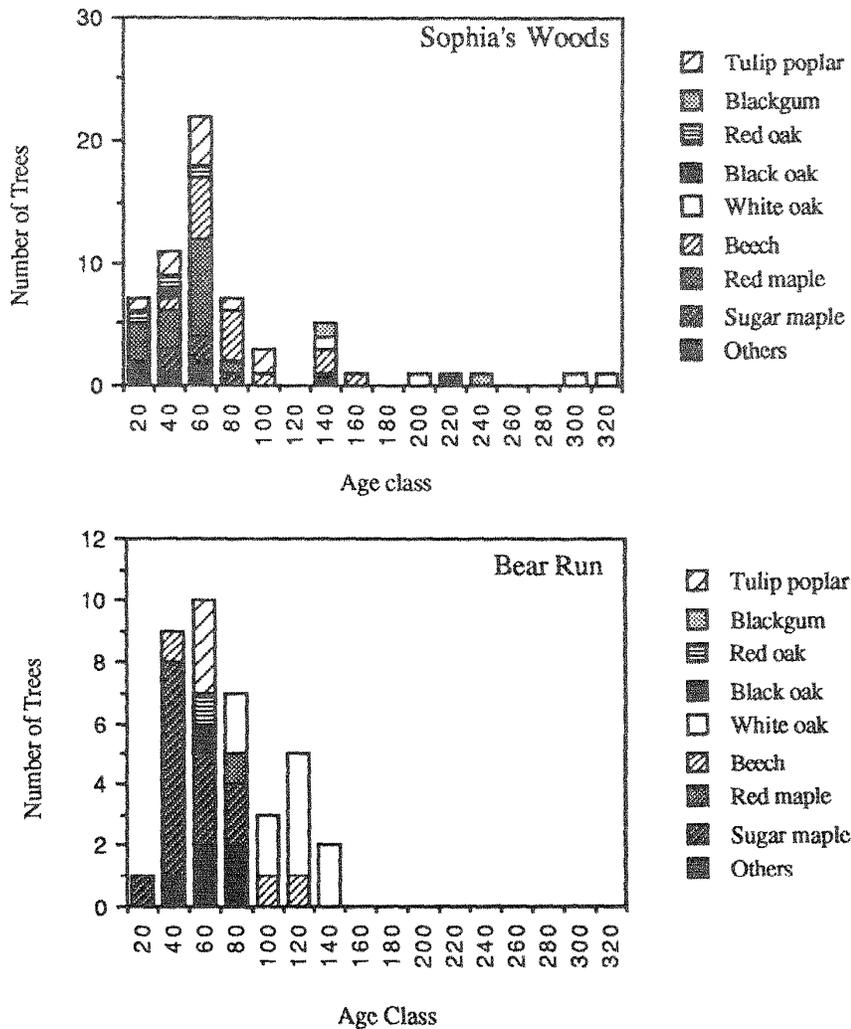


Figure 2. Age distribution of tree species in an old-growth oak forest (Sophia's Woods) and a second-growth oak forest (Bear Run) in southwestern Pennsylvania. Other species include *Betula lenta*, *Prunus serotina*, *Tilia americana*, *Cornus florida* and *Aesculus* spp. in Sophia's Woods and *Prunus serotina*, *Carya* spp. and *Ulmus* spp. in Bear Run.

DISCUSSION

Presettlement forests of southwestern Pennsylvania were dominated by white oak (Braun 1950, Jenning 1927). Beech may have been a codominant with white oak in the original forests (Braun 1950), and at Friendship Hill one beech and two white oak were among five trees present in a 1787 survey of the property corners. The age of beech trees relative to white oak in the original forests is unknown, but they were distinctly younger than the white oaks in Sophia's Woods, despite that beech can live over 300 years. Periodic fire by Native Americans and lightning seems to be responsible, at least in part, for the predominance of oak

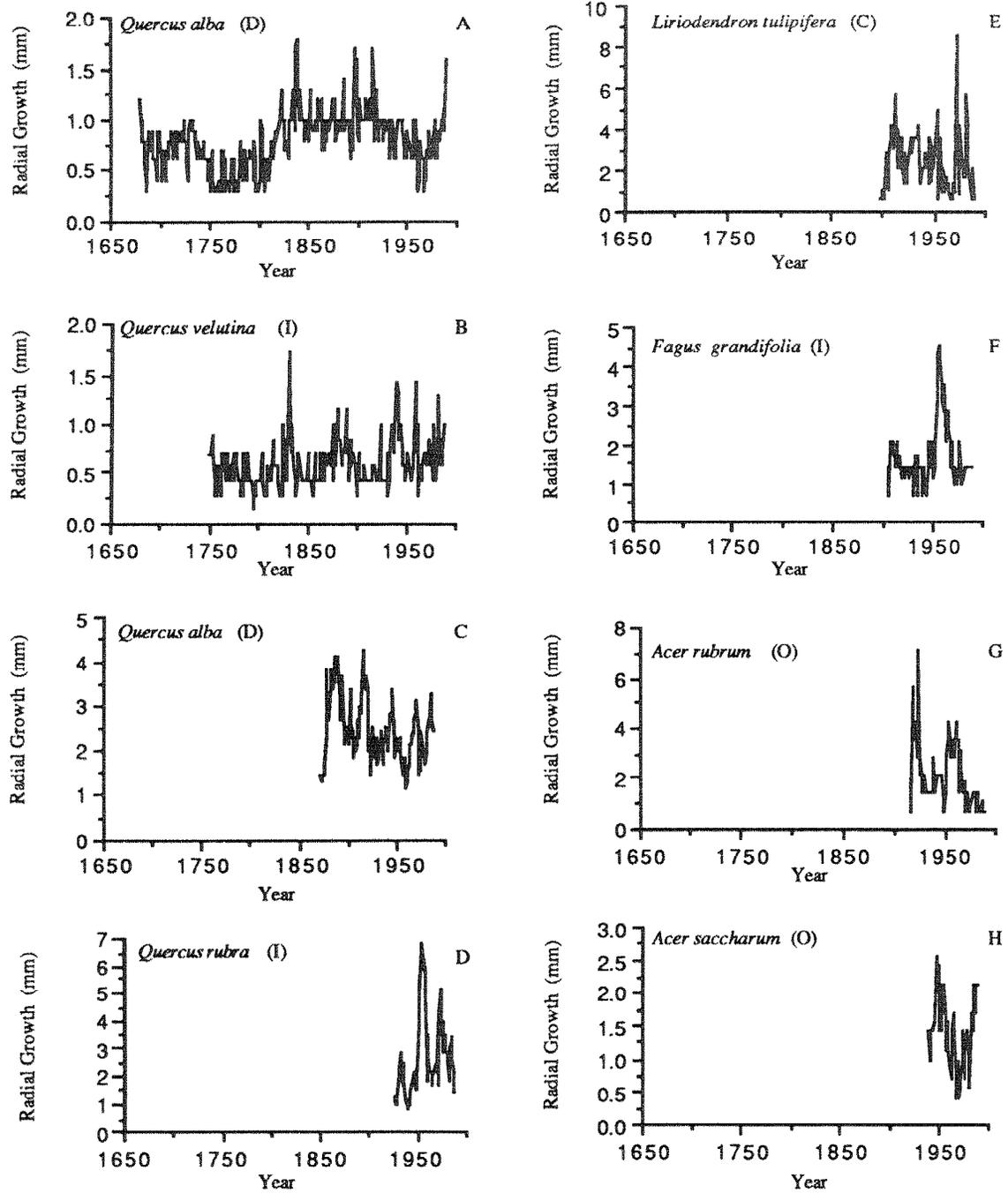


Figure 3. Radial growth of representative trees in an old-growth white oak forest (Sophia's Woods) located in southwestern Pennsylvania. Letters in parentheses indicate canopy class as follows: D = dominant, C = codominant, I = intermediate, O = overtopped (cf. Smith 1986).

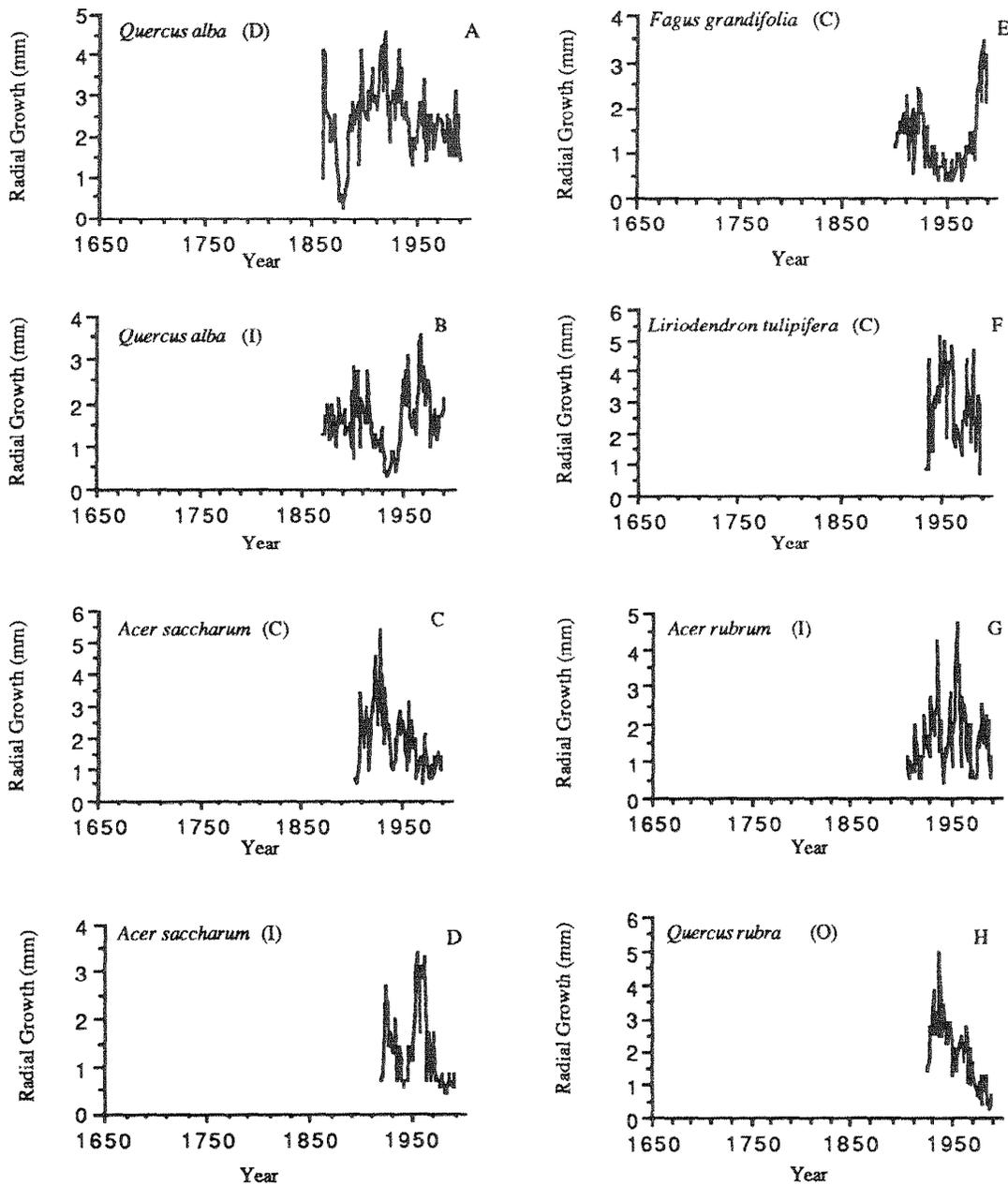


Figure 4. Radial growth of representative trees in a young-mature white oak forest (Bear Run) located in southwestern Pennsylvania. Letters in parentheses indicate canopy class as follows: D = dominant, C = codominant, I = intermediate, O = overtopped (cf. Smith 1986).

in the region prior to European settlement (Buell et al. 1954, Lorimer 1984). Not surprisingly, however, fire scarring on trees was not observed at Sophia's Woods, which has been a country estate for the last 200 years. Sophia's Woods was probably dominated by white oak in the 1600-1700's. Five trees (four oak and one blackgum) in the stand were over 195 years and the two oldest trees were white oak of over 300 years.

All of the older trees surveyed at Sophia's Woods exhibited slow radial growth of approximately 0.60-0.75 mm/yr. The specific reason for slow growth of the oldest white oak is unknown, but may be related to growing up in small gaps of an uneven-aged forest, or to the differential survival of slow growing individuals in an even-aged oak cohort. In contrast, the white oak of Bear Run originated directly after logging and exhibited high growth rates (> 1.5-2.0 mm/yr) probably in response to growing in high light. Likewise, many present-day northeastern, Lake States and Central Plains oak forests have an even-aged cohort of oak that originated either directly after large-scale disturbances, such as logging and fire, or the cessation of prairie fires and exhibited relatively high growth rates (Abrams 1986, Knox 1984, Lorimer 1981, Nowacki et al. 1990, Oliver and Stephens 1977). The younger northern red oaks in Sophia's Woods had much higher radial growth than the older white oaks and black oaks, suggesting that these individuals benefited from greater understory light conditions created by periodic logging or other gap-creating events. Relatively high growth rates with little or no periods of prolonged suppression were also exhibited by younger trees of beech, tulip poplar, red maple and sugar maple at Sophia's Woods, which matched the growth rates of those species at Bear Run. The general scarcity of trees > 195 years and the consistently high growth rates of younger individuals in Sophia's Woods suggest the occurrence of selective logging not reported in the historical record.

Oaks at both study sites were represented almost exclusively in the older age and middle to larger diameter classes, with the slight exception of northern red oak. Northern red oaks were also present in the smaller diameter classes of two virgin hemlock-pine forests in northwestern Pennsylvania (Morey 1936a), and were able to maintain a minor place in the forest canopy by infrequent gap capture in a southern Appalachian hardwood forest (Barden 1981). A scarcity of young oak trees is typical of many forests in eastern North America, and this has been used as evidence for predicting oak replacement by more shade tolerant species (Abrams 1986, Adams and Anderson 1980, Fralish 1988, Host et al. 1987, Lorimer 1984, Nowacki et al. 1990, Parker et al. 1985).

In both Sophia's Woods and Bear Run, beech, tulip poplar, red maple and sugar maple dominated the smaller and middle tree classes. In addition, many beech and tulip poplar and some blackgum, *Tilia americana* (L.) (basswood) and black birch also dominated the upper canopy at Sophia's Woods. This contrasted with the predominance of white oak at Bear Run and suggests that Sophia's Woods is in a later stage of oak replacement. Red maple and sugar maple trees at Sophia's Woods were generally smaller in diameter and height than the other mesophytic hardwoods, but showed every indication of becoming a codominant in the canopy in the near future. Red maple and sugar maple were present as codominants and dominated as understory trees at Bear Run. Thus, a pattern of decreasing oak and increasing sugar and red maple importance was also apparent in this stand. The more advanced status of maples at Bear Run versus Sophia's Woods may be due to the more extensive or complete

logging of that stand. We were somewhat surprised at the higher importance of sugar maple at Bear Run which has soil with lower moisture holding capacity than that at Sophia's Woods. Other studies reported higher red maple than sugar maple in drier oak forests (Host et al. 1987, Nowacki et al. 1990).

A pattern of gradual decreasing oak and increasing tulip poplar, beech and some red maple trees in Sophia's Woods was apparent before the selective logging in the 1930-40's. However, peak recruitment of these species and sugar maple occurred during and shortly after logging. Thus, this stand seems to have experienced accelerated succession of mixed-mesophytic hardwoods following logging (cf. Abrams and Scott 1989, Lorimer 1985). Similarly, gaps created by oak wilt or gypsy moth in eastern and Lake States forests became dominated by sugar maple or red maple (Collins 1961, Menges and Loucks 1984, Tryon et al. 1983). Beech has been reported to grow slowly as saplings beneath overstory conifers or hardwoods and then extend to the canopy following subsequent disturbance (Foster 1988, Spurr 1956). The small number of younger trees (in the 20-year age class) and saplings in both stands may be due to monopolization of resources (e.g. from canopy closure) by older, shade tolerant or gap-specialist trees.

Red maple was a dominant seedling at Sophia's woods and Bear Run, which was consistent with its importance as an understory tree at both sites. Red maple is the dominant seedling in many eastern and Lake States oak forests (Christensen 1977, Host et al. 1987, Lorimer 1984, Nowacki et al. 1990). Beech was poorly represented as seedlings at both sites which contrasts with its reputation of forming a dense seedling layer even in heavily shaded understories (Curtis and Rushmore 1958, Fowells 1965). However, beech seedlings were also scarce in many southeastern Pennsylvania hardwood forests, where reproduction of this species occurs mainly from root suckers (Keever 1973). Regardless, beech was present in most age classes in both stands. Tulip poplar also dominated the overstory but was not surveyed in the seedling layer at either site. Tulip poplar is intolerant of shade, but is a component of old-growth forests because it is an aggressive gap-phase species that often dominates its own gaps, and because trees of this species obtain great size and age (Buckner and McCracken 1978). Northern red oak and white oak were well represented as seedlings at Sophia's Woods, but they were poorly represented at Bear Run. Northern red oak has had some recruitment into the tree size class over the last 80 years in Sophia's Woods whereas white oak has not. Oak recruitment in closed stands may be limited to whether or not a substantial number of oak seedlings are present (Abrams 1986, Nowacki et al. 1990).

Black cherry seedlings dominated at Bear Run and were second in abundance to red maple at Sophia's Woods, despite the presence of only a few black cherry trees in both stands. The adults in Sophia's Woods were only about 20-years-old, which suggests that black cherry invaded the stand relatively recently. Black cherry recruitment in response to canopy gaps has been reported for oak woods in Wisconsin (Auclair and Cottam 1971, McCune and Cottam 1985), and has been observed in mesic white oak stands in central Pennsylvania (Nowacki and Abrams, unpublished data). We anticipate a gradual increase of black cherry into the canopy of Sophia's Woods and Bear Run.

In conclusion, Sophia's Woods is a remnant white oak forest in a late stage of oak replacement. Presettlement white oak forests in the region were probably maintained by periodic fire. Younger mixed-oak forests in the region are most likely a direct response to wide-spread cutting and subsequent fire in the mid-to late-1800's (Powell and Considine 1982). Sophia's Woods has been a part of a country estate since the late 1700's, during which time fire frequency was most likely reduced and a succession from white oak to mixed-mesophytic species has occurred. No white oaks under 130-years-old were surveyed, whereas numerous beech, tulip poplar, red maple, and sugar maple trees less than 120 years-old were present. A succession toward these mixed-mesophytic species was also apparent at Bear Run, but because of the relatively young stand age white oak still dominated. Replacement of oaks on undisturbed sites is relatively slow due to their longevity, but the results of this and previous studies of second growth oak forests indicate the inevitability of this process in many eastern forests.

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CHANGES IN THE RELATIONSHIP BETWEEN ANNUAL TREE GROWTH
AND CLIMATIC VARIABLES FOR FOUR HARDWOOD SPECIES

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Abstract: A study was conducted to characterize temporal and spatial variability in the growth response of four major hardwood species (white oak, chestnut oak, northern red oak, and yellow-poplar) to climatic fluctuations, and to evaluate the role of environmental factors associated with differences in response among individuals. The study incorporated tree-ring data collected by the Tennessee Valley Authority from a system of permanent forest inventory plots. Results of the dendroclimatic modelling indicated that there is a great deal of temporal variability in the climate/growth relationship for the species and sites included in this study. Statistically significant trends in growth showed a decrease in sensitivity to climate occurring in the tree-ring series. Changes in tree sensitivity did not appear to coincide with changes in climate. Environmental factors were effective in explaining groupings of tree core series as long as interactions between variables were considered. These factors indicate that differences in growth response to climate may be a function of changes in stand structure, competitive interactions and soil moisture holding capacity.

INTRODUCTION

Climate is often considered one of the most prominent and consistent factors affecting year to year variability in tree growth and, depending on the existence of other growth limiting factors, may be one of the most difficult to understand (Fritts 1976). In areas such as the arid southwest United States where moisture is the limiting growth factor, response to rainfall fluctuations is strong and predictable, especially at the forest - desert interface where conditions are marginal for tree survival (Fritts et al. 1965, Stahle 1987). However, moving towards more mesic sites, where moisture is less limiting, response to climate becomes less predictable due to the effects of factors such as nutrient availability and stand competition and their interactions with climate. The dynamic nature of these factors along with their inherent variability further obscures direct climatic effects resulting in a great deal of temporal and spatial variability in tree growth response. As these relationships increase in complexity from the moisture limited "sensitive" trees of the arid southwest to the "complacent" trees growing on more mesic sites, the level of detail of investigation of other factors and the sophistication of analytical techniques must also increase if tree growth response to climate is to be understood.

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As moisture becomes less limiting, other growth-limiting factors increase in relative importance, particularly in that stress due to some other factor may predispose a tree to injury attributable to climate. Site quality changes over time as a result of the natural aging processes of ecosystems, as well as stochastic events that cause significant disturbances. These changes bring about both abrupt and gradual changes in soil properties and species composition before a constant vegetation composition associated with a mature soil is reached (Pritchett and Fisher 1987). Over the life of a forest stand, changes occur in 1) soil physical and chemical properties as well as soil biota (Carmean et al. 1976, Whittaker and Woodwell 1972); 2) the physiology of individual trees and their sensitivity to stresses (Boyce 1961, Daubenmire 1974, Kim and Siccama 1987, Kozłowski 1979, Waring and Cleary 1967); and 3) stand structure and competition among trees (Haines and Cleveland 1981, Hornbeck et al. 1986, Van Deusen 1987, 1988). In addition, microsite differences within a stand modify individual tree response to various stresses.

Variability in tree growth response to climate across geographical gradients can be anticipated due to: 1) varying site requirements for different species (Fowells 1965); 2) differences in soils reflected in moisture availability and nutrient content (Bassett 1964, Kim and Siccama 1986, Pritchett and Fisher 1987); 3) local fluctuations in climate not accounted for in available data (Daubenmire 1974, Haines and Cleveland 1981); 4) intraspecific genetic variability as a result of species adaptation to a particular site; and 5) interactions with other trees (Doyle 1983). Spatial variability is, of course, a function of scale. However, variability in forest ecosystems can be extreme, as conditions influencing tree growth can change substantially over a small area.

The objective of this study was to characterize temporal and spatial variability in tree growth response to climate for four major hardwood species that occur within the Tennessee Valley region: white oak (*Quercus alba*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), and yellow-poplar (*Liriodendron tulipifera*). Temporal variability was examined using a time-variant response function, the Kalman filter (Kalman 1960), to model the relationship between climatic variables and annual increment. The hypothesis that environmental factors could explain differences in growth response in terms of spatial variability was tested using corollary site information and multivariate statistics.

METHODS

In 1986 the Tennessee Valley Authority (TVA) initiated a study to assess factors contributing to forest condition with regard to the possible impact of atmospheric deposition. The research described here utilizes data collected in that study. The study was designed to determine growth trends in uneven-aged, mixed species, second-growth natural hardwood stands occurring in the Tennessee Valley region and was built on an existing framework of permanent forest inventory plots. Since the objectives of the study were to determine the effects of natural factors on growth, plots were selected to represent a variety of sites and stocking levels. Three study sites (figure 1) were selected based on geographic distribution, spatial distribution of plots, and number of remeasurements: 1) the Emory River Land

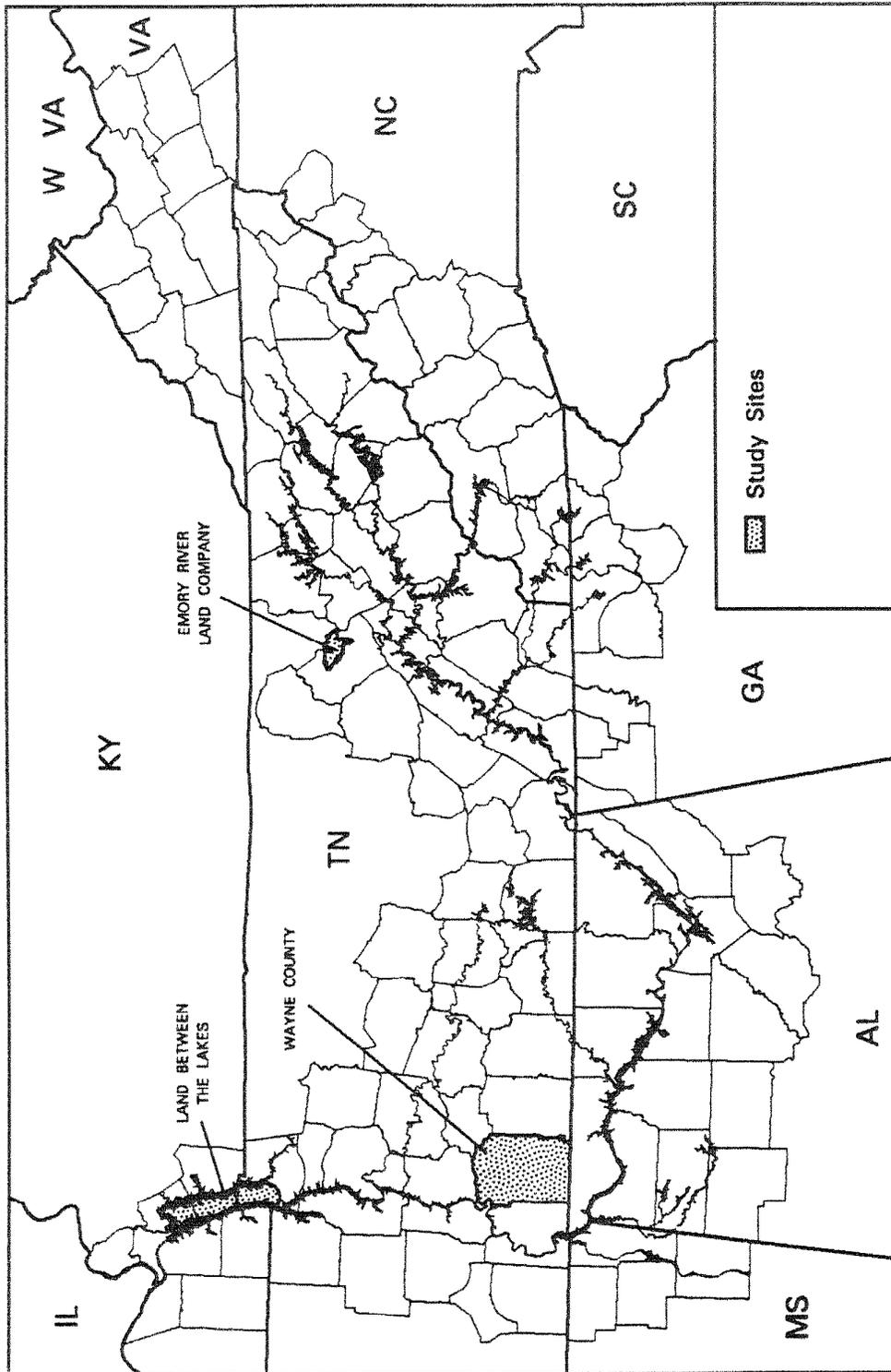


Figure 1. Map showing location of study sites.

Company, a 14,770 ha private land ownership located in Morgan County in northeast Tennessee; 2) "Land Between The Lakes" (LBL), a 68,797 ha national demonstration area managed by TVA and located in northwest Tennessee and southwest Kentucky; and, 3) Wayne County, located in southwest Tennessee, encompassing a total area of 191,903 ha. Together, these sites are considered representative of the forests of the Tennessee Valley region. Plots included in the study were selected from the total inventory based on forest type (white oak--black oak--northern red oak forest cover type and variants, Eyre 1980), size of trees (predominantly large sawtimber size trees -- greater than or equal to 28 cm dbh), and lack of substantial recent disturbance. A total of 267 0.08 ha plots were actually remeasured in the spring and summer of 1987 after preliminary screening.

Increment cores were collected from every living dominant and codominant tree on the plot (regardless of health). Core trees were not selected to represent site condition strata as the intention was to assess growth for a population and the relative importance of each of the many candidate site descriptors was unknown. Additional cores were collected from trees off the plot but in the immediate vicinity to increase core tree sample size. Ideally, five samples per species were collected but because of time constraints the total number of cored trees did not exceed 15 (unless more than 15 dominant and codominant trees occurred on the plot). Diameter at breast height (dbh) was recorded for all core trees to facilitate later age estimation. A prism count was made around every cored tree as a measure of individual competitive pressure. Notes regarding injury or other conditions affecting growth were also recorded for each core tree.

Tree cores were mounted according to the procedures described by Phipps (1985) and sorted by species. Crossdating was done by standard dendrochronological technique and was verified by a computer program COFECHA (Holmes 1985). Measurement of annual radial increment from individual trees was done using a Bannister incremental measuring device linked to an IBM-XT microcomputer. Tree-ring series from a total of 1843 trees were analyzed in this study (table 1). A wide range of ages was represented in each species sample with the youngest tree being a yellow-poplar at LBL with an estimated age of 34 years up to a total estimated age of 319 years for an individual chestnut oak at Emory River.

In complacent species growing in closed-canopy forests, the natural growth trend is often confounded with stand dynamics such as competition. This can complicate standardization of tree-ring series as it is difficult to determine what portion of the year-to-year variation in growth is due to climate and what portion is due to other factors. Therefore, in this study tree-ring series were standardized using first differences of natural logarithms, resulting in values that represent relative annual growth rates (Van Deusen 1990a). This technique avoids subjective decisions about what type of growth curve to use to remove the natural growth trend, or how stiff a spline is necessary to remove the low frequency variation due to endogenous disturbances while maintaining the high frequency variance associated with exogenous disturbances or climate.

Next, series from each species-site combination were scanned to identify a period for which there were measurements in common (table 2). A cluster analysis was run on standardized data for this common period to identify trees that had similar growth patterns. The

Table 1.--Number of trees and range of ages by site and species.

	White oaks	Chestnut oaks	Northern red oaks	Yellow-poplar
Emory River	229 trees (48-206 yrs.)	276 trees (49-319 yrs.)	143 trees (48-185 yrs.)	237 trees (34-161 yrs.)
LBL	384 trees (39-214 yrs.)	123 trees (51-267 yrs.)	15 trees (65-136 yrs.)	26 trees (34-130 yrs.)
Wayne County	193 trees (47-256 yrs.)	106 trees (42-157 yrs.)	62 trees (60-151 yrs.)	49 trees (42-127 yrs.)
Total trees:	806	505	220	312

Table 2.--Common measurement period used for clustering tree-ring data.

Site and Species	measurement period	number of years
Emory River white oak	1949 - 1983	35
LBL white oak	1952 - 1986	35
Wayne Co. white oak	1956 - 1986	31
Emory River chestnut oak	1951 - 1986	36
LBL chestnut oak	1947 - 1986	40
Wayne Co. chestnut oak	1955 - 1986	32
Emory River northern red oak	1956 - 1986	31
LBL northern red oak	1942 - 1986	45
Wayne Co. northern red oak	1948 - 1986	39
Emory River yellow-poplar	1968 - 1986	19
LBL yellow-poplar	1968 - 1986	19
Wayne County yellow-poplar	1960 - 1986	27

FASTCLUS procedure in SAS was run iteratively to group tree-ring series in clusters with high within-cluster correlation. FASTCLUS performs a disjoint cluster analysis on the basis

of Euclidean distances computed from one or more variables, which in this case were individual measures of annual increment for the common measurement period. FASTCLUS utilizes *nearest centroid sorting* (SAS 1985). In this procedure, *n* clusters are specified and a set of *n* points known as *cluster seeds* are selected as a first guess of means of the clusters. Each observation is then assigned to the nearest cluster and the cluster seeds are updated according to these temporary cluster groupings. The process is repeated until no further changes occur in the clusters.

Initial sizes of clusters were determined based on the computer memory limitations of the software used in the following analyses; each cluster could have a maximum of 87 series with 91 years of data per series (to be used with climate data available from 1895-1986 minus one year for the differencing). After working with the white oak data, a criterion was established of cluster sizes having a maximum distance from seed to observation equal to or less than approximately 2.5. The initialization method used by FASTCLUS makes it sensitive to outliers; clusters that contained four or less series were discarded as outliers. The resulting number of clusters and associated statistics are given in table 3.

Table 3.--Cluster statistics for each species at the three study sites.

Species/ Site	Percent of Plots with Species	Number of Resulting Clusters	Mean Cluster Size (trees)	Coefficient of Variation for Cluster Size
White oaks				
ER ¹	68	9	24.3	96%
LBL	63	9	42.7	48%
WC	75	6	32.2	67%
Chestnut oaks				
ER	75	7	39.4	64%
LBL	17	4	30.8	55%
WC	42	3	35.3	71%
Northern red oaks				
ER	58	2	71.5	13%
LBL	6	2	7.5	47%
WC	35	3	20.7	44%
Yellow-poplars				
ER	48	4	59.3	41%
LBL	6	1	23.0	-
WC	28	4	12.3	52%

¹ ER = Emory River, LBL = Land Between the Lakes, and WC = Wayne County.

Climate data, consisting of monthly averages of temperature and monthly totals for precipitation, for the period 1895 through 1986 were made available from Oak Ridge National

Laboratory (ORNL) for state climatic divisions in which the study sites occurred. These data were also standardized using the first differences of the natural logarithm so that subsequent analyses would assess the relationship between rates of change in tree growth and rates of change in the climate data. Due to the large amount of data processed in this study, climate variables were selected for each cluster using multiple regression techniques rather than fitting a Kalman filter model one parameter at a time because the latter is a very time-intensive technique.

A stepwise regression was performed using annual values from a cluster mean chronology as the dependent variable with climatic variables for the current year through the end of the growing season and variables lagged one year as independent variables. To enter the model, variables had to be significant at the 0.15 level, and to remain in the model the parameter had to be significant at the 0.05 level. Coincident with fitting the regression, tolerance values were calculated for the variables used in each of the models to determine if there was a potential problem with collinearity. Tolerance values are defined as $1-R^2$ for a variable with respect to all other regressor variables in the model (SAS 1985). Collinearity did not appear to be a problem with the selected variables.

Once climate variables were selected from the stepwise regression, dendroclimatic modelling using the Kalman filter proceeded using the software package DYNACLIM (Van Deusen and Koretz 1988). The Kalman filter has been proposed to address problems in tree-ring analysis arising from temporal nonstationarity in the relationship between annual increment and climate (Van Deusen 1987, 1988; Visser 1986; Visser and Molenaar 1987, 1988). The formulation used here, described by Van Deusen and Koretz (1988), is a generalization of an ordinary regression equation that allows for dynamic parameters which are estimated using maximum likelihood. Models were specified using a non-varying intercept while regression coefficients for all climate variables were allowed to vary through time. DYNACLIM software produced smoothed parameter estimates for each of the climate variables for every year and their associated variances.

Verification of dendroclimatic models traditionally involves demonstration of time stability by comparing a model developed from data from one time period (known as the calibration period) with data from another (known as the verification period). By using the Kalman filter to develop dendroclimatic models we are allowing the relationship between climatic variables and tree growth to be non-stable through time because of the dynamic nature of the trees' growing environment. Therefore, other means of verification must be used. Van Deusen (1990b) suggests a number of statistical tests to assess the possibility of model misspecification or the absence of a systematic component in the resulting model. These include observation of the cumulative sum of the prediction errors and their confidence intervals according to Brown et al. (1975), assessment of recursive residuals using the modified Von Neumann ratio (Harvey 1981), and use of the C^* statistic calculated from the cumulative sum of prediction errors for time t (Harvey 1981). Each of these tests were applied to the models produced using DYNACLIM and no evidence was found of either model misspecification or missing components. Additionally, each tree-ring data set was tested for remaining autocorrelation up to a five-year lag. Although there was evidence of some autocorrelation, it occurred in amounts small enough (generally less than 0.10) to be

considered unimportant. Verification was also provided through replication of results. Models developed for clusters within a species generally consisted of the same climatic parameters, although coefficient values differed. Once model testing was completed, a normal distribution for the variance among individual trees was assumed and ninety-five percent confidence intervals were calculated for each of the climate parameters to assess if these values were significantly different from zero.

Observed trends in parameter coefficients were tested using a *runs* test (Draper and Smith 1981) to determine if changes in coefficient values followed a pattern that might be associated with a change in sensitivity to climate or if they occurred randomly and therefore did not reflect true changes in sensitivity. The runs test was performed for individual clusters by calculating a mean coefficient over time for specific climate parameters that were common to a large proportion of the clusters over each site. Deviations from the mean were calculated on a year by year basis and assigned a value of "+" if they were greater than zero and "-" if less than zero. Changes in sign within a sequence of pluses and minuses denote the beginning of a new run. The Z statistic described in Draper and Smith (1981) was used to determine if the number of runs is an "extreme" arrangement as opposed to one which would occur randomly. A small number of runs (the minimum would be 2) indicates a trend in coefficient value, while a large number of runs indicates lack of a trend or a random pattern similar to white noise. The climate data, standardized and non-standardized, were also tested for trends using the runs test.

The last part of the analysis was to determine which environmental factors could be associated with different clusterings and might therefore affect differences in response to climatic fluctuations. This was accomplished using a discriminant analysis on a set of environmental factors that was associated with each individual increment core tree. Each tree was identified with a cluster number and the environmental factors (quantitative variables) were used to discriminate the trees into cluster groupings (classification variables).

Environmental factors consisted of variables associated with individual trees and site variables determined for each plot. Individual tree data consisted of the dbh of the core tree, an estimated age based on average annual increment and tree radius, and the prism count collected for each tree. Site information included descriptive variables such as elevation, slope percent, topographic classification, aspect, and fire and grazing codes. Information calculated from the inventory data included: 1) a productivity index calculated as average annual basal area increment for the plot; 2) relative frequency of each of the four core tree species; 3) an importance value for each of the core tree species calculated as that species' basal area per acre divided by total basal area per acre; 4) mean age of all cored trees; 5) basal area of mortality trees; 6) basal area of cut trees; and 7) percent of trees in the stand affected by the different injury classifications. Soils data consisted of horizon depth and texture for each plot. Horizons were aggregated into an A and E horizon and a B horizon -- deeper horizon data were not included. Soil textures were assigned a categorical name in the field. These data were ranked according to a gradient reflecting change in texture from fine to coarse and assigned a numerical value representative of this gradient. Presence of an argillic zone (Bt horizon) or a fragipan (Bx horizon) was indicated with a presence code of 1 or an absence code of 0 for a variable representing each type of horizon.

Canonical discriminant analysis was applied to the data using the SAS procedure CANDISC. This procedure is a dimension-reduction technique related to PCA and canonical correlation. CANDISC calculates linear combinations of the quantitative variables (known as *canonical variables*) that summarize between-class variations and that have the highest possible multiple correlation with the groups, then tests the hypothesis that resulting canonical correlations are zero in the population. A variable's importance in determining groupings can be evaluated by observing the value of the standardized canonical coefficients associated with it. In conjunction with CANDISC, univariate statistics in the form of one-way analyses of variance were calculated for each environmental variable.

A classificatory discriminant analysis was also performed on the data using the SAS procedure DISCRIM. This procedure generates a linear discriminant function for each group of data as well as probabilities of misclassification (error rates). This provided an evaluation of how well the environmental factors explained the cluster groupings of tree growth.

RESULTS

Clustering of tree-ring series by species and sites resulted in a total of 54 groups. All clusters incorporated trees of different ages and sizes. Series from trees in close proximity to one another sometimes grouped in the same cluster but often did not. Cluster groupings were observed on a plot-by-plot basis to determine the degree of spatial heterogeneity that occurred for each species-site combination. A count was made of the number of plots with more than one sample tree on which all of the trees of a species were grouped into a single cluster. This revealed a great deal of spatial variability with a range of values showing plot homogeneity on only 2% of the plots with chestnut oak at Emory River, up to a high of 39% for northern red oak at Emory River (table 4). Plots with many cluster groupings were compared to those with a single cluster grouping to see if any differences were apparent to explain the degree of heterogeneity. Examination of soils diagrams made in the field showed that the number of cluster groupings could not be explained by differences in soils. Disturbance history accounts were also compared. Plots that were very homogeneous in tree growth response included histories that indicated no apparent disturbance, disturbance by Timber Stand Improvement (TSI), insects, disease, fire and widespread adjacent mortality. Spatial homogeneity did appear to relate to the percent of the stand that was occupied by the individual species. Plots that consisted of only one species generally had core trees that clustered together, while plots with a number of species often exhibited heterogeneity in growth response for each species.

For white oaks, June temperature was overall the most important variable selected in the stepwise regression, exhibiting a negative relationship with growth. Later variables that entered the climate models differed somewhat by site -- at Emory River, generally past August rainfall (a positive relationship) was the next most important variable, while at LBL past December rain (a positive relationship) usually entered the model second, and at Wayne County, each cluster had a different variable entering in the second place position.

Table 4.--Percent of plots in which all trees of one species clustered into the same group.

	White oaks	Chestnut oaks	Northern red oaks	Yellow-poplar
Emory River	5%	2%	39%	24%
LBL	29%	29%	14%	-
Wayne County	24%	16%	33%	18%

June temperature was also the most important variable for chestnut oak, although at Emory River, May rain was a close competitor for first place. June rain was also important, especially at LBL. Northern red oaks behaved similarly, with June temperature the unanimous choice for first entry. Past August rain was important at Emory River, showing similar associations as the white oaks. Summer rains were important to Emory River yellow-poplar, especially June rain. No other clear relationships were apparent for a species or site.

Kalman filter estimates of parameter values for each of the 54 tree-ring clusters indicated some interesting differences and similarities between species and overall time trends in the climate/growth relationship. Changes in parameter coefficients over time were compared with graphs of monthly climatic data over time to determine if changes were coincident with trends in climate. No associations were determined. Additionally, the runs test indicated that the number of runs was not significantly different than random (i.e. no trends) for both standardized and non-standardized climate data. For the most part, each cluster model revealed that through time, these trees become less sensitive (i.e. coefficient values for these parameters approached zero over time) to climate variables such as summer temperature and rainfall.

Trends in coefficient values for June temperature and past August rain were assessed for all clusters which incorporated these parameters in the dendroclimatic model. These variables were not always the most significant for each cluster, however, they were the most prevalent overall and therefore were used to gain insight into the general relationship between climate and tree growth. Figures 2-7 show the percentage of clusters that had a coefficient that was significantly different from zero by year. This graphical display provides an overview of what appears to be a general trend towards decreasing sensitivity to climate. In each graph except for past August rain in Wayne County (figure 7), there is first a trend towards increasing significance in coefficient values, followed by a drop in the percent of clusters which included values that were significantly different from zero. The early low values reflect relatively wide confidence intervals for each coefficient value resulting from a large amount of variation between individuals and small sample sizes for older trees. Later decreases in the percentages of significant values are associated with coefficient values that approach zero over time, reflecting a decreasing sensitivity to these climate variables for most trees.

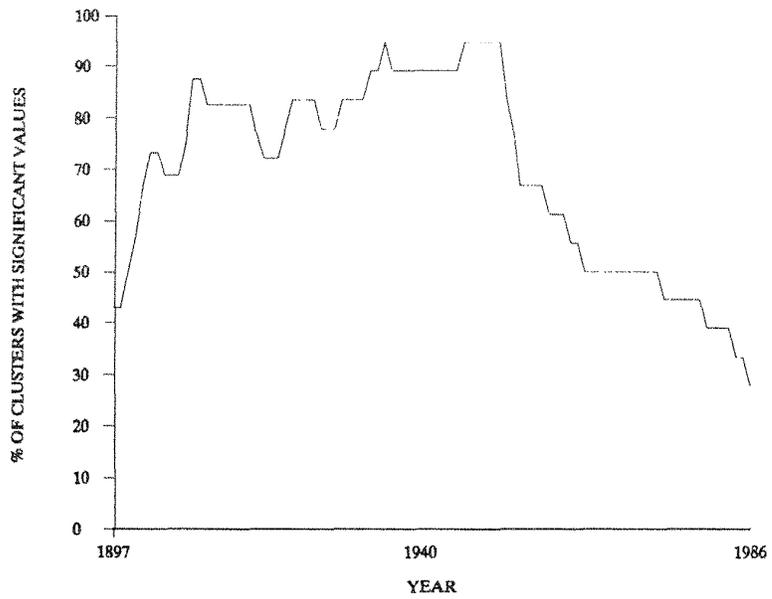


Figure 2. Percent of Emory River clusters with June temperature coefficients that are significantly different than zero by year.

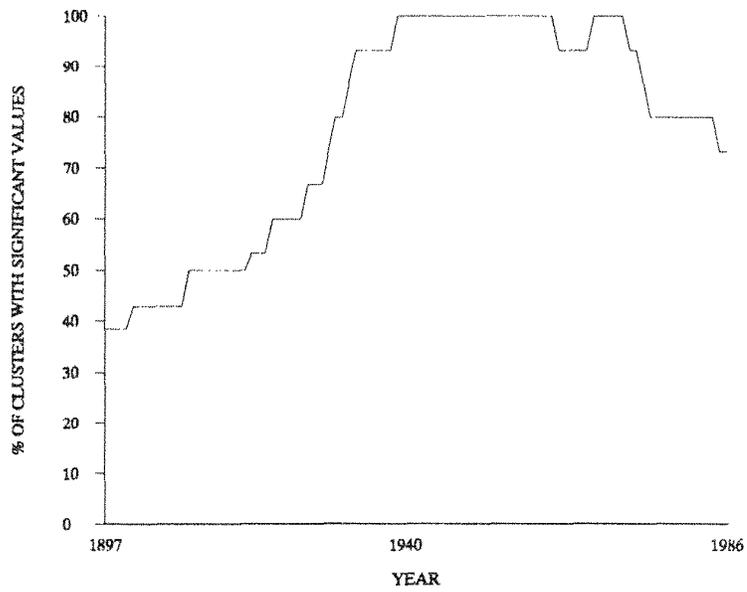


Figure 3. Percent of Emory River clusters with past August rain coefficients that are significantly different than zero by year.

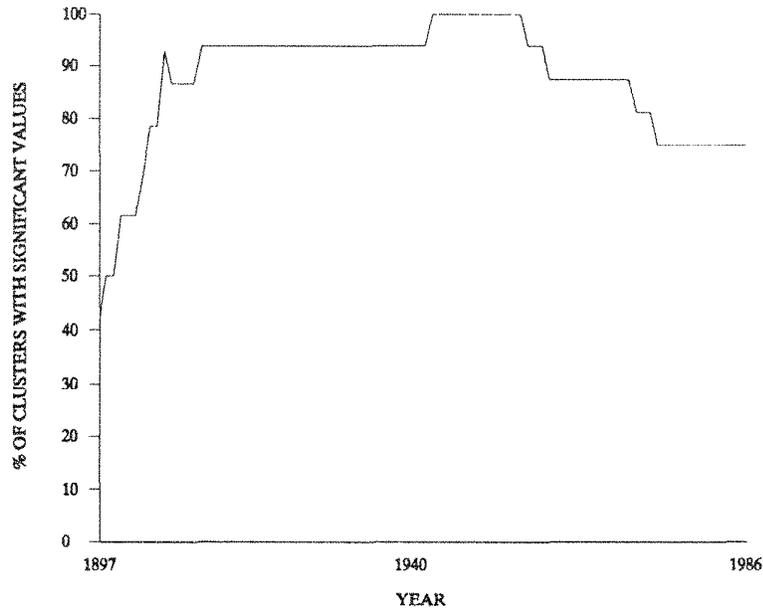


Figure 4. Percent of Land Between the Lakes clusters with June temperature coefficients that are significantly different than zero by year.

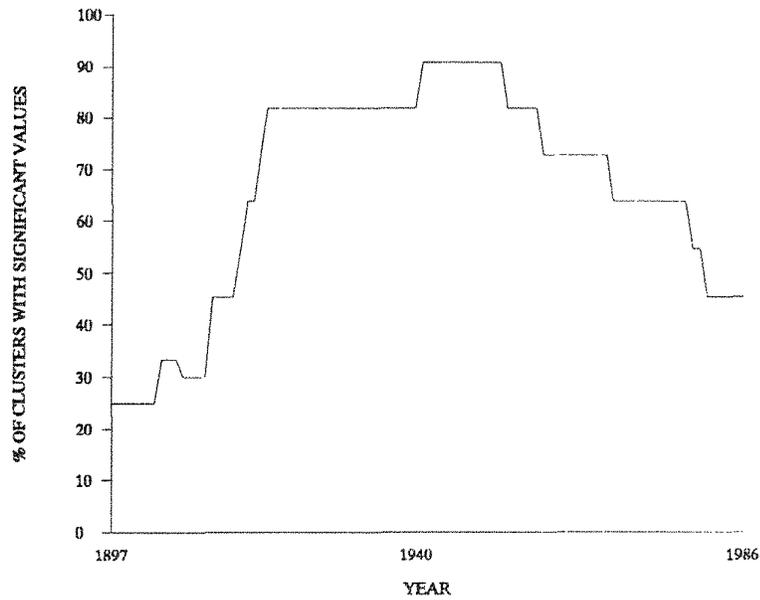


Figure 5. Percent of Land Between the Lakes clusters with past August rain coefficients that are significantly different than zero by year.

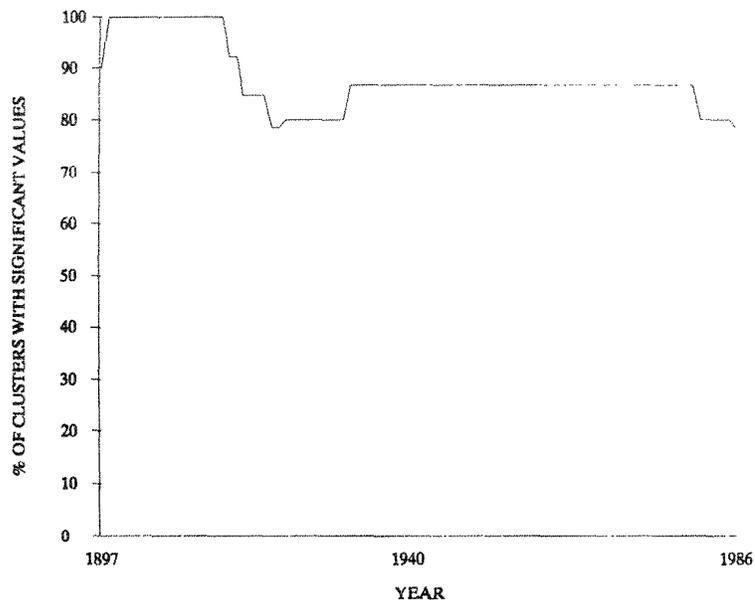


Figure 6. Percent of Wayne County clusters with June temperature coefficients that are significantly different than zero by year.

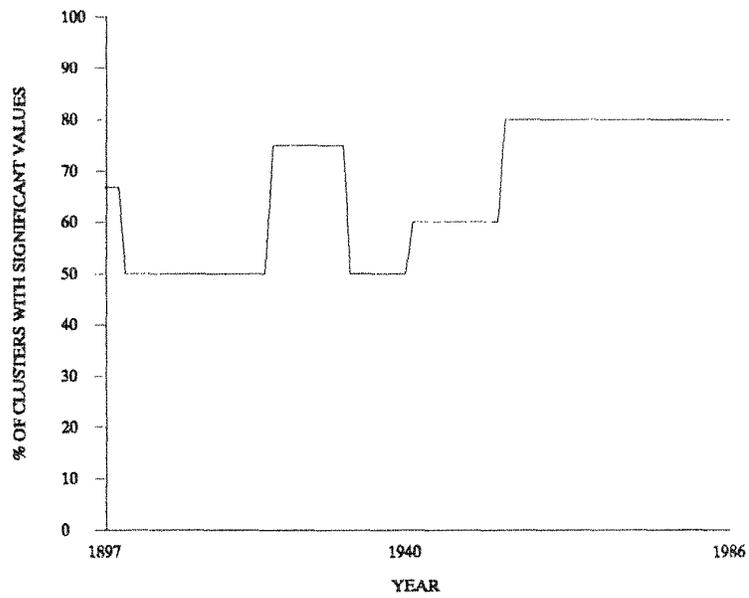


Figure 7. Percent of Wayne County clusters with past August rain coefficients that are significantly different than zero by year.

A runs test was done on June temperature and past August rain for those clusters in which these variables contributed to the explanation of variation in growth. Decreased sensitivity to June temperature is indicated by a change towards less negative coefficients (denoted by a plus sign), while a change towards more negative coefficients (denoted by a minus sign) indicates increased sensitivity. At Emory River, all clusters that exhibit temporal variation in coefficient value showed a trend towards decreasing sensitivity to June temperature that was significantly different than random changes in the relationship (figure 8). One yellow-poplar cluster (number 1) showed a reversal in this trend, towards increased sensitivity. Similar trends were observed for all species at LBL, except where there was no temporal variability in June temperature coefficients. At Wayne County, the pattern was more confused. All white oaks again showed a trend towards decreased sensitivity. Two clusters, chestnut oak number 1 and northern red oak number 1, showed a reversed trend, towards increased sensitivity.

Changes in sensitivity to past August rainfall were not as apparent, although general patterns did exist (figure 9). Decreased sensitivity to past August rain was signified by a less positive coefficient (denoted by a minus). A more positive coefficient (denoted by a plus sign) indicated increased sensitivity. No temporal variation was represented by zeros. Of the 16 clusters at Emory River, four showed no temporal variation, five showed a significant trend towards decreased sensitivity, and seven showed a trend towards increased sensitivity. At LBL, all clusters except white oak number 9 showed a significant trend towards decreased sensitivity. In white oak number 5 there was a recent change towards increased sensitivity. Of the five clusters incorporating past August rain at Wayne County, two showed no temporal variability, and the remaining three showed increased sensitivity to this variable.

Analyses of variance provided little insight into which environmental factors were important in differentiating growth responses to climatic variables. Although a number of environmental variables were significant ($P < 0.01$) in explaining differences among groupings, the amount of variation explained by individual factors was very low (table 5). This result was expected because of the nature of the data and its collection. The data base consisting of tree-ring series from 1843 individual trees selected from 267 sites located over a large geographic area was created to represent the forests of the Tennessee Valley and therefore incorporates a wide variety of site conditions and potential stresses. Trees were not selected to represent a specific suite of environmental variables, but rather to represent the population of each of these species within the region.

Discriminant analysis based on environmental variables collected in the study was generally successful in reclassifying tree-ring clusters. Total error count estimates ranged from 0% for northern red oaks at LBL, up to 75% for chestnut oaks at Emory River (table 6). Overall, site statistics outperformed individual tree statistics in discriminatory power, and when analyzed as multivariate data, presence and predominance of competing species was the most important factor influencing tree-ring groupings (table 7). Other factors that commonly had high canonical coefficient values included variables related to soil moisture conditions such as soil depths and textures, topographic position, and aspect; and variables related to changes in stand density, including current basal area, and basal areas of cut and mortality trees.

Table 5.--Results of one-way analyses of variance - average R²s weighted by variance for environmental variables, by site and species.

Site/Species	R ²
ERWO ¹	0.10
LBLWO	0.16
WCWO	0.16
ERCO	0.01
LBLCO	0.08
WCCO	0.12
ERNRO	0.15
LBLNRO	0.01
WCNRO	0.11
ERYP	0.07
LBLYP ²	-
WCYP	0.04

¹Site/Species identification consists of a combination of letters designating site: ER = Emory River, LBL = Land Between the Lakes, WC = Wayne County; followed by letters designating species: WO = white oak, CO = chestnut oak, NRO = northern red oak, and YP = yellow-poplar.

²LBL had only one grouping of yellow-poplar series.

Individual tree age was only important for Wayne County yellow-poplar, indicating that variability in growth response was not strongly influenced by changes in tree physiology.

DISCUSSION AND CONCLUSIONS

The results of this study indicate that, for the 4 hardwood species studied within the Tennessee Valley region, relationships between climatic variables and tree growth change over time. Maximum sensitivity to monthly values of temperature and precipitation did not coincide with extreme values of these variables. Instead, maximum sensitivity generally occurred at the beginning of the time series and decreased over time. Patterns of change in sensitivity (parameter coefficient values) were significantly different ($P < 0.001$) from random indicating a trend in the relationship. However, statistical tests indicated only random variation in the climatic data. This implies that tree growth sensitivity to climate is not merely a function of climate, or that other factors work to modify the influence of climate. In natural, mixed-species hardwood stands in the Tennessee Valley, these factors are apparently dynamic.

Table 6.--Error count estimates (percent) for linear discriminant functions on non-transformed data.

Species/Site	Cluster #									Total	
	1	2	3	4	5	6	7	8	9		
White oaks											
ER ¹	50	25	29	41	60	50	0	26	33	42	
LBL	15	56	11	44	33	35	53	32	28	36	
WC	23	26	30	26	40	24				27	
Chestnut oaks											
ER	54	63	60	52	63	53	75			57	
LBL	50	47	11	23						28	
WC	7	27	22							14	
Northern red oaks											
ER	21	20								21	
LBL	0	0								0	
WC	6	8	22							10	
Yellow-poplars											
ER	25	32	37	32						30	
LBL	-									-	
WC	0	11	43	27						20	

¹ER = Emory River; LBL = Land Between the Lakes; WC = Wayne County.

Table 7.--Environmental factors determined important in producing differences in tree growth response to climate from canonical discriminant analysis, by site and species.

Site/Species	Important Environmental Factors
ERWO ¹	Relative frequency and importance values for core tree species, presence of a fragipan
LBLWO	Relative frequency and importance values for core tree species, soil texture
WCWO	Relative frequency and importance values for core tree species, current basal area, elevation
ERCO	Relative frequency and importance values for core tree species, topographic position, presence of an argillic horizon
LBLCO	Relative frequency and importance values for core tree species, aspect
WCCO	Relative frequency and importance values for core tree species, aspect, topographic position, presence of insect damage
ERNRO	Relative frequency and importance values for core tree species, elevation, soil depth and texture
LBLNRO	Current basal area, size distribution of trees, basal area of mortality trees, slope, topographic position, aspect
WCNRO	Relative frequency and importance values for core tree species, grazing damage, aspect
ERYP	Relative frequency and importance values for core tree species, aspect, basal area of mortality trees, soil depth and texture
WCYP	Relative frequency and importance values for core tree species, slope, current basal area, basal area of cut trees, basal area of mortality trees, individual tree age

¹Site/Species identification consists of a combination of letters designating site: ER = Emory River, LBL = Land Between the Lakes, WC = Wayne County; followed by letters designating species: WO = white oak, CO = chestnut oak, NRO = northern red oak, and YP = yellow-poplar.

Factors that could modify climatic effects include those related to changes that occur within the individual or within the forest stand. Individual or physiological changes occurring within a single tree should be highly correlated with age or size. However, except for yellow-poplar at Wayne County, both of these variables lacked statistical significance in differentiating growth response patterns when analyzed as either univariate or multivariate data. However, factors representing changes in stand density were important for some clusters. Changes that occur within the forest stand may affect attributes associated with climate such as moisture availability which would appear as a change in sensitivity to climate in this analysis. It is well known that climatic extremes are buffered within a fully-developed forest stand through shading and the wind-breaking effect of stand structure (Daubenmire 1974, Haines and Cleveland 1981). Site conditions have also been shown to improve over time with stand development (Whittaker and Woodwell 1972, Carmean et al. 1976). The trend towards decreased growth sensitivity to climatic variables over time is synchronous with a period of increased forest protection and improved forest management within the Tennessee Valley. In general, this has resulted in a transition from poorly-stocked, cutover stands to more productive forests with increased stocking levels. Thus, it appears that decreases in individual tree sensitivity to climate are associated with stand development as the changes in stand structure and site quality buffer climatic variation.

Spatial variation in tree growth response to climate is more difficult to characterize. Univariate statistical analyses (one-way analyses of variance) were ineffective in identifying environmental factors important in producing the different patterns of growth response identified through cluster analysis. However, multivariate analyses of environmental factors were, in most cases, very effective in discriminating differences in patterns of annual increment. Unfortunately, these results are more difficult to interpret, as they indicate that interactions between environmental factors can significantly alter a tree's growth response.

Standardized coefficient values for canonical components indicate the relative importance of each environmental factor as it impacts the relationship between climate and growth. Overall, the most important factors were relative frequency and importance values for the predominant species. This indicates that differences in size and species composition of neighboring trees is associated with differences in pattern of growth response. This could reflect competitive interactions, signifying that trees behave differently according to the company they are in, or it may denote a difference in site quality or some type of ecological gradient. Ermich et al. (1976) suggested that homogeneity of tree growth patterns was related to site quality. Their premise was that low site quality results in increased susceptibility to additional stresses that increase the variability in annual increment among individuals. The results of the current study indicate that spatial heterogeneity increases as the predominance of a species on a site decreases, a fact that may be due to site quality, competitive interactions, or both.

Factors typically associated with soil moisture conditions were also identified as relatively important in producing differences in growth. As expected, there were identifiable differences in growth pattern between mesic and xeric sites. Trees on drier sites generally appeared more sensitive to climate (i.e. coefficient values were of greater magnitude). However, interactions with other, often more subtle, environmental factors exhibited the potential to alter characteristic growth patterns. For example, insect infestation on a mesic site was observed

to increase tree sensitivity to climate producing a response more typical of a tree located at a drier site.

The literature on forest tree growth indicates that there is a great deal of both temporal and spatial variability in tree growth response to climate, and that reasons for the variability are not obvious. The results of this study were similar to those reported in the literature. Temporal variability in growth response to climate can be characterized as a trend towards decreased sensitivity to climate that apparently occurs primarily as a result of stand development rather than as a function of changes in individual trees. Spatial variability was profound, occurring in part as a result of changes in site conditions and potentially as a function of competitive interactions among individual trees of different species. Environmental factors were generally useful in explaining similarities in growth response to climate among individual trees, as long as interactions between factors were incorporated into the analysis. Use of additional site variables, information specific to individual trees, and more detailed climate data might provide a better understanding of what response to climate might be expected under various combinations of environmental factors.

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COMMUNITY AND EDAPHIC ANALYSIS OF MIXED OAK FORESTS IN THE
RIDGE AND VALLEY PROVINCE OF CENTRAL PENNSYLVANIA

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Abstract: Forty-two relatively undisturbed mixed oak stands on nine different physiographic units in the Ridge and Valley Province of central Pennsylvania were surveyed to investigate the ecological status of oak species in the region. *Quercus* species were primarily restricted to the canopy, with the exception of *Quercus ilicifolia* Wangenh. (a shrub). The most species rich forest stands were located along an indented stream and on fine-textured, valley floor sites where *Quercus alba* L., *Quercus velutina* Lam. and/or *Quercus rubra* L. dominated the overstories and *Acer rubrum* L. and *Prunus serotina* Ehrh. dominated the understories. The importance of *Quercus prinus* L. was positively correlated with percent sand and elevation, and this species dominated steep inclines and xeric ridgetop communities. *Quercus velutina*, *Carya* spp. and *Q. rubra* occurred on all topographic sites, however the latter was most abundant on cool, north-facing slopes.

Most present-day stands were initiated following heavy cutting and fire around the 1900's, and the oak component tended to be even-aged. Regeneration data suggest that succession to more shade tolerant species, primarily *A. rubrum*, is occurring in all but the most xeric oak stands. Frequent understory associates with *A. rubrum* included *P. serotina*, *Acer saccharum* Marsh. and *Fraxinus americana* L. on mesic toe slopes, indented stream bank and valley floor sites and *Betula lenta* L. and *Acer pensylvanicum* L. on and near ridgetops. Although *Quercus* species were well represented as seedlings in most stands, recruitment into larger classes was infrequent, except on the driest sites.

INTRODUCTION

The topography of Ridge and Valley Province of central Pennsylvania leads to an diverse floristic pattern across the landscape, in which *Quercus* species predominate. Typical of most eastern forests, large-scale logging and subsequent fires following European settlement drastically altered the original vegetation in central Pennsylvania (Hough and Forbes 1943, Whitney 1987, Crow 1988, Nowacki et al. 1990). Braun (1950) had classified this area as oak-chestnut (*Castanea dentata* [Marsh.] Borkh.) forest type, though most ecologists now consider it an oak-hickory (*Carya* spp.) or mixed-oak association (Keever 1953, McCormick and Platt 1980, Johnson and Ware 1982). Braun also suggested that the mixed mesophytic

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forest is the potential climax in the region, but that topographic diversity would lead to physiographic or edaphic climaxes, including mixed oak communities on mountain slopes, hemlock-dominated (*Tsuga canadensis* [L.] Carr.) communities within mountain coves, white oak (*Q. alba*) forests on valley floors and mixed mesophytic communities on ravine slopes along indented streams. Whether the oak communities are actually true or edaphic climaxes in this or other regions of eastern North America is uncertain. Recent studies indicate a transition from oak to more shade tolerant species in many forests (Christensen 1977, Lorimer 1984, Parker et al. 1985, Abrams 1986, McGee 1986, Nowacki et al. 1990). Successional trends in oak forests of central Pennsylvania have not been well established, although regional surveys indicate poor oak development under shaded conditions (Lorimer 1984, Russell and Schuyler 1988, Abrams and Downs 1990).

In this study, mixed oak stands on nine different physiographic units in the Ridge and Valley Province in central Pennsylvania were surveyed to investigate the effect of edaphic factors on stand composition and structure. From these data we attempt to predict the successional status of mixed oak forests in the region and how successional pathways may vary with physiographic changes.

METHODS

During the summers of 1988-1989, 42 relatively undisturbed mixed oak forests in central Pennsylvania were surveyed. Stands selected for sampling were 1) relatively homogeneous vegetative units located on uniform topography and restricted to a single soil type and 2) showed little or no evidence of recent disturbance by fire, cutting, etc. Trees (≥ 10 cm dbh) were sampled using the point-quarter method (Cottam and Curtis 1956) at 20 points within each stand. Points were systematically located along transects at intervals of 20 to 30 m depending on stand size. Transects were positioned to avoid forest edges. Tree information included distance from the sample point, dbh, species name and canopy position (dominant, codominant, intermediate, or overtopped). Crown class definitions followed those of Smith (1986).

Saplings and seedlings were recorded by species at each sampling point within nested circular plots of 10 and 5 m², respectively. Saplings were classified as tree species < 10 cm at dbh but ≥ 1.5 m in height, whereas seedlings were < 1.5 m in height. Average slope and aspect were estimated for each stand using a clinometer, compass and topographic maps.

Soils were described at a centrally-located pit within each stand. Horizons comprising the upper 50 cm solum were identified and their depth recorded. Soil samples were collected from the mineral surface (A or E horizon) for particle-size analysis using the Hydrometer Method (Bouyoucos 1962). Soil pH was also recorded by use of a pH meter (calibrated at pH 4.0) and a prepared soil slurry consisting of 5 g soil and 10 ml distilled water.

Species importance percentages were calculated from the tree data for each stand (importance percentage = [relative density + relative dominance + relative frequency]/3; Cottam and Curtis

1956). Statistical analyses were accomplished using simple correlation, ANOVA and Scheffe's mean separation procedure at $p < 0.05$.

Table 1.--Edaphic features of the nine physiographic units studied in the Ridge and Valley Province of central Pennsylvania.

Physio. Unit	% sand	% silt	% clay	pH	Predominant texture	Representative soil type	% slope ¹	Elev. ¹ (m)
Stream	46 ^{ab}	41 ^{ab}	14 ^a	6.1 ^b	loam	Ultic Hapludalfs	19 _± 6	306 _± 6
Fine-Valley	26 ^a	59 ^a	15 ^a	4.9 ^a	silt loam	Typic Hapludalfs	7 _± 1	344 _± 6
Cove	65 ^{ab}	27 ^b	8 ^a	3.5 ^c	sandy loam	Typic Fragidults	7 _± 3	547 _± 21
North-Lower	52 ^{ab}	34 ^b	14 ^a	4.3 ^{ac}	loam	Typic Fragidults	28 _± 3	464 _± 4
South-Lower	53 ^{ab}	34 ^{ab}	14 ^a	4.4 ^{ac}	loam	Typic Fragidults	30 _± 0	472 _± 1
North-Upper	60 ^{ab}	30 ^{ab}	10 ^a	3.9 ^{ac}	loam	Typic Dystrochrepts	35 _± 6	501 _± 21
South-Upper	67 ^b	26 ^b	7 ^a	3.7 ^c	sandy loam	Typic Dystrochrepts	28 _± 7	568 _± 16
Coarse-Valley	70 ^b	21 ^b	9 ^a	4.1 ^{ac}	sandy loam	Ultic Hapludalfs	6 _± 1	407 _± 9
Crest	75 ^b	19 ^b	6 ^a	4.1 ^{ac}	sandy loam	Typic Dystrochrepts	4 _± 0	598 _± 22

¹ Mean_±S.E.

Values in a column with the same letter are not significantly different at $p < 0.05$.

RESULTS

Stand Classification Based On Edaphic Factors

Forty-two forest stands were grouped into nine physiographic units based on topographic position and soil characteristics (Table 1). The physiographic groups were indented stream bank, fine textured-valley floor, coarse textured-valley floor, cove, northern-lower slope, northern-upper slope, crest, southern-upper slope, and southern-lower slope (Fig. 1). Soil factors were correlated with changes in elevation. In particular, percent sand increased and percent silt, clay and pH decreased with elevation ($p < 0.05$, $r = .58, -.57, -.49$ and $-.77$, respectively). Fine textured-valley sites contained significantly less sand and more silt than coarse textured-valley, crest, and southern-upper sites (Table 1). Average soil pH was highest

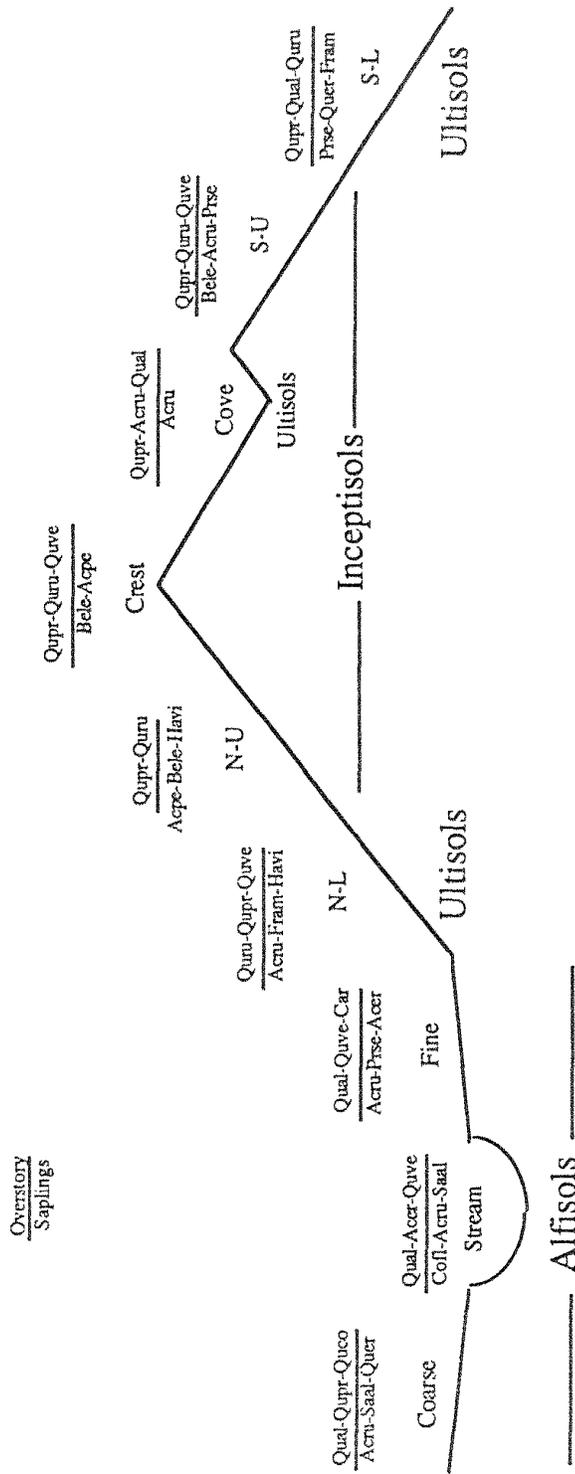


Figure 1. Dominant overstory and regenerating species on nine physiographic areas in the Ridge and Valley Province of central Pennsylvania arranged along a topographic gradient.
 Acer=*Acer saccharum/platanoides*, Acpe=*Acer pensylvanicum*, Acru=*Acer rubrum*, Bele=*Betula lenta*, Car=*Carya* spp., Cofl=*Cornus florida*, Fram=*Fraxinus americana*, Havi=*Hamamelis virginiana*, Prse=*Prunus serotina*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Quer=*Quercus* spp., Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*, Saal=*Sassafras albidum*.

along streams, intermediate on valley sites and lower slopes and lowest on upper slopes and coves. A general shift in soil type occurred with elevation, with Alfisols dominating valley floor and stream bank sites, Ultisols along lower slopes and coves and Inceptisols located on upper slopes and ridgetops (Fig. 1).

Stand Composition and Structure

The overstory of all groups was dominated by *Quercus* (Fig. 1 and 2), however significant differences in species importance occurred among groups (Table 2). The three most abundant oaks, *Q. alba*, *Q. rubra*, and *Q. prinus*, varied with elevation. *Quercus alba* was most important on gently sloping, valley and indented stream locations, although it was also important in mesic cove forests. *Quercus alba* importance was negatively correlated with slope ($r = -.38$), elevation ($r = -.50$) and the importance of *Q. rubra* and *Q. prinus* ($r = -.66$ and $-.67$, respectively). *Quercus rubra* and *Q. prinus* were most abundant on lower slopes and crest sites, respectively. *Quercus prinus* importance was correlated with percent sand, silt, clay, elevation, and pH ($r = .56, -.54, -.49, .79$ and $-.58$, respectively). Similar to *Q. alba*, *Quercus coccinea* Muenchh. was most frequent on valley sites, although it was associated with coarser soils. *Quercus velutina* was fairly common on all sites, but its highest importance occurred at lower elevations. Overstory trees other than *Quercus* were primarily *A. rubrum*, *A. saccharum*, *Pinus strobus* L., *P. serotina*, and *Carya* spp. Most of these species were infrequent, intermediate in crown size, and restricted to stream bank, valley floor and/or cove sites.

A larger number of species were present as understory trees, including *Quercus*, *Carya*, *Acer*, *Prunus* and *P. strobus* (Fig. 2). In general, understory trees of *Quercus* were most abundant on xeric areas (i.e. coarse textured-valley, crest, and upper slope sites) and in younger stands regardless of physiographic location. *Carya*, *Acer*, *Prunus* and *P. strobus* were most abundant in the understory on stream banks and fine textured-valley sites. *Acer rubrum* was a common understory tree in most stands.

Regeneration Trends Across An Environmental Gradient

Total seedling number tended to be greatest on the coarse textured-valley sites and least on the upper slopes (Table 3). Seedling number was negatively correlated with stand basal area and percent slope ($p < 0.05$, $r = -.43$ and $-.41$). *Quercus* species were well represented as seedlings in all physiographic units and seedling density closely followed importance values of the overstory species. Seedlings of *Q. alba* were most abundant on stream bank and valley sites, *Q. rubra* on slopes and *Q. prinus* on slopes, ridges and coarse textured-valley sites. *Quercus prinus* seedlings were significantly correlated with percent sand, silt and clay ($p < 0.05$, $r = .50, -.47$ and $-.42$, respectively), as exhibited with its overstory importance. *Acer rubrum* and *P. serotina* were common seedlings on all sites, however the latter were most

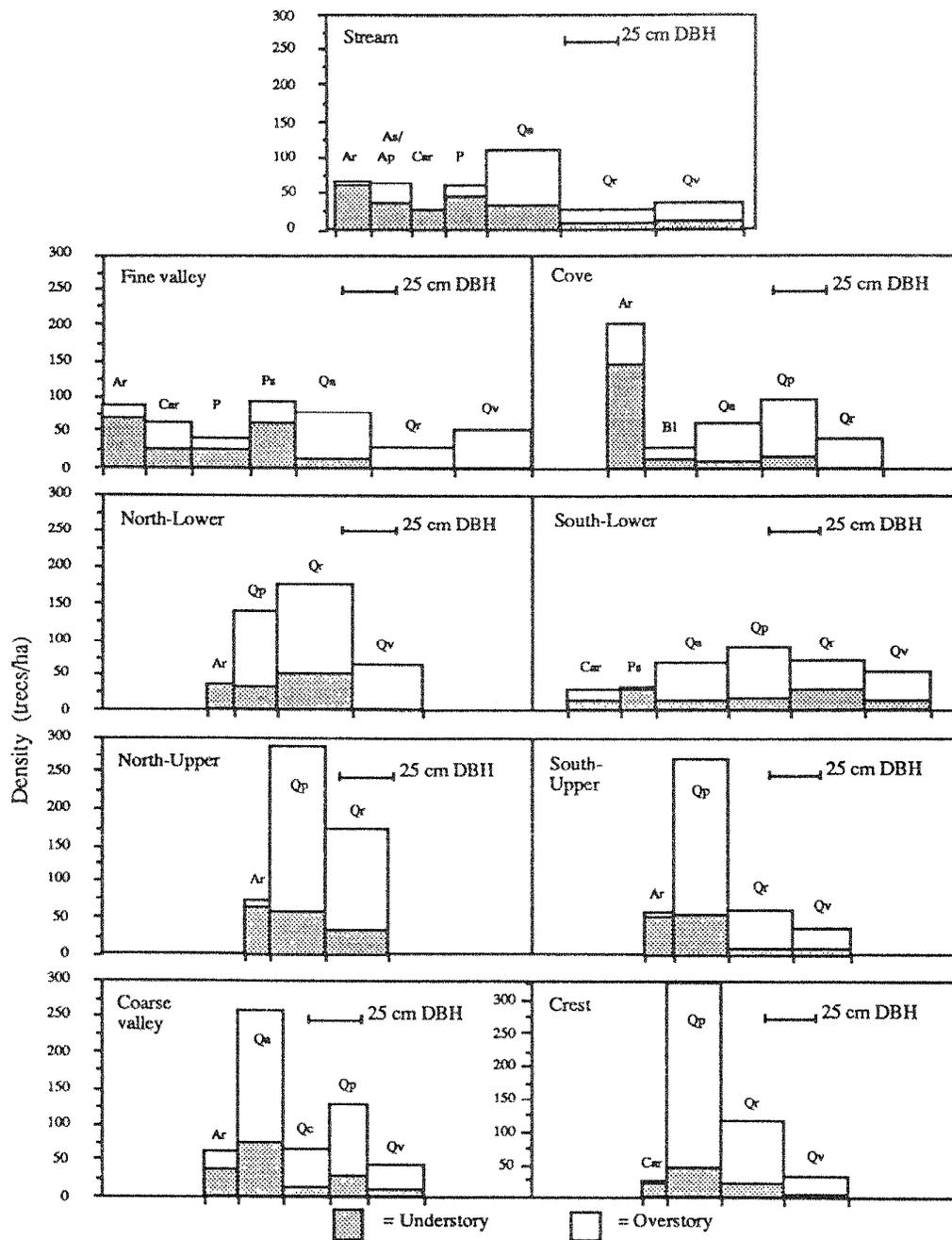


Figure 2. Stand structure on nine physiographic areas in the Ridge and Valley Province of central Pennsylvania based on mean density of overstory and understory trees and mean diameter of principal species (mean importance percentages of 5 or greater). Ar=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bl=*Betula lenta*, Car=*Carya* spp., P=*Pinus strobus*, Ps=*Prunus serotina*, Qa=*Quercus alba*, Qc=*Quercus coccinea*, Qp=*Quercus prinus*, Qr=*Quercus rubra*, Qv=*Quercus velutina*.

Table 2.--Mean importance percentages¹ (+S.E.) of principal species and mean stand density (trees/ha) and basal area (m²/ha) of 42 mixed oak forest stands organized by physiographic unit.

	Fine Stream Valley Cove			North Lower	South Lower	North Upper	South Upper	Coarse Valley	Crest
Acru	10+3 ^{ab}	15+2 ^{ab}	30+5 ^b	6+2 ^a	1+0 ^a	9+7 ^{ab}	10+4 ^{ab}	10+2 ^a	2+1 ^a
As/Ap	8+6 ^a	2+1 ^a	0+0 ^a	0+0 ^a	1+1 ^a	0+0 ^a	0+0 ^a	0+0 ^a	0+0 ^a
Bele	0+0 ^{ab}	0+0 ^a	6+4 ^b	2+1 ^{ab}	0+0 ^{ab}	1+1 ^{ab}	1+1 ^{ab}	0+0 ^a	2+1 ^{ab}
Carya*	5+1 ^a	11+3 ^a	3+3 ^a	1+1 ^a	9+5 ^a	1+1 ^a	3+3 ^a	2+1 ^a	5+1 ^a
Pist*	9+4 ^a	8+3 ^a	0+0 ^a	1+1 ^a	1+1 ^a	4+2 ^a	2+2 ^a	1+1 ^a	0+0 ^a
Prav	1+1 ^a	3+2 ^a	0+0 ^a	0+0 ^a	1+0 ^a	0+0 ^a	0+0 ^a	0+0 ^a	0+0 ^a
Prse	4+2 ^b	15+2 ^a	1+1 ^b	1+1 ^b	7+2 ^{ab}	0+0 ^b	0+0 ^b	1+1 ^b	1+1 ^b
Qual	27+9 ^{ab}	20+5 ^{ab}	15+9 ^{ab}	1+1 ^b	18+3 ^{ab}	0+0 ^{ab}	1+1 ^b	38+9 ^a	1+1 ^{ab}
Quco	4+2 ^{ab}	1+1 ^a	2+2 ^{ab}	0+0 ^a	1+0 ^{ab}	0+0 ^a	1+0 ^a	14+3 ^b	0+0 ^a
Qupr	0+0 ^{ab}	0+0 ^a	22+1 ^{abc}	32+6 ^{abc}	22+5 ^{abc}	47+1 ^{bc}	52+8 ^c	17+9 ^{abc}	54+4 ^c
Quru	9+3 ^{ac}	8+4 ^a	11+4 ^{ac}	39+4 ^b	19+3 ^{ab}	34+6 ^{bc}	17+5 ^{ab}	3+2 ^a	27+1 ^{ab}
Quve	11+4 ^a	15+5 ^a	5+3 ^a	13+5 ^a	14+5 ^a	1+1 ^a	10+4 ^a	10+3 ^a	8+2 ^a
# of Stands	4	7	3	5	3	3	5	9	3
Density	507 ^a	498 ^a	501 ^a	478 ^a	390 ^a	575 ^a	472 ^a	617 ^a	530 ^a
Basal Area	34 ^{ab}	35 ^a	24 ^{ab}	37 ^a	30 ^{ab}	31 ^{ab}	24 ^{ab}	20 ^b	31 ^{ab}

¹ Importance percentage = (relative density + relative dominance + relative frequency)/3. Values in a row with the same letter are not significantly different at p < 0.05.

* Significant differences based on ANOVA, but not detected by Scheffe's mean separation procedure.

Acru=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bele=*Betula lenta*, Carya=*Carya* species, Pist=*Pinus strobus*, Prav=*Prunus avium*, Prse=*Prunus serotina*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*.

abundant on southern lower slopes and fine textured-valley sites. *Acer saccharum*, *Acer platanoides* L. and *Prunus avium* L. seedlings were restricted primarily to mesic sites, specifically fine textured-valley and stream bank sites. In contrast, *A. pensylvanicum* and *B. lenta* seedlings occurred primarily on more severe, ridge sites.

Sapling density was not consistent among species, although higher density was skewed towards shade tolerant species (Table 4). The most prevalent sapling was *A. rubrum*, which commonly occurred on all physiographic sites. *Prunus serotina* saplings were similar in number to *A. rubrum* on all sites except for coarse textured-valley and cove sites. *Acer saccharum*, *A. platanoides* and *Cornus florida* L. were frequent saplings in mesic, fine

Table 3.--Mean seedling number (stems/ha) of principal species of 42 mixed oak forest stands organized by physiographic unit.

	Stream	Fine Valley	Cove	North Lower	South Lower	North Upper	South Upper	Coarse Valley	Crest
Acpe	0 ^a	0 ^a	900 ^{ab}	380 ^a	0 ^a	6733 ^{ab}	1180 ^a	11 ^a	13600 ^b
Acru	20200 ^a	6329 ^a	57033 ^a	15440 ^a	4100 ^a	7767 ^a	10980 ^a	36322 ^a	9200 ^a
As/Ap	3225 ^a	3886 ^a	0 ^a	20 ^a	33 ^a	0 ^a	0 ^a	0 ^a	0 ^a
Bele [*]	0 ^a	0 ^a	1567 ^a	420 ^a	0 ^a	433 ^a	480 ^a	11 ^a	4333 ^a
Carya [*]	1125 ^a	857 ^a	0 ^a	1560 ^a	1733 ^a	467 ^a	200 ^a	633 ^a	367 ^a
Cade [*]	0 ^a	0 ^a	0 ^a	60 ^a	0 ^a	33 ^a	20 ^a	244 ^a	0 ^a
Cofl	925 ^a	386 ^a	33 ^a	100 ^a	67 ^a	0 ^a	0 ^a	89 ^a	267 ^a
Fram	3025 ^{ab}	1171 ^{ab}	33 ^{ab}	10700 ^b	11067 ^{ab}	467 ^{ab}	500 ^{ab}	222 ^a	0 ^{ab}
Havi [*]	600 ^a	43 ^a	633 ^a	1520 ^a	0 ^a	1067 ^a	500 ^a	33 ^a	500 ^a
Nysy	0 ^a	0 ^a	300 ^a	100 ^a	0 ^a	0 ^a	340 ^a	0 ^a	0 ^a
Osvi [*]	1650 ^a	43 ^a	0 ^a	200 ^a	0 ^a	0 ^a	0 ^a	44 ^a	0 ^a
Pist	425 ^a	0 ^a	200 ^a	0 ^a	0 ^a	33 ^a	0 ^a	67 ^a	0 ^a
Prav [*]	325 ^a	6629 ^a	0 ^a	20 ^a	67 ^a	0 ^a	20 ^a	56 ^a	0 ^a
Prse	5075 ^{ab}	14457 ^{ab}	2933 ^{ab}	2660 ^a	27333 ^{ab}	2333 ^{ab}	5420 ^b	6100 ^{ab}	3067 ^{ab}
Prvi [*]	0 ^{ab}	8686 ^a	0 ^{ab}	60 ^{ab}	67 ^{ab}	0 ^{ab}	80 ^{ab}	11 ^b	0 ^{ab}
Qual [*]	3575 ^a	3557 ^a	3800 ^a	200 ^a	4233 ^a	0 ^a	20 ^a	29589 ^a	0 ^a
Quco	325 ^a	29 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	2200 ^b	0 ^a
Quil	0 ^{ab}	0 ^a	0 ^{ab}	0 ^{ab}	0 ^{ab}	0 ^{ab}	0 ^{ab}	2933 ^b	0 ^{ab}
Qupr	0 ^a	43 ^a	3700 ^a	6560 ^a	26267 ^a	19333 ^a	14640 ^a	28756 ^a	10207 ^a
Quru [*]	400 ^a	271 ^a	533 ^a	2200 ^a	1333 ^a	1600 ^a	1880 ^a	756 ^a	1100 ^a
Quve [*]	1050 ^a	314 ^a	233 ^a	780 ^a	2133 ^a	333 ^a	1020 ^a	2178 ^a	1533 ^a
Saal [*]	4450 ^a	0 ^a	200 ^a	20 ^a	133 ^a	267 ^a	720 ^a	6444 ^a	67 ^a
Total	51675 ^{ab}	48786 ^a	96000 ^{ab}	44280 ^a	82667 ^a	42467 ^{ab}	39060 ^{ab}	124744 ^b	44700 ^{ab}

Values in a row with the same letter are not significantly different at $p < 0.05$.

* Significant differences based on ANOVA, but not detected by Scheffe's mean separation procedure.

Acpe=*Acer pensylvanicum*, Acru=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bele=*Betula lenta*, Carya=*Carya* spp., Cade=*Castanea dentata*, Cofl=*Cornus florida*, Fram=*Fraxinus americana*, Havi=*Hamamelis virginiana*, Nysy=*Nyssa sylvatica*, Osvi=*Ostrya virginiana*, Pist=*Pinus strobus*, Prav=*Prunus avium*, Prse=*Prunus serotina*, Prvi=*Prunus virginiana*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Quil=*Quercus ilicifolia*, Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*, Saal=*Sassafras albidum*.

textured-valley and stream bank communities, whereas *Hamamelis virginiana* L., *A. pensylvanicum*, and *B. lenta* saplings were common on slopes and ridgetops. The latter two species were positively correlated with elevation ($p < 0.05$, $r = .36$ and $.37$, respectively). *Sassafras albidum* (Nutt.) Nees saplings frequently occurred on coarse textured-valley sites.

Table 4.--Mean sapling number (stems/ha) of principal species of 42 mixed oak forest stands organized by physiographic unit.

	Fine Stream Valley		Cove	North Lower	South Lower	North Upper	South Upper	Coarse Valley	Crest
Acpe*	0 ^a	0 ^a	0 ^a	170 ^a	0 ^a	1467 ^a	50 ^a	0 ^a	1017 ^a
Acru	187 ^a	1136 ^a	2250 ^a	420 ^a	100 ^a	67 ^a	440 ^a	1333 ^a	50 ^a
As/Ap	62 ^a	321 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a
Bele	0 ^a	0 ^a	87 ^a	146 ^a	29 ^a	987 ^a	442 ^a	17 ^a	2330 ^a
Carya	25 ^a	50 ^a	0 ^a	110 ^a	133 ^a	0 ^a	20 ^a	33 ^a	0 ^a
Cade	0 ^a	0 ^a	0 ^a	10 ^a	10 ^a	0 ^a	0 ^a	89 ^a	0 ^a
Cofl	475 ^b	129 ^{ab}	0 ^a	40 ^a	50 ^a	17 ^a	0 ^a	28 ^a	0 ^a
Fram	25 ^a	250 ^a	0 ^a	280 ^a	150 ^a	33 ^a	0 ^a	6 ^a	0 ^a
Havi	0 ^{ab}	0 ^a	17 ^{ab}	270 ^b	0 ^{ab}	100 ^{ab}	20 ^{ab}	0 ^a	67 ^{ab}
Nysy	0 ^a	0 ^a	33 ^a	10 ^a	20 ^a	0 ^a	0 ^a	0 ^a	0 ^a
Osvi	87 ^a	14 ^a	0 ^a	40 ^a	0 ^a	0 ^a	0 ^a	22 ^a	0 ^a
Pist	13 ^a	7 ^a	0 ^a	0 ^a	30 ^a	0 ^a	0 ^a	44 ^a	0 ^a
Prav	0 ^a	71 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a
Prse	62 ^a	729 ^a	33 ^a	80 ^a	1850 ^b	67 ^a	190 ^a	128 ^a	17 ^a
Prvi*	0 ^a	129 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a
Qual	13 ^a	0 ^a	0 ^a	0 ^a	50 ^a	0 ^a	0 ^a	83 ^a	0 ^a
Quco	13 ^a	0 ^a	83 ^a	0 ^a					
Quil	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	0 ^a	94 ^a	0 ^a
Qupr	0 ^a	0 ^a	0 ^a	10 ^a	50 ^a	0 ^a	10 ^a	78 ^a	0 ^a
Quru	13 ^a	14 ^a	0 ^a	30 ^a	33 ^a	17 ^a	10 ^a	6 ^a	0 ^a
Saal	187 ^{ab}	7 ^a	0 ^{ab}	0 ^a	10 ^a	0 ^{ab}	0 ^{ab}	456 ^b	0 ^{ab}
Total	1350 ^a	3000 ^a	2400 ^a	1580 ^a	2917 ^a	2450 ^a	1050 ^a	2583 ^a	2667 ^a

Values in a row with the same letter are not significantly different at $p < 0.05$.

* Significant differences based on ANOVA, but not detected by Scheffe's mean separation procedure.

Acpe=*Acer pensylvanicum*, Acru=*Acer rubrum*, As/Ap=*Acer saccharum/platanoides*, Bele=*Betula lenta*, Carya=*Carya* spp., Cade=*Castanea dentata*, Cofl=*Cornus florida*.

Fram=*Fraxinus americana*, Havi=*Hamamelis virginiana*, Nysy=*Nyssa sylvatica*, Osvi=*Ostrya virginiana*, Pist=*Pinus strobus*, Prav=*Prunus avium*, Prse=*Prunus serotina*, Prvi=*Prunus virginiana*, Qual=*Quercus alba*, Quco=*Quercus coccinea*, Quil=*Quercus ilicifolia*, Qupr=*Quercus prinus*, Quru=*Quercus rubra*, Quve=*Quercus velutina*, Saal=*Sassafras albidum*.

DISCUSSION

Mixed oak forests of the Ridge and Valley Province of central Pennsylvania differ appreciably in composition and structure due to differences in edaphic factors. General

decreases in soil moisture with increasing elevation from mesic indented stream sites to xeric ridgetops occurred due to increases in percent sand and slope, decreases in soil thickness and percent silt and clay, and changes in substrate (limestone to sandstone) and soil type (Alfisol to Inceptisol)(cf. Whittaker 1956). This gradient is rather uniform across the landscape except for two physiographic outliers, the coarse textured-valley floor and cove units. These units encompass xerophytic and mesophytic communities, respectively, which contrast sharply with surrounding forests. Otherwise, changes in forest composition were rather subtle between adjoining physiographic units, representing a continuum of community organization (Gleason 1926). Although changes in forest composition seemed to be closely linked with moisture availability, changes in fertility and pH may also play important roles (Peet and Loucks 1977, Balter and Loeb 1983, Campbell 1987).

Quercus species were consistently the largest and presumably oldest individuals on all sites, and dominated the overstories of all physiographic units. These attributes seem to be quite characteristic of *Quercus* in other eastern forests (Cottam 1949, Parker et al. 1985, Abrams 1986, McGee 1986, Nowacki et al. 1990). General shifts in *Quercus* dominance from *Q. alba* through *Q. rubra* to *Q. prinus* occurred from mesic to xeric sites, and is consistent with regional surveys (Niering 1953, Keever 1973, Overlease 1978, Russell and Schuyler 1988). In contrast, both coarse textured-valley and cove sites had overstories dominated by *Q. alba* and *Q. prinus*. This is rather unusual considering that these two physiographic units occur at the opposite extremes of the moisture spectrum and the co-occurrence of these two species on other sites is infrequent.

The mixed oak forests in this study are considered early- to mid-successional on most sites based on regeneration trends. Replacement of the oak component to varying degrees by more shade tolerant species seems likely in the future, though the transition may be rather gradual due to long life span of *Quercus* species (Abrams and Downs 1990). Understory trees and saplings are probably the best predictor of future composition, barring large-scale disturbances to the site (cf. Ohmann and Buell 1968). On mesic sites, *A. rubrum* and *P. serotina* were the most abundant understory species, which is consistent with other forests in the region (Gysel and Arend 1953, Crow and Miller 1983, Lorimer 1984, Russell and Schuyler 1988, Abrams and Downs 1990). The distribution of *A. rubrum* on a wide variety of sites in central Pennsylvania can be explained, in part, by genotypic variation and physiological plasticity (Abrams and Kubiske 1990). Some studies indicate poor performance of *P. serotina* in understory conditions (cf. Mackey and Sivec 1973), however we found this species growing rather vigorously and recruiting well in most cases. *Acer saccharum*, usually a dominant understory species in other *Quercus* forests (Crow and Miller 1983, Parker et al. 1985, Nowacki et al. 1990), was lacking on most mesic areas, probably due to its low overstory importance in the area. On the drier upper slopes, trends towards *A. pensylvanicum*, *H. virginiana*, *B. lenta*, *A. rubrum* were apparent, though only the latter two species have overstory potential. Regeneration on the crest was primarily made up of *B. lenta* and *A. pensylvanicum*. Successful seedling-to-sapling recruitment of *Quercus* species occurred only on coarse textured-valley floor locations, combining with *A. rubrum*, *P. strobus* and *S. albidum* to form the understory. Abundant *Quercus* regeneration on xeric sites has been documented elsewhere (Gysel and Arend 1953, Overlease 1978, McCune and Cottom 1985,

Abrams 1986), and may be explained by higher light levels at the forest floor and fewer competing seedlings of less drought tolerant species. We conclude from these data that future decreases of *Quercus* will probably occur, with corresponding increases of *A. rubrum* and *P. serotina* on mesic sites and *A. rubrum* and *B. lenta* on drier slopes and ridgetops. In the most xeric communities, *Quercus* seems to be a rather stable component, although slight increases in *A. rubrum*, *S. albidum* and/or *B. lenta* may occur.

Betula lenta often dominates recently disturbed areas in central Pennsylvania, however it can also occur in shaded forest understories (Fowells 1965). Successional trends in this and other studies of northeastern forests suggest that *B. lenta* has been increasing in importance over the past few decades, possibly in response to canopy gaps (Good 1968, Russell and Schuyler 1988, Loeb 1990). Nonetheless, the distribution of *B. lenta* in this study was restricted to high-elevational or xeric valley-floor forests.

Present-day mixed oak stands seem to be intrinsically linked with intense anthropogenic disturbances. Most stands included in the survey are associated with recurring logging and fire from 1760 to 1900. Even though *Quercus* species were an important component in eastern presettlement forests (Sears 1925, Braun 1950, Spurr 1951, Russell 1981, Abrams and Downs 1990), it seems likely that their dominance has been maintained or even promoted from recurring disturbances due to their resistance to fire and competitiveness in post-disturbance environments (Lorimer 1985, Crow 1988, Lorimer 1989, Nowacki et al. 1990). However, decreased disturbance this century has led to conditions favoring shade tolerant species, with few opportunities for *Quercus* establishment and canopy recruitment. Under today's low-disturbance regime, *Quercus* species will most likely decline on all but the most xeric sites.

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EXTRAPOLATION OF FOREST COMMUNITY TYPES WITH A GEOGRAPHIC INFORMATION SYSTEM

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Abstract: A geographic information system (GIS) was used to project eight forest community types from a 1,190-acre (482-ha) intensively sampled area to an unsampled 19,887-acre (8,054-ha) adjacent area with similar environments on the Western Highland Rim of Tennessee. Both physiographic and vegetative parameters were used to distinguish, extrapolate, and map communities. Accuracy of the GIS-generated community map was tested by sampling community types from 211 plots and assessing whether the predicted communities actually occurred. Probability statements were formulated to assess map accuracy within a specified confidence level for each community type. The extrapolated composite community map was 85 percent correct at the 90 percent confidence level. Maps of six community types - American beech, northern red oak, black oak-hickory, yellow-poplar, post oak, and scarlet oak - were also 85 percent correct at the 90 percent confidence level. The map was accurate less often, 70 percent and 80 percent correct at the 90 percent confidence level, for American sycamore-sweetgum and chestnut oak communities respectively. These results indicate that when forest communities across a landscape are similar in species composition, structure, and physiography, sampling and inventories of these communities can be reduced or eliminated.

INTRODUCTION

The use of Geographic Information Systems (GIS) by natural resource organizations has expanded greatly beyond just map making capabilities in the last 5 years. Lipscomb and Williams (1989) described some of the more specific uses of a GIS for forest management activities such as fire weather danger simulations and logging transportation costs. The Tennessee Wildlife Resources Agency (TWRA) is using its system as a tool to model wildlife habitat parameters for improved management of wildlife species (Davis 1982). The objective of this paper was to determine if GIS technology could be used to model and predict with an acceptable degree of confidence, forest attributes or community types across the landscape. Can a vegetational and physiographic database obtained from intensively sampled portions of the landscape be used to accurately describe forest communities with similar biotic and physiographic environments? Such a process would conserve substantial sampling and

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inventory costs while generating forest community databases for wildlife habitat management much more quickly than could be obtained through 100 percent inventories.

STUDY AREA

The study was conducted on the 19,887-acre (8,054-ha) Cheatham Wildlife Management Area (CWMA), situated in the Western Highland Rim physiographic region of Tennessee (Fenneman 1938), and managed by the TWRA. The CWMA is located approximately 25 miles (40 km) west of Nashville, TN (36012'N, 8705'W). Braun (1950) described the vegetation of the Western Highland Rim as part of the Western Mesophytic Forest, a transition area between the Mixed Mesophytic Forest Region of the mountains to the east and the Oak-Hickory Region to the west. The CWMA consists of narrow to broad ridges, steep dissected side slopes, and V-shaped upland stream valleys. Elevations range from 480 ft (146 m) in the valleys to 820 ft (250 m) on the ridges. Site index for upland oaks ranges from 55 ft (17 m) at 50 years on the exposed dry south slopes to 85 ft (26 m) on the well-drained footslopes and cooler moist north slopes (Schnur 1937).

According to Smalley's (1980) hierarchical classification of forest sites, the CWMA is within the Highland Rim and Pennyroyal physiographic province, Western Highland Rim region, Highland Rim plateau subregion, and two landtype associations: strongly dissected plateau and moderately dissected plateau. Six landtypes from the two landtype associations are present on the CWMA: narrow ridges and convex upper slopes; broad ridges - north aspect; broad ridges - south aspect; cherty north slopes; cherty south slopes; and footslopes, terraces, streambottoms, and upland depressions with good drainage (Smalley 1980). Agronomical, climatological, and geological characteristics of the region are described by Smalley (1980). Prevalent tree species on the study area include white oak (*Quercus alba* L.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muenchh.), post oak (*Q. stellata* Wangenh.), chestnut oak (*Q. prinus* L.), hickories (*Carya* spp.), yellow-poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), sweetgum (*Liquidambar styraciflua* L.), white ash (*Fraxinus americana* L.), American sycamore (*Platanus occidentalis* L.), dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* Marsh.), sourwood (*Oxydendrum arboreum* L.), and sassafras (*Sassafras albidum* (Nutt.) Nees).

PROCEDURES

In a previous study, eight statistically discrete community types (yellow-poplar, northern red oak, post oak, American beech, chestnut oak, scarlet oak, black oak-hickory, and sycamore-sweetgum) were defined and mapped on an intensively sampled 1,190-acre (482-ha)

compartment within the CWMA.² The community classification was expanded to cover the entire 19,887-acre (8,054-ha) CWMA. The process of projecting these community types to unsampled areas will be referred to as extrapolation in this paper. The variation and landscape heterogeneity associated with the community classification system were recognized and accepted as a source of the variation encountered during the extrapolation process.

GIS Extrapolation

The extrapolation procedure involves two steps. We first describe or define each community according to physiographic features, i.e., landtype, topographic slope, aspect, and then integrated these features to produce maps of forest community types. The second step involves evaluating the accuracy of the community map. Thus, the extrapolation procedure is not only a test of differentiating and defining communities by physiographic parameters, but also a test of projecting those parameters or community entities on the landscape.

The projection of the community classification system on the landscape was accomplished with a Geographic Information System (GIS) that assembles, stores, retrieves, and manipulates data in formats to allow information to be mapped and spatially analyzed. The GIS uses different coverages, i.e., layers, of information such as topography, vegetation, soil, hydrology, etc. in a point, line, or polygon form that are referenced to a coordinate system. Roads, easement right-of-ways, waterways, and specific units of the landscape such as fields or ponds can be digitized and geographically referenced. These coverages are superimposed on each other to yield a geographically connected information system which can be used in planning and decision-making analyses.

The GIS database for the CWMA was compiled during previous TWRA inventories. Earth Resource Data Analysis System (ERDAS) software (ERDAS, Inc. 1987) was used to organize data geographically. Grid cell size was 0.67 acre (0.27 ha), and each cell contained information on landtype, topographic slope, and aspect of locations within CWMA. Communities were defined according to these geographic parameters; ERDAS was used to integrate and manipulate these coverages to produce maps of community types. The GIS output was a gray map of eight computer symbols, with each symbol representing one grid cell and its corresponding community type.

²Clatterbuck, W.K. 1988. Classification and analysis of forest plant communities on Cheatham Wildlife Management Area in north-central Tennessee. Unpublished USDA Forest Service Report, RWU-4102, Study No. 1.45. Southern Forest Experiment Station, New Orleans, LA.

Map Accuracy

Accuracy testing involved selecting sample points from each community type on the map, "ground-truthing" those points, and assessing whether the predicted communities actually occurred. Departures were recorded and evaluated for future refinements in the extrapolation process as well as in the community classification system. A probability statement concerning the accuracy of the projected community types was formulated and used to determine the degree of accuracy within some level of confidence (e.g., a community type on the map is 85 percent accurate at the 95 percent confidence level). The equations and reasoning used in these methodologies are in accordance with those reported by Ginevan (1979) and modified by Aronoff (1982) who used hypothesis testing to determine consumer and producer risks. Consumer's risk, i.e., probability of accepting an inaccurate map is as follows:

$$A \geq \frac{\sum_{x=0}^{X'} N!}{[X!(N-X)!]QL^{(N-X)}(1-QL)^X} \quad (1)$$

To use this equation, a minimum acceptable map accuracy (QL), a sample size (N), and a consumer's risk (A) are selected. The maximum number of allowable misclassifications (X') is found such that the cumulative probability of having X' or fewer misclassifications is less than or equal to A.

Producer's risk (B) is the probability of incorrectly rejecting an acceptable map of some high accuracy (QH) by having more than X' misclassifications. The equation for producer's risk is:

$$B = \frac{\sum_{x=X'+1}^N N!}{[X!(N-X)!]QH^{(N-X)}(1-QH)^X} \quad (2)$$

The primary consideration in evaluating extrapolation success is determining the number of samples to take and the maximum number of misclassified samples to allow to attain a prescribed map accuracy.

Approximately 30 samples per community type were adequate to achieve an accuracy of 85 percent with a 90 percent level of precision. Samples for each community type were selected at random from the map where the same community type covered five contiguous grids. Each sample represented at least 3 acres (1.2 ha) of the predicted community type. Map accuracy and confidence levels were altered when community misclassifications were more frequent than desired or if 30 samples for a community type were not represented on the map. A total of 211 sample plots was used for a sampling density of one plot per 94 acres (38 ha).

RESULTS AND DISCUSSION

Community Matrix

To predict community occurrence on CWMA, a matrix of aspect and percent slope that described the eight communities was constructed (Table 1). Six of the community types were adequately defined by aspect and percent slope: northern red oak, black oak-hickory, yellow-poplar, scarlet oak, American beech, and post oak; chestnut oak and sycamore-sweetgum were not. However, both chestnut oak and sycamore-sweetgum communities were delineated by landtype: chestnut oak on broad undulating ridges greater than 250 ft (76 m) wide, and sycamore-sweetgum in the stream valleys. The two landtypes depicting chestnut oak and sycamore-sweetgum communities were superimposed onto the coverage created by the aspect and percent slope matrix to generate a composite map for all eight communities. The overlay of the landtype map effectively replaced communities defined by the matrix (Table 1) in the 0 to 8 percent slope range that occurred on the broad ridge crests and in stream valleys with chestnut oak and sycamore-sweetgum communities respectively. Thus the only communities defined by the matrix at 0 to 8 percent slope were on narrower ridge crests less than 250 ft (76 m) wide. The percentage of land area within CWMA in each community type, as predicted by the aspect-slope percent matrix superimposed with landtype maps, is shown in Table 2.

Table 1.--Community types by aspect and percent slope, as used in the extrapolation analysis.¹

Aspect	Percent slope		
	0-23	24-35	>35
North	Yellow-poplar	Northern red oak	Northern red oak
Northeast	Yellow-poplar	Northern red oak	Northern red oak
East	Black oak-hickory	Black oak-hickory	American beech
Southeast	Black oak-hickory	Black oak-hickory	American beech
South	Scarlet oak	Scarlet oak	Post oak
Southwest	Scarlet oak	Scarlet oak	Post oak
West	Scarlet oak	Scarlet oak	Post oak
Northwest	Yellow-poplar	Northern red oak	American Beech

¹The map created by this matrix was overlaid with landtype maps to define the two communities (chestnut oak and sycamore-sweetgum) that could not be defined by aspect and/or percent slope.

Table 2.--Extrapolation analysis: predicted area by community type and mapping accuracy.

Community type	Predicted land area --Percent--	Sample plots	Correctly identified plots -----Number-----	Map accuracy -----Percent-----	Confidence level of map	Allowable plot misclassifications
Yellow-poplar	1.4	12	10	85	90	3
Northern red oak	17.8	31	26	85	90	7
Black oak-hickory	17.4	31	28	85	90	7
Chestnut oak	16.3	25	18	80	90	8
American beech	20.9	30	24	85	90	6
Scarlet oak	8.8	22	17	85	90	5
Post oak	14.0	32	29	85	90	7
Sycamore-sweetgum	3.4	28	19	70	90	10
Total	100.0	211	171	85	90	44

Map Accuracy

Six of the GIS generated communities were within map accuracies of 85 percent at the 90 percent confidence level: yellow-poplar, scarlet oak, post oak, northern red oak, black oak-hickory, and American beech (Table 2). Communities that were misclassified usually appeared as communities that occur adjacent to the predicted communities. The scarlet oak and yellow-poplar communities only contained 22 and 12 samples, respectively, as contiguous map grids for these communities were scarce. Although 30 samples for each community type were initially sought, the scarlet oak and yellow-poplar communities at the smaller sample size were within the prescribed map accuracies.

The map was accurate less often for sycamore-sweetgum and chestnut oak communities. Both these communities were defined by landtype rather than the aspect-percent slope matrix in the extrapolation. Communities were often classified as American beech and northern red oak rather than sycamore-sweetgum, and black oak-hickory rather than chestnut oak (Table 3). The landtype representing sycamore-sweetgum communities extended into narrow, V-shaped, second-order streams on the GIS map, locations where this community does not occur. Generally, sycamore-sweetgum communities appeared more often as stream width increased and as valleys became more U-shaped. Adjustments in the data base could be made so that the stream bottom landtype would not extend into V-shaped, second-order streams.

Chestnut oak communities were defined on ridge crests greater than 250 ft (76 m) wide. Ridge crests in the compartment where the community type classification was developed rarely exceeded 400 ft (122 m) in width and occupied a very small portion of the compartment. Several ridges on the CWMA were wider than 400 ft (122 m), but less than 1,000 ft (305 m), and constituted a much larger percentage of the total land base within CWMA (Table 2) than represented in the sampled compartment. Several oak species (white oak, scarlet oak, black oak, post oak, and chestnut oak) were present on these ridges. Accordingly, many of these wider ridges (>400 but <1,000 ft or >122 but <305 m) contained black oak-hickory communities rather than the predicted chestnut oak community. Alterations in the community classification system will be necessary to accommodate extrapolation of these different communities on these wider ridges.

Approximately 4.3 percent or 867 acres (350 ha) of the GIS generated map contained blocks of 20 or more continuous grids that were composed of three or more communities. Within these blocks, no one community was continuous or connected. Refinements in the database and modeling procedures should allow each unit of the landscape to be mapped and interpreted more clearly. One refinement currently being implemented by TWRA is changing their GIS modeling procedure from a grid to a polygon format so that areas of varying shape and size can be mapped.

Table 3.--Extrapolation: accuracy of community type projections.

Predicted community	Actual community							Sample size	
	Sycamore-sweetgum	Scarlet oak	Post oak	Yellow-poplar	American beech	Black oak-hickory	Chestnut oak		Northern red oak
Sycamore-sweetgum	19				5			4	28
Scarlet oak		17	3			2			22
Post oak			29		1	2			32
Yellow-poplar				10				2	12
American beech					24			6	30
Black oak-hickory						28	3		31
Chestnut oak						7	18		25
Northern red oak					1	4		26	31
Total									211

¹Of the 211 extrapolated classifications, 40 were misclassified.

SUMMARY

The use of the GIS was instrumental in generating a landscape model of forest community types. The composite CWMA community map was 85 percent correct at the 90 percent confidence level. All but two community type projections were within the prescribed limits. The slightly lower map accuracies and confidence levels for the chestnut oak and sycamore-sweetgum communities would not alter forest management or habitat modeling for these communities. Although some variation is present in both the community classification system and the extrapolation, the level of map accuracy achieved was more than adequate to serve as a database in modeling vegetation for wildlife and forest management.

Perhaps the greatest usefulness of GIS generated community classification modeling is the characterization and estimation of vegetational properties across the landscape. Great advances in forest management and habitat planning can be made if a treatment successfully applied to a community at one location can be expected to be successful on the same community type at another location. Currently, the community classification is being used to assess habitat potential. Community classification is also playing a role in the planning and decision-making processes used to appraise the effect of forest management on wildlife habitat. This study provides a broad qualitative extrapolation of communities. Further research should quantify the variation and consistency of forest communities and community properties or values across even broader landscapes of the Western Highland Rim.

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