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Anatomical and phenological Variation of Liquidambar Styraciflua L. Under Controlled Environmental Conditions

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ANATOMICAL AND PHENOLOGICAL VARIATION OF *LIQUIDAMBAR STYRACIFLUA* L. UNDER CONTROLLED ENVIRONMENTAL CONDITIONS

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ANATOMICAL AND PHENOLOGICAL VARIATION IN *LIQUIDAMBAR STYRACIFLUA* L. UNDER CONTROLLED ENVIRONMENTAL CONDITIONS

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A large degree of variation in fiber tracheid length, wood specific gravity, and time of apical bud formation existed within two populations of *Liquidambar styraciflua* L. from south central Kentucky. The variation exhibited by these populations may be attributed to the self-sterility of *Liquidambar* and the variable environment of south central Kentucky.

Variation of fiber tracheid length and wood specific gravity within the two populations was significant. Fiber tracheid length was dependent on temperature and photoperiod while wood specific gravity was primarily dependent on temperature. A significant level of variation was also evident between the two populations regarding tracheid length.

Phenologically the populations showed a very large amount of variation in the total number of hours darkness required for bud formation. A pattern of decreasing photoperiods resulting in a decrease in the total number of hours darkness required for bud formation is also suggested. Limited studies revealed a period of cold temperature is required for bud bursting.

INTRODUCTION

The original work of Turesson (1922) on the concept of ecotypic differentiation gave botanists a tool for examining the range of genetic variation in those species having a wide geographic distribution. Hiesey and Milner (1965) have pointed out that only a small fraction of the world's plant species have been examined for ecotypic differentiation. In those species that have been studied, the emphasis has been placed on detecting the interpopulational variation. Few, if any, studies examined each individual population for the extent of intrapopulational variation. One species that has recently been intensively investigated for interpopulational variation is Liquidambar styraciflua L. Studies on this species (Winstead, 1968, 1971, 1972; Williams, 1971, 1971a; and Williams and McMillan, 1971, 1971a) have confirmed that populational differentiation is multidimensional over its wide range of distribution in the United States, Mexico and Central America. These studies provide a framework for more intensive study of variation at the intrapopulational level. Until the extent of intrapopulational variation is known for many specific populations proper management techniques in such areas as reforestation and improved wood quality cannot be properly applied. This may be of critical importance in light of the increasing destruction of natural habitats and the potential shrinking of gene pools. To offset this destruction and to meet the increased demand for wood products, emphasis is being placed on the manipulation of the remaining gene pools for increased production. As the potential stock from which to select decreases it is important to

examine and characterize the remaining gene pools. Noticeably lacking are studies involving this species within its range of distribution in Kentucky. For these reasons the present study was undertaken.

Based on Winstead's work (1972) on fiber tracheid length and wood specific gravity, and Williams and McMillan's study (1971) on time required for apical bud formation as ecotypic characters of Liquidambar, it was decided to investigate the full range of variation these characters exhibit in two south central Kentucky populations of Liquidambar when grown under controlled environmental conditions. In addition to examining the range of variation, the effects of temperature and photoperiod on these ecotypic characters were also studied. To complement the work on apical bud formation it was also decided to make a limited study of the cold temperature requirement for bud bursting.

Liquidambar styraciflua L. ranges from the swamp forests of Massachusetts across the southeastern one-third of the United States to east Texas. It reoccurs in the montane regions of Mexico and in scattered locations as far south as Honduras and Nicaragua (Martindale, 1958). Liquidambar has been referred to as one of the most important hardwood species in America by the U. S. Forest Service. The wood of Liquidambar is used for lumber, veneer, plywood, fine grades of paper, corrugated board, and rayon (Martindale, 1958).

Harms (1930) recognized four species of Liquidambar and placed them in two sections. Section Euliquidambar contains three species, L. styraciflua L. found in the United States and Mexico, L. macrophylla Oerst. found in Central America, and L. orientalis Mill. found in Asia. Section Cathayambar contains one species, L. formosana Hance. found in Southeast Asia.

MATERIALS AND METHODS

Seed collections were made during the fall of 1973 from two areas in south central Kentucky. The two collection sites, though not greatly separated by latitude, represent two distinct habitats approximately thirty miles apart. The more northern site near Morgantown in Butler County, 37° 14' north latitude, is in the Hill Section of the Western Mesophytic Forest (Braun, 1950). In contrast, the southern site close to Alvaton in Warren County, 36° 52' north latitude, is in the Mississippi Plateau Section of the Western Mesophytic Forest. All seedlings utilized in the study were given a symbol which identified the seed tree from which it originated.

The plants were grown in the laboratory under controlled environmental conditions using Environator Corporation growth chambers (Model E3448). Seeds were germinated in sand under constant light and an alternating thermoperiod of 15 hour-32°C, 9 hour-24°C. After germination the seedlings were repotted in 17 ounce plastic cups containing a 3:1 peat-perlite mixture.

The controlled environmental chambers were used for two experimental programs. The two programs were designed to furnish material for wood character analysis and determination of the number of hours of darkness required for apical bud formation.

Four growth chambers were utilized in the first program. Two of the chambers were programmed for a day-night temperature of 32° - 24°C. The

remaining two chambers were programmed for a day-night temperature of 24° - 16°C. In each temperature regime two photoperiods were programmed. One chamber received a 12-hour photoperiod using both incandescent and fluorescent lighting. The other chamber had a 15-hour photoperiod. The first 12 hours of this photoperiod used incandescent and fluorescent lighting while the last 3 hours used only incandescent lighting.

Seedlings utilized in the first program were 38 days old when removed from the germination trays and repotted. They were watered daily with tap water and given one-half concentration Hoagland's solution fortified with chelated iron twice weekly. Seed material from both collection sites was used in the first program.

Three growth chambers were used in the second program. All three chambers were programmed for a day-night temperature of 32° - 24°C. Three different photoperiods were employed. Of the three chambers, one received an 8-hour photoperiod, another a 10-hour photoperiod, and the third a 14-hour photoperiod for the first thirty days with that being reduced to a 12-hour photoperiod for the duration of the program. All photoperiods used incandescent and fluorescent lighting.

Seedlings in the second program were 77 days old when removed from the germination trays and repotted. They were watered and cared for in the same manner as the seedlings in the first program. Due to the small quantity of seed material available from the northern collection site, seed material from the southern collection site only was used in the second program.

The racks in the growth chambers on which the seedlings were placed were lowered periodically so that the distance from the plant tops to the light source remained as constant as possible. Combined light intensity

for incandescent and fluorescent bulbs at the plant tops ranged from 600 - 800 foot-candles.

Measurements of stem height from the point of attachment of the cotyledons to the terminus and stem diameter at the point of attachment of the cotyledons were made at the beginning of a program, at the time of bud formation, and at the termination of the program. Each seedling was checked regularly for apical bud formation. The criteria for determining bud formation were absence of embryonic leaves and the presence of bud scales.

At the termination of the program a one-centimeter section of wood just above the point of attachment of the cotyledons was removed. This section of wood was used in the specific gravity determination and the fiber tracheid analysis.

The specific gravity determinations were made using the maximum moisture content method developed by Smith (1954). Using this method only the ovendry weight and the weight of the saturated wood sample in air need to be obtained. Stamm (1938) found the specific gravity of wood substances to be 1.53. The specific gravity was determined by substituting the three values into the formula developed by Smith:

$$\frac{1}{\frac{\text{weight saturated - weight ovendry}}{\text{weight ovendry}} + \frac{1}{1.53}}$$

Fiber tracheids were analyzed by macerating the one-centimeter section of wood used previously in specific gravity determinations in Jeffery's solution, staining the resulting cells in safranin-O stain, and permanently mounting the cells. Permount was used as the mounting medium for the slides made from the seedlings of the first program. The slides

made from the seedlings of the second program were made using diaphane as the mounting medium.

In program one, fiber tracheids of six seedlings from each chamber were measured. Three of these six seedlings were from the northern collection site and three from the southern collection site. Three slides were made from each seedling. Using a calibrated ocular, a total of fifty randomly selected fiber tracheids were measured for length from each plant. Seventeen fiber tracheids were measured on two of the three slides with sixteen fiber tracheids measured on the third slide.

Fiber tracheids of three seedlings from each chamber of program two were measured. Three slides were made from each seedling and a total of fifty fiber tracheids were measured from each plant in the same manner as in program one.

In addition to length measurements, fiber tracheid diameter and cell wall thickness were measured in plants from the southern collection site. Three plants from each test condition were measured. Ten cells were measured from each plant. The measurements were made at the widest portion of the fiber tracheid.

Buds from naturally growing trees were collected from both the northern and southern sites and tested for the amount of cold treatment required for bud burst. Buds from four trees at the southern site and three trees at the northern site were collected early in December, 1973. The buds were cut such that a length of stem approximately eight centimeters remained. They were placed in water and set in a refrigerator at 4°C. At regular intervals ten buds from each collection tree were removed from the refrigerator and placed in a growth chamber with a day-night temperature of 32° - 24°C and a 15-hour photoperiod. Ten buds

from each collection tree were also collected periodically from the field at the southern site and placed directly into the growth chamber.

After being placed under the growth chamber condition the buds were examined daily for signs of bud bursting. A bud was considered to have burst when the first embryonic leaf emerged through the bud scales.

In order for the amount of cold temperature received by buds in the field to be compared with those in the refrigerator at $4^{o}C$, the number of days the temperature in the area of the collection dropped below $4^{o}C$ was determined. This data was obtained from monthly reports of the National Oceanic and Atmospheric Administration, Environmental Data Service, Asheville, North Carolina.

RESULTS

Analysis of two populations of Liquidambar styraciflua L. indicates a large degree of variation existing within populations with regard to fiber tracheid length, wood specific gravity, and hours darkness required for apical bud formation. This study also showed interpopulational variation in fiber tracheid length. In addition, a cold requirement for bud bursting was demonstrated.

Progeny of trees from the southern collection site exhibited significant (.05 level of confidence) and highly significant (.01 level of confidence) differences in fiber tracheid length when compared on a seed tree basis in two of the four test conditions of program one. Table 1 shows that under the 32° - 24°C, 15-hour photoperiod test condition there was a significant difference in fiber tracheid length between the progeny from different seed trees. There was no significant difference in fiber tracheid length between progeny from the same seed tree. In both the 32° - 24°C, 12-hour photoperiod test condition and the 24° - 16°C, 15-hour photoperiod test condition there were no significant differences between neither progeny from different seed trees nor from the same seed tree. Under the 24° - 16°C, 12-hour photoperiod test condition there was a highly significant difference in fiber tracheid length between progeny from different seed trees. Again, there was no significant difference in fiber tracheid length among progeny from the same seed tree.

The collective response of the seedlings from the southern collection site to the four test conditions of program one is shown in Table 2.

TABLE 1

INTRAPOPULATIONAL VARIATION IN FIBER TRACHEID LENGTHS OF *LIQUIDAMBAR* SEEDLINGS FROM THE SOUTHERN COLLECTION SITE.[a]

32 - 24°C, 15-hour photoperiod test condition		
	length (mm)	
Seedling 1[b]	.975	seed tree 1
Seedling 2	1.021	seed tree 1
Seedling 3	1.129	seed tree 2
Mean	1.042	
Standard deviation	.081	
32 - 24°C, 12-hour photoperiod test condition		
	length (mm)	
Seedling 1	1.040	seed tree 1
Seedling 2	1.063	seed tree 2
Seedling 3	1.091	seed tree 1
Mean	1.065	
Standard deviation	.039	
24 - 16°C, 15-hour photoperiod test condition		
	length (mm)	
Seedling 1	.821	seed tree 1
Seedling 2	.863	seed tree 2
Seedling 3	.877	seed tree 1
Mean	.853	
Standard deviation	.040	
24 - 16°C, 12-hour photoperiod test condition		
	length (mm)	
Seedling 1	.737	seed tree 1
Seedling 2	.751	seed tree 1
Seedling 3	.821	seed tree 2
Mean	.769	
Standard deviation	.047	

[a] Data connected by lines not significantly different at .05 level.

[b] Each seedling value represents an average of 50 fiber tracheid measurements.

TABLE 2

FIBER TRACHEID LENGTH RESPONSE OF SEEDLINGS FROM THE SOUTHERN COLLECTION SITE TO DIFFERENT PHOTOPERIODS AND TEMPERATURES.[a]

32 - 24°C 15 hour	32 - 24°C 12 hour	24 - 16°C 15 hour	24 - 16°C 12 hour
1.042	1.065	.853	.769

[a]Composite sample of 150 fiber tracheids from three seedlings are represented under each condition. Data connected by lines are not significantly different at the .05 level. Values are in mm.

Fiber tracheid lengths in the 32° - 24°C, 15-hour photoperiod test condition, and the 32° - 24°C, 12-hour photoperiod test did not vary significantly from one another. Those grown under the 24° - 16°C, 15-hour photoperiod test condition had significantly shorter fiber tracheids than the two 32° - 24°C test conditions. The fiber tracheids grown under the 24° - 16°C, 12-hour photoperiod test conditions had the shortest fiber tracheids of the four conditions. There was a highly significant difference between the fiber tracheids of this test condition compared to all others.

Progeny from the northern collection site also exhibited significant and highly significant differences when compared on a seed tree basis in two of the four test conditions of program one. Table 3 shows that under the 32° - 24°C, 15-hour photoperiod test condition a highly significant difference existed among progeny from different seed trees. Under this particular test condition a check for variance among progeny of the same seed tree was absent. Under the 32° - 24°C, 12-hour photoperiod test condition a significant difference was shown among progeny from different seed trees and, again, no significant difference existed between progeny from the same seed tree. No significant difference existed among progeny from the same seed tree under the 24° - 16°C, 15-hour photoperiod test condition. No comparisons are available on seedlings from the 24° - 16°C, 12-hour photoperiod test condition. The majority of the seedlings from the northern collection site did not survive under this test condition.

Response of seedlings from the northern collection site to the four test conditions of program one is the same as that shown by the seedlings from the southern collection site (Table 4). Seedlings from the two 32° - 24°C test condition show no significant difference in fiber tracheid length. Seedlings of the two 24° - 16°C test conditions show a highly

TABLE 3

INTRAPOPULATIONAL VARIATION IN FIBER TRACHEID LENGTHS OF LIQUIDAMBAR SEEDLINGS FROM THE NORTHERN COLLECTION SITE.[a]

32 - 24°C, 15 hour photoperiod test condition		
	length (mm)	
Seedling 1	.933	seed tree 2
Seedling 2	1.017	seed tree 1
Seedling 3	1.068	seed tree 3
Mean	1.006	
Standard deviation	.063	
32 - 24°C, 12 hour photoperiod test condition		
	length (mm)	
Seedling 1	.933	seed tree 2
Seedling 2	.942	seed tree 2
Seedling 3	1.012	seed tree 1
Mean	.962	
Standard deviation	.045	
24 - 16°C, 15 hour photoperiod test condition		
	length (mm)	
Seedling 1	.723	seed tree 2
Seedling 2	.727	seed tree 2
Seedling 3	.746	seed tree 2
Mean	.737	
Standard deviation	.032	
24 - 16°C, 12 hour photoperiod test condition		
	length (mm)	
Seedling 1	.658	seed tree 1
Seedling 2	----	
Seedling 3	----	
Mean	----	
Standard deviation	----	

[a]Data connected by lines not significantly different at the .05 level. Each seedling is represented by an average of 50 fiber tracheids.

TABLE 4

FIBER TRACHEID LENGTH RESPONSE OF *LIQUIDAMBAR* SEEDLINGS FROM THE NORTHERN COLLECTION SITE TO DIFFERENT PHOTOPERIODS AND TEMPERATURES.[a]

32 - 24°C 15 hour	32 - 24°C 12 hour	24 - 16°C 15 hour	24 - 16°C 12 hour
1.006	.962	.732	.658

[a]Composite sample of 150 fiber tracheids from three seedlings are represented under each condition. Data connected by lines are not significantly different at the .05 level. Values are in mm.

significant difference from seedlings of the 32° - 24°C test conditions and each other. The fiber tracheids of seedlings from the 24° - 16°C test conditions are shorter with fiber tracheids produced under the 24° - 16°C, 12-hour photoperiod test condition being the shortest.

Variation in fiber tracheid length between the two collection sites was highly significant in three of the four test conditions. Only in the 32° - 24°C, 15-hour photoperiod test condition was there no significant difference in fiber tracheid length. In each of the four test conditions the northern collection site had shorter fiber tracheids as is shown in Table 5.

Results from the second program which utilized only one seed source from the southern collection site indicate a larger degree of intrapopulational variation of fiber tracheid length. In the 32° - 24°C, 14-12-hour photoperiod test condition, one of the three seedlings measured showed a highly significant difference in fiber tracheid length when compared to the other two seedlings of that test condition. Under the 32° - 24°C, 10-hour photoperiod test condition highly significant differences in fiber tracheid length also existed among the progeny from the same seed tree. Significant differences in fiber tracheid length existed among the seedlings under the 32° - 24°C, 8-hour photoperiod (Table 6).

Response of the seedlings to the different photoperiods of program two is shown in Table 7. In all instances, as the photoperiod decreased the mean fiber tracheid length decreased. The differences in the fiber tracheid length between treatment conditions were highly significant.

Wood specific gravity of seedlings grown under controlled conditions also showed a great deal of intrapopulational variation. Values from program one for the seedlings from the southern collection site are given

TABLE 5

VARIATION IN FIBER TRACHEID LENGTH BETWEEN THE TWO SOUTH CENTRAL KENTUCKY POPULATIONS UNDER FOUR TEST CONDITIONS.[a]

	32 - 24°C 15 hour	32 - 24°C 12 hour	24 - 16°C 15 hour	24 - 16°C 12 hour
Southern collection site	1.042	1.065	.853	.769
Northern collection site	1.006	.962	.732	.658

[a]Each population is represented by a composite sample of 150 fiber tracheids from three seedlings grown under each condition. Data connected by lines are not significantly different at the .05 level. Values are in mm.

TABLE 6

INTRAPOPULATIONAL VARIATION IN FIBER TRACHEID LENGTHS OF *LIQUIDAMBAR* SEEDLINGS FROM THE SOUTHERN COLLECTION SITE WHEN GROWN UNDER THREE TEST CONDITIONS.[a]

32 - 24°C, 12 - 14 hour photoperiod test condition	
	length (mm)
Seedling 1[b]	.858
Seedling 2	.891
Seedling 3	.998
Mean	.916
Standard deviation	.066
32 - 24°C, 10 hour photoperiod test condition	
	length (mm)
Seedling 1	.649
Seedling 2	.825
Seedling 3	.905
Mean	.793
Standard deviation	.117
32 - 24°C, 8 hour photoperiod test condition	
	length (mm)
Seedling 1	.672
Seedling 2	.713
Seedling 3	.737
Mean	.707
Standard deviation	.037

[a]Data connected by lines not significantly different at .05 level.

[b]Each seedling value represents an average of 50 fiber tracheid measurements.

TABLE 7

FIBER TRACHEID LENGTH RESPONSE OF *LIQUIDAMBAR* SEEDLINGS FROM THE SOUTHERN COLLECTION SITE TO DIFFERENT PHOTOPERIODS AND TEMPERATURES OF PROGRAM TWO.[a]

32 - 24°C 12 - 14 hour	32 - 24°C 10 hour	32 - 24°C 8 hour
.916	.793	.707

[a]Composite sample of 150 fiber tracheids from three seedlings are represented under each test condition. Values are in mm.

in Table 8. Under each test condition the standard deviation is relatively high and the spread between the lowest and highest value is large.

Response of the seedlings from the southern collection site to the four test conditions with regard to specific gravity is similar to the response of fiber tracheid lengths. The specific gravity of the seedlings under the two 32° - 24°C test conditions did not vary significantly. The specific gravity of seedlings under the two 24° - 16°C test conditions differed significantly not only from the 32° - 24°C test conditions but also from each other. Under these conditions the specific gravity was greater with the 24° - 16°C, 12-hour photoperiod test condition producing the greatest specific gravity.

Seedlings from the northern collection site also showed a high degree of intrapopulational variation in specific gravity under the four test conditions of program one. The values are given in Table 9. Again, a relatively high standard deviation with a large spread between the lowest and highest values indicates the high degree of variation.

The specific gravity response of the seedlings from the northern collection site to the four test conditions was similar to that of the southern site. The specific gravity values for seedlings of the two 32° - 24°C test conditions did not vary significantly. Seedling specific gravity of the 24° - 16°C, 15-hour photoperiod test condition was significantly larger than the specific gravity of either of the 32° - 24°C test conditions. The specific gravity value for seedlings of the 24° - 16°C, 12-hour photoperiod test condition is suspect due to the small number of seedlings from the northern collection site surviving this test condition.

In comparing the specific gravity of seedlings from the two collection sites, it was found that no significant differences existed between them under any of the test conditions.

TABLE 8

VARIATION IN SPECIFIC GRAVITY OF LIQUIDAMBAR SEEDLINGS FROM THE SOUTHERN COLLECTION SITE GROWN UNDER FOUR TEST CONDITIONS.[a]

	32 - 24°C 15 hour	32 - 24°C 12 hour	24 - 16°C 15 hour	24 - 16°C 12 hour
Mean	.37	.38	.42	.48
Standard deviation	.05	.03	.04	.02
Lowest individual value	.31	.32	.34	.47
Highest individual value	.43	.43	.47	.53

[a]Data connected by lines not significantly different at .05 level. Mean specific gravity values from 5 - 13 seedlings grown under each condition.

TABLE 9

VARIATION IN SPECIFIC GRAVITY OF LIQUIDAMBAR SEEDLINGS FROM THE NORTHERN COLLECTION SITE GROWN UNDER FOUR TEST CONDITIONS.[a]

	32 - 24°C 15 hour	32 - 24°C 12 hour	24 - 16°C 15 hour	24 - 16°C 12 hour
Mean	.37	.39	.43	.44
Standard deviation	.04	.04	.05	.04
Lowest individual value	.32	.35	.40	.40
Highest individual value	.40	.44	.49	.49

[a]Data connected by lines not significantly different at .05 level. Mean specific gravity values from 3 - 9 seedlings grown under each condition.

Results on specific gravity from the second program (Table 10) in which only seedlings from the southern collection site were used indicate intrapopulational variation but not to the extent found in program one. In two of the three test conditions the standard deviation and the spread from lowest to highest are not as large as in program one yet variation within the population does exist.

The specific gravity of the seedlings in the second program, which had three 32° - 24°C test conditions, was comparable to the seedling specific gravity of the 32° - 24°C test conditions of program one. Seedling specific gravity in two of the three test conditions of program two did not differ significantly from the specific gravity of seedlings in the warm temperature test conditions of program one even though all were of different photoperiods. Only the specific gravity of seedlings in the 32° - 24°C, 8-hour photoperiod test condition of program two differed from the specific gravity of seedlings from other warm temperature programs (Tables 8, 9, and 10).

Analysis of cell diameter and cell wall thickness revealed that differences in specific gravity were primarily due to differences in total cell diameter. Under all test conditions the cell wall thickness of fiber tracheids remained constant at 3.10 microns. The 24° - 16°C test conditions produced cells with a narrower mean diameter at the widest point than the 32° - 24°C test conditions (Table 11). Variation in cell diameter among plants under the same test conditions was slight. Only one of the seven test conditions (32° - 24°C, 15-hour photoperiod) of the study showed any significant difference in cell diameter between the plants grown under the same test conditions.

TABLE 10

VARIATION IN SPECIFIC GRAVITY OF *LIQUIDAMBAR* SEEDLINGS FROM THE SOUTHERN COLLECTION SITE GROWN UNDER THREE TEST CONDITIONS.[a]

	32 - 24°C 12 - 14 hour	32 - 24°C 10 hour	32 - 24°C 8 hour
Mean	.39	.39	.35
Standard deviation	.03	.02	.04
Lowest individual value	.35	.38	.29
Highest individual value	.42	.43	.41

[a]Data connected by lines not significantly different at .05 level. Mean specific gravity values are from 18 seedlings grown under each condition.

TABLE 11

MEAN CELL DIAMETERS (MICRONS) OF LIQUIDAMBAR SEEDLINGS FROM THE SOUTHERN COLLECTION SITE GROWN UNDER SEVEN DIFFERENT TEST CONDITIONS.[a]

24 - 16°C 12 hour	24 - 16°C 15 hour	32 - 24°C 8 hour	32 - 24°C 15 hour	32 - 24°C 12 hour	32 - 24°C 10 hour	32 - 24°C 12 - 14 hour
15.19	17.05	18.91	19.22	19.22	19.22	20.77

[a] Each mean represents a composite of 30 cell diameters measured from three seedlings grown under each condition. Data connected by lines not significantly different at .05 level.

The total number of hours darkness required for apical bud formation in program one varied widely in seedlings from the same collection site under the same test conditions. The greatest total number of hours darkness required for fifty percent apical bud formation in seedlings from both the southern and northern collection site occurred under the 32° - 24°C, 12-hour photoperiod test condition (Table 12). The 32° - 24°C, 15-hour photoperiod and the 24° - 16°C, 15-hour photoperiod test conditions produced almost the same results. The 24° - 16°C, 12-hour photoperiod test condition caused very rapid apical bud formation. No significant difference in time of apical bud formation existed between the seedlings from the two collection sites.

A particularly interesting occurrence was the bursting of the apical buds a short time after formation. This occurred under each test condition. At the 32° - 24°C, 15-hour photoperiod and the 24° - 16°C, 15-hour photoperiod test conditions the occurrence was rare. The bursting occurred frequently under the 32° - 24°C, 12-hour photoperiod test condition. Under the 24° - 16°C, 12-hour photoperiod test condition the occurrence of bursting was near one hundred percent.

Reformation of apical buds in the two 32° - 24°C test conditions and the 24° - 16°C, 15-hour photoperiod test condition was rare due to the time required for reformation being greater than the time remaining in the program. Reformation of buds in the 24° - 16°C, 12-hour photoperiod test condition was complete. Under this test condition the average total number of hours darkness required for bud reformation was 786.

The total number of hours darkness required for apical bud formation of seedlings in program two also exhibited substantial variation. Seedlings grown under the same test conditions responded to different amounts

TABLE 12

MEAN NUMBER OF HOURS DARKNESS REQUIRED FOR 50% APICAL BUD FORMATION

	32-24°C 15 hour	32-24°C 12 hour	24-16°C 15 hour	24-16°C 12 hour
Southern Collection Site[a]				
Mean	1,209	1,532	1,251	552
Standard Deviation	142	140	136	---
Northern Collection Site[b]				
Mean	1,116	1,464	1,121	552
Standard Deviation	111	123	46	---

[a]Mean values represent 6 - 8 seedlings grown under each condition.

[b]Mean values represent 4 - 5 seedlings grown under each condition.

of darkness resulting in the relatively large standard deviation as shown in Table 13. Seedlings grown under the 32° - 24°C, 14-12 hour photoperiod test condition required the greatest number of hour darkness for bud formation. The 32° - 24°C, 10-hour photoperiod test condition required less darkness and the 32° - 24°C, 8-hour photoperiod test condition required the least hours darkness for bud formation.

The pattern of shorter photoperiods resulting in a lower total number of hours darkness required for bud formation shown in program two can also be seen by comparing all the 32° - 24°C test conditions from both programs (Table 14). The only exception to the pattern is the 32° - 24°C, 12-hour photoperiod test condition of program one.

Average values of height and diameter of seedlings at the time of bud formation and program termination are given in Table 15. It is readily discernible that lateral growth did not cease at the time of bud formation. Also of interest are the average values of seedling height under the two 32° - 24°C test conditions at the time of bud formation. The seedlings grown under the 32° - 24°C, 15-hour photoperiod test condition are taller than those of the 32° - 24°C, 12-hour photoperiod test condition even though the seedlings of the shorter day test condition required more hours darkness to form apical buds. This does not mean the seedlings of the 32° - 24°C, 12-hour photoperiod test condition took longer to form apical buds. Seedlings under the 32° - 24°C, 15-hour photoperiod test condition required an average of 134 days with a 15-hour photoperiod to form apical buds while the 32° - 24°C, 12-hour photoperiod test condition required an average of 128 days with a 12-hour photoperiod to form apical buds. The greater value in height for the seedlings under the 32° - 24°C, 15-hour photoperiod test condition can be attributed to the more favorable growth conditions.

TABLE 13

MEAN NUMBER OF HOURS DARKNESS REQUIRED FOR 50% APICAL BUD FORMATION, PROGRAM TWO.[a]

	32 - 24°C 14 - 12 hour	32 - 24°C 10 hour	32 - 24°C 8 hour
Mean	1,072	859	679
Standard deviation	24	177	120

[a]Mean values represent nine seedlings grown under each condition.

TABLE 14

MEAN NUMBER OF HOURS DARKNESS REQUIRED FOR 50% APICAL BUD FORMATION UNDER WARM TEMPERATURE.[a]

	32 - 24°C 15 hour	32 - 24°C 12 hour	32 - 24°C 14 - 12 hour	32 - 24°C 10 hour	32 - 24°C 8 hour
Mean	1,184	1,498	1,072	859	679

[a]Mean values under the 15 and 12 hour photoperiod test conditions represent 5 - 8 seedlings. Mean values for the remaining test conditions represent nine seedlings.

TABLE 15

MEAN VALUES[a] OF HEIGHT AND DIAMETER OF SEEDLINGS AT THE TIME OF BUD FORMATION AND PROGRAM TERMINATION.[b]

	32-24°C 15 hour	32-24°C 12 hour	24-16°C 15 hour	24-16°C 12 hour
Diameter at Bud Formation	8.4	8.4	9.0	8.1
Diameter at Termination	9.0	9.4	10.3	11.2
Height at Bud Formation	79.2	60.4	26.5	14.4
Height at Termination	79.4	61.2	26.8	14.7

[a]Mean height and diameter values from 9 - 13 plants grown under each test condition. The seedlings from the northern and southern collection sites were pooled.

[b]Diameter in mm. Height in cm.

Buds collected in the field brought into the laboratory and stored for a specified time at 4°C showed a cold temperature requirement for bud bursting. The amount of time required for bud bursting under the 32° - 24°C, 15-hour photoperiod test condition was inversely proportional to the amount of time spent at 4°C. This is shown for both the northern and southern collection sites in Table 16.

Buds that were collected periodically, brought into the laboratory and placed directly into the 32° - 24°C, 15-hour photoperiod test condition showed the same response as the buds receiving the cold treatment in the laboratory (Table 17).

The percent survival of buds collected in the field and stored at 4°C and those collected periodically and placed directly into the growth chambers was low. The values ranged from 37 to 7 percent.

TABLE 16

TIME REQUIRED FOR FIELD-COLLECTED BUDS STORED AT 4°C TO BURST UNDER CONTROLLED CONDITIONS.

Southern collection site

Number of days at 4°C	Average number of days at 32 - 24°C for bud burst	Percent of 40 buds surviving to burst
0	65	28%
14	45	23%
30	33	30%
44	27	17%
54	28	23%
66	20	7%

Northern collection site

Number of days at 4°C	Average number of days at 32 - 24 C for bud burst	Percent of 40 buds surviving to burst
12	38	23%
28	26	17%
42	20	27%
52	24	17%
64	23	7%

TABLE 17

TIME REQUIRED FOR BUDS RECEIVING COLD TREATMENT IN THE FIELD TO BURST UNDER CONTROLLED CONDITIONS.

Number of days below 4°C (in field)	Average number of days at 32 - 24°C for bud burst	Percent of 40 buds surviving to burst
12	56	13%
39	25	37%
46	20	10%
69	22	27%

DISCUSSION

The data presented in this study outline anatomical and phenological responses of two populations of Liquidambar styraciflua L. from south central Kentucky under different photoperiods and temperatures. The two populations exhibited a large degree of intrapopulational variation in fiber tracheid length, wood specific gravity, and total number of hours darkness required for bud formation. Interpopulation variation in fiber tracheid length was also present. Results show that fiber tracheid length, and the total number of hours darkness required for bud formation were dependent on photoperiod and temperature. Wood specific gravity was dependent on temperature. A limited study on bud bursting showed a definite cold requirement.

Each population of Liquidambar studied demonstrated intrapopulational variation among progeny from the same and/or different seed trees. This variation can be ascribed to two factors. One, the self-sterility of Liquidambar (Schmitt and Perry, 1964); two, the broad natural selective forces existing in south central Kentucky. Self-sterility alone could account for a large part of the variation demonstrated. That such a large amount of variation is present in the gene pools of these populations may be due to the broad natural selective forces existing in these areas. Exactly how much variation can be attributed to the environmental conditions cannot be measured. Some of the genotypes adding to the amount of variation under controlled conditions could be selected

against under natural conditions and thus lessen the amount of variability exhibited in the surviving progeny.

As previously mentioned, fiber tracheids attained maximum length under the 32° - 24°C, 15- and 12-hour photoperiod test conditions. Photoperiods of 10 hours or less at 32° - 24°C caused shortening of fiber tracheid lengths. The two 24° - 16°C test conditions produced shorter fiber tracheids than the warm temperature test conditions. Under these conditions, photoperiod responses were evident with the shorter photoperiod (12 hours) producing shorter fiber tracheids. Fiber tracheid length also bears a direct relationship to stem height which is a function of the apical meristem. Dinwoodie (1963) working with Picea sitchensis Carr. found a positive relation to exist between rate of height growth and the length of tracheids during the first growing season. Seedlings with a fast rate of height growth had longer tracheids than those with slow terminal growth rates. Dinwoodie (1963) also found that an increase in the rate of diameter growth will produce shorter tracheids than a slow rate of diameter growth. Rapid growth in girth must be accompanied by an increase in anticlinal division if the cambial cylinder is to be maintained. Bannon (1967a and 1967b) found that an inverse relationship exists between frequency of anticlinal division of cambial initials and xylem cell length in coniferous trees. This is due to the new cambial initials, formed from anticlinal division of existing cambial initials, undergoing periclinal cell division before maximum length is attained. This results in a short xylem mother cell producing a short xylem element. The data from this study does show that seedlings with a greater diameter have shorter fiber tracheids. Richardson and Dinwoodie (1960) showed tracheid length in conifers to increase with an increase in day or night

temperature. From the previous work cited and the results of this study, it could be concluded that under the warmer temperatures (32° - 24°C) and longer photoperiods the conditions were near optimum for the apical meristem to initiate growth. Associated with the active meristem might have been an increase in hormone production, probably an auxin, which caused elongation of the fiber tracheids. A possibility other than hormone production exists in that the actively dividing apical meristem utilized the available energy resulting in low cambial activity. The lower cambial activity could allow the cambial initials to attain maximum length before periclinal division. Under the cooler temperatures the apical meristem was not as active. The lateral meristem was very active as evidenced by the significantly larger stem diameters produced under the cool temperature regimes. It is logical to assume that this fast rate of diameter growth was accompanied by an increase in anticlinal division of the cambial initials which resulted in shorter fiber tracheids. Whether the increased cambial activity is due to hormonal influence or energy availability or both is not known and points up the need for further study. Under the 24° - 16°C, 12-hour photoperiod test condition not only were the shortest fiber tracheids produced but also the largest stem diameters indicating the most rapid rate of diameter growth. It would seem the seedlings under the 24° - 16°C, 15-hour photoperiod would have a greater amount of energy for cambial division resulting in more anticlinal division which would ultimately cause shorter fiber tracheids. Since this is not the case, it might be concluded that the rate of cambial division is more dependent on hormones than available energy. In further support of hormonal control is the fact that the two test conditions differ from one another only in length of photoperiod. Photoperiod control of hormone production is a known occurrence (Galston and Davies, 1970).

Under each test condition the fiber tracheid lengths of seedlings from the northern collection site were shorter than those from the southern collection site. Correlation of fiber tracheid length and latitude of origin is well documented in the literature. Winstead (1972) showed in Liquidambar styraciflua L. that as latitude increased fiber tracheid length decreased. Webb (1964) showed that in field collected wood samples fiber tracheid length generally decreased to the north. Rickson (1963) showed that Liquidambar plants from Central America had longer fibers that those from the United States. Tracheid length has also been correlated with latitude of origin in a number of coniferous species. Dinwoodie (1963) working with Picea sitchensis Carr. and Echols (1958) working with Pinus sylvestris L. found that as latitude increased tracheid length decreased. The fact that latitudinal differences in fiber tracheid length do occur brings up the question of how tracheid length has been naturally selected. Dinwoodie (1961) states that "it is more likely that tracheid length is associated with some factor or factors that have been naturally selected. Richardson and Dinwoodie (1960) and Dinwoodie and Richardson (1961) have shown tracheid length is a function of temperature and it is possible that latitudinal differences in tracheid length result from genetically controlled adaptation to topoclinal differences in temperature during the growing season."

The data on wood specific gravity indicates the same response pattern to temperature and photoperiod as fiber tracheid length. All of the seedlings grown under the 32° - 24°C test conditions produced wood with a lower specific gravity than those grown under the 24° - 16°C test condition. With one exception, the 32° - 24°C, 8-hour photoperiod test condition of program two, the seedlings of the 32° - 24°C test conditions did

not vary significantly in their wood specific gravity regardless of the photoperiod. The photoperiod of the seedlings grown under the 24 - 16°C test conditions did, however, influence the specific gravity. The shorter photoperiod (12 hour) produced the greater wood specific gravity. A correlation also existed between wood specific gravity and seedling diameter. The greater the seedling diameter the greater the wood specific gravity. Differences in specific gravity also correlate to the lumen to cell wall ratio. The wood with higher specific gravity had smaller cell lumens. In all cases the cell wall thickness remained the same. Richardson and Dinwoodie (1960) working with Pseutotsuga menziesii (Mirb.) Franco and Sequoia sempervirens (Lamb.) Endl. found specific gravity to be a function of night temperature. Under cool night temperatures (7°C and 17°C) specific gravity increased. They also showed that an increase in cell wall thickness and a decrease in lumen diameter occurred at the lower temperatures. Richardson and Dinwoodie (1960) concluded by stating that differences in wood specific gravity were due to increased cell wall thickness which resulted from higher net assimilation rates at the lower night temperatures. Winstead (1972) showed that in Liquidambar styraciflua L. wood specific gravity differences due to latitude of origin were caused by differences in lumen diameter. The cell wall thickness remained constant. It could be concluded from the present study that specific gravity is primarily dependent on temperature. At lower temperatures specific gravity is secondarily dependent on photoperiod. Specific gravity differences at the cellular level in this study are due to the lumen to cell wall ratio. The size of the lumen is the variable factor. The same correlation that exists between fiber tracheid length and frequency of anticlinal division might exist between cell diameter and frequency of

periclinal division. As a cambial initial divides periclinally the resulting daughter cells are each approximately one-half the diameter of the cambial initial. Subsequent periclinal division by the cell remaining a cambial initial before attaining maximum diameter could influence the diameter of the xylem mother cell and the xylem elements. If during this process the cell wall thickness remained constant the lumen would be smaller resulting in an increase in specific gravity.

The question arises whether fiber tracheid length and wood specific gravity bear a direct relationship. Richardson and Dinwoodie (1960) showed in Pseudotsuga menziesii (Mirb.) Franco and Sequoia sempervirens (Lamb) Endl. that the two anatomical characters are under separate physiological control. They stated that specific gravity was a function of net assimilation rate and cell size was determined by at least two processes, temperature and a photosensitive process. In comparing the data from tables 1, 6, 8, and 10, and considering only the plants grown under the warm temperature programs, a decrease in fiber tracheid length is seen with a decrease in photoperiod, but the specific gravity remained relatively constant except for the shortest photoperiod. Although much more detailed work is needed, the information from the above comparisons indicates separate physiological controls for cell length and wood specific gravity.

The total number of hours darkness required for bud formation showed considerable variation under each test condition. A comparison of the two temperature programs showed that a decrease in the total number of hours darkness required for bud formation occurred under the 24° - 16°C test conditions. Under the two cool temperature test conditions a decrease in photoperiod caused a decrease in the total number of hours darkness

required for bud formation. With one exception, results from the warm temperature test conditions also showed that a decrease in photoperiod decreased the total number of hours darkness required for bud formation. The exception was the 32° - 24°C, 12-hour photoperiod test condition under which bud formation required the greatest total number of hours darkness. This is contrary to what would normally be expected as other studies on Liquidambar (Winstead, 1968) indicate that populations grown under 12-hour photoperiods and warm temperatures (29° - 24°C day night cycle) show bud formation sooner when compared to populations grown at the same temperatures but under longer days (16-hour photoperiod). The variation of the current study from what was expected points out an area of research with this species that needs further investigation. Williams and McMillan (1971) working with latitudinally diverse populations of Liquidambar under the same test conditions as program one of this study showed populations differed as to which test condition required the largest total number of hours darkness for bud formation. They found for the more northern populations that the length of photoperiod in the test condition requiring the largest number of hours darkness for bud formation closely approximated the photoperiod length at the site of origin of the population during the spring flush of growth. Their data also indicated that southern populations are less sensitive to photoperiod in relation to their total growth. Tennessee populations studied by Williams and McMillan (1971) required the largest total number of hours darkness for bud formation under the 24° - 16°C, 15-hour photoperiod test conditions. As previously mentioned the south central Kentucky population required the largest total number of hours darkness for bud formation under the 32 - 24°C, 12-hour photoperiod test condition. The average

daylength (sunrise to sunset) for both the Tennessee and south central Kentucky populations from March 15 to June 1 is approximately 13.5 hours. This value falls between the two test condition photoperiods used in Williams and McMillan's study (1971) and the present work. This, along with differences in the genetic makeup of each population, Williams and McMillan's (1971) findings of less sensitivity of southern populations to photoperiod, and the large amount of variation in time required for bud formation exhibited in the present study could account for a part of the differences between the present study and Williams and McMillan's work (1971) and the seemingly out-of-place value for the 32° - 24°C, 12-hour photoperiod test condition. Further studies in which the naturally occurring daylength is more closely approximated are needed.

Varying numbers of the buds formed under each test condition reinitiated growth. This occurred to a greater extent under the 12-hour photoperiod test conditions with the greatest occurrence under the 24° - 16°C, 12-hour photoperiod test condition. The reinitiation of growth after a short period of inactivity raises the question of whether or not the buds were representing a dormant state. With reinitiation of growth occurring so soon after bud formation the possibility exists that the plants were entering a state of quiescence rather than true dormancy. That true dormancy was never effected is also supported by the fact that stem diameter continued to increase even after bud formation. This state of quiescence could have been in response to some adverse environmental factor encountered during germination or early seedling growth. If, indeed, part or all of the seedlings in each test condition were in a complete or partial state of quiescence the highly variable and conflicting results could be more easily explained. One point in support of this

is the value for the total number of hours darkness required for bud reformation under the 24° - 16°C, 12-hour photoperiod test condition of 786 hours. This is very near the average value (723 hours) obtained by Williams and McMillan (1971) for the three Tennessee populations studied to form apical buds under the same test conditions. The total number of hours darkness required for bud reformation under the other test conditions is not known since the program ended before any reformation could occur. More work is certainly needed on this problem.

Field collected buds of Liquidambar show a definite cold temperature requirement for bud bursting. Buds receiving a cold treatment under laboratory conditions reacted similarly to those receiving a cold treatment in the field. The value of a cold temperature requirement is obvious as a protective mechanism preventing bud bursting during a brief warm period in the winter. Also, the cold requirement for reinitiating growth further supports the hypothesis that the seedlings which formed buds and later reinitiated growth were merely in a state of quiescence and not dormant since they reinitiated growth quickly without any cold treatment.

SUMMARY

1. The two south central Kentucky populations examined in this study exhibited a large degree of intrapopulational variation in fiber tracheid length, wood specific gravity, and total number of hours darkness required for bud formation. This probably can be correlated with the self-sterility of Liquidambar and the relatively broad natural selective forces existing in this area.

2. Analysis of fiber tracheid length of seedlings grown under seven test conditions revealed that cell length is influenced by temperature and photoperiod. Warm temperatures (32° - 24°C) produced longer fiber tracheids than cool temperatures (24° - 16°C). Photoperiods of 10 hours or less were effective in decreasing fiber tracheid length.

3. Latitudinal differences in fiber tracheid length were demonstrated which support previous studies indicating more northern populations have inherently shorter fiber tracheids.

4. Differences in specific gravity under the seven test conditions were due to the size of the cell lumen and not cell wall thickness as indicated in previous work. Cell lumen size was dependent primarily on temperature with warmer temperatures (32° - 24°C) producing larger cell lumens. Only at cool temperatures (24° - 16°C) did photoperiod affect lumen size.

5. The total number of hours darkness required for bud formation was influenced by temperature and photoperiod. Cool temperatures (24° - 16°C) caused a decrease in this number. A general pattern of decreasing photoperiods decreasing the total number of hours darkness required for bud formation was suggested.

6. Limited studies revealed a period of cold temperature is required for bud bursting.

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