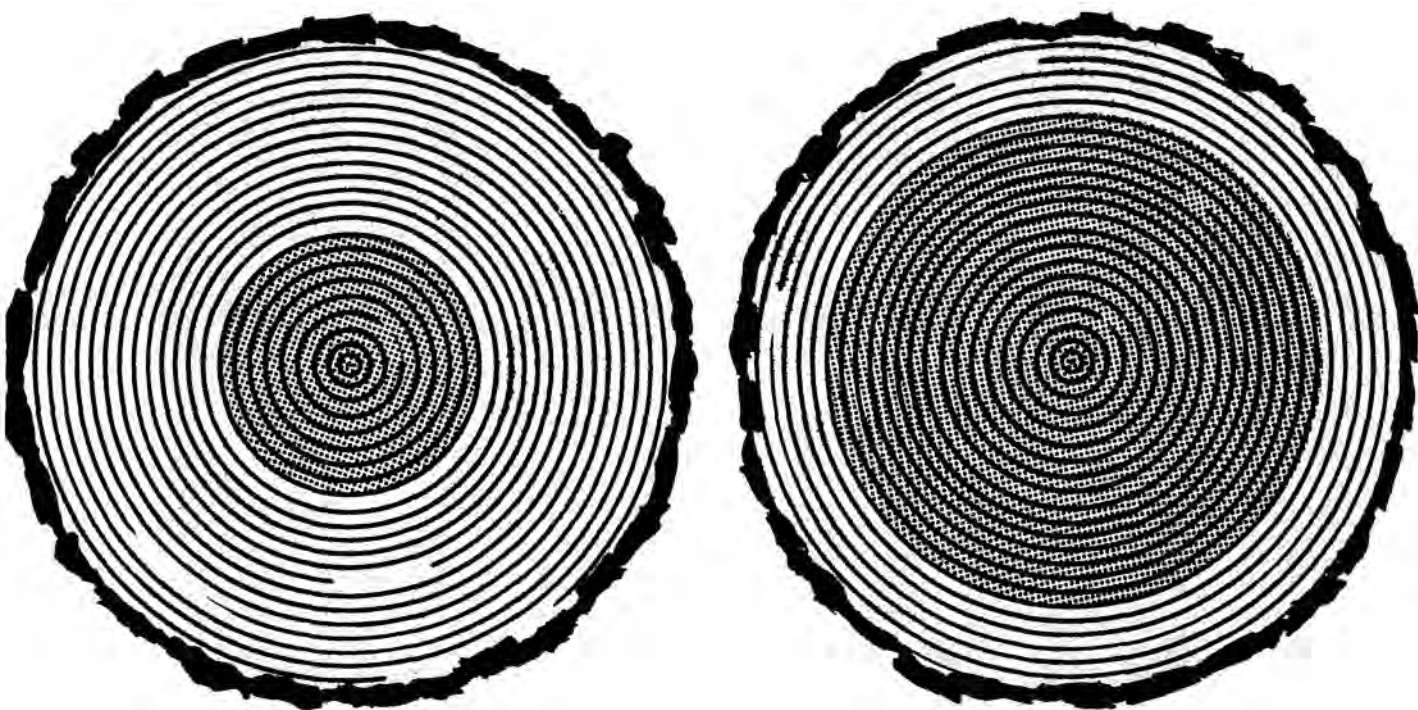


GROSS INFLUENCES ON HEARTWOOD FORMATION IN BLACK WALNUT AND BLACK CHERRY TREES



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ABSTRACT

Heartwood formation in black walnut (*Juglans nigra* L.) and black cherry (*Prunus serotina* Ehrh.) was studied in relation to tree age, size, and growth rate, vertical position in tree, morphological characteristics of heartwood-sapwood transition zones, between-tree and between-stand variation, and the broad organizations of physiological control over the process. Variability data, the concept of temporal and spatial control of xylem parenchyma senescence, and tentative genetic selection criteria were derived to aid hardwood geneticists and silvicultulists.

Heartwood formation (near ground level) commences at 3-8 years tree age in walnut, 3-9 years in cherry. In walnut, both between-stand and between-tree variation

contribute significantly to total variation in sapwood ring number. In cherry, of these two sources of variation, only between-tree variation is important. Walnut shows little correlation between number of sapwood rings and recent rates of radial growth, while cherry exhibits a compensation for fast radial growth through a reduction in the number of sapwood rings.

Results indicate that sapwood will be excessively wide in walnut grown under intensive culture in the absence of genetic or silvicultural control of heartwood formation, and that such control is biologically feasible. The results are equivocal regarding severity and control of this wood quality problem in rapidly grown cherry.

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INTRODUCTION

The proportion of heartwood to sapwood is an important criterion of timber quality in many tree species. The relative amount of heartwood has a major impact on the effectiveness of wood preservative treatments, on the gluing, drying, and pulping of wood, and on the value and utilization efficiency of high value hardwood species where heartwood is desired for aesthetic reasons (e.g., 5,8,7,10,12).²

Black walnut (*Juglans nigra* L.) and black cherry (*Prunus serotina* Ehrh.) are two species in which heartwood-sapwood proportions are commercially important for aesthetic reasons. Sapwood limitations are part of the lumber grading rules for walnut and veneer grading rules for both species (14,23), and sapwood thickness is important in the determination of walnut log values. According to the fine hardwoods industry, excessively wide sapwood in walnut can result in Cog value reductions of 10-70 percent as well as increased manufacturing costs and waste.

During the past decade a number of public and private organizations have responded to shortages of high-quality fine hardwood species (21-22), by intensifying their programs of research and development on these species. The Forest Service and other institutions have significant silvicultural and genetic programs for both walnut

and cherry, with a major goal being the development of improved trees which can be grown to commercial maturity in a much shorter time than is now typical. Recently, recognition has been given to the possibility that the rapid growth rates associated with such intensive cultural systems may favor significant increases in sapwood thickness in the resulting timber (4). This recognition has produced active interest in applying manipulations of heartwood-sapwood proportions to silviculture and tree improvement programs for walnut and cherry.

Evaluation of the potential problem of wide sapwood and derivation of methods for controlling it require a knowledge of the normal progression of heartwood formation and of the factors that influence the process. This report describes the characteristics of heartwood-sapwood transition zones, the magnitude and patterns of within-tree, between-tree, and between-stand variation, the effects on heartwood formation of age, size, and growth rate, and the broad organization of physiological control over the process.

¹Maintained in Madison, Wis., in cooperation with the University of Wisconsin.

²Underlined numbers in parentheses refer to literature cited at end of this report.

MATERIALS AND METHODS

The study data were obtained from 155 walnut trees in west-central Missouri, southern and northern Illinois, southern Indiana, and southern Wisconsin, and 159 cherry trees in northwestern Pennsylvania and northeastern West Virginia. The sample trees were selected to represent a wide range of ages (1-77 yr for walnut, 3-80 yr for cherry) and a wide range of sizes and growth rates. Heartwood and sapwood widths and annual ring counts were recorded for 0-0.23 meter above ground level³ for all trees and for various heights within the butt log for a limited number of trees. For most trees, ground level measurements were made on a

single increment core per tree, extracted from a random circumferential position. The heartwood-sapwood boundary is clearly distinguishable in both species without staining. Measurements of distances from pith to cambium and pith to heartwood boundary were made to ± 0.5 millimeter with the wood in the green condition. Annual ring counts in heartwood and sapwood were made on microtome-smoothed surfaces in most cases, magnified up to 550 times.

³References to "ground level" in report refer to this portion of stem.

RESULTS

Transition Zones

The heartwood-sapwood transition zone is the area of the xylem which the evidence favors as the site of the primary metabolic processes of heartwood formation (9,18-19).

The heartwood boundary area in walnut exhibits only sporadic occurrence of a light brown zone, which may be a transition zone, between the dark brown heartwood and white sapwood. When this zone does occur, it is often not readily visible without magnification. It usually covers 1/2 to 2 growth rings. A transition zone is apparently always present in black cherry trees which contain heartwood. It is generally an easily visible gray band (rarely greenish-brown) between the reddish-brown heartwood and white sap-

wood zones, and usually includes 1 to 5 annual rings.

Natural Variation

Magnitude and Patterns

Near-ground-level heartwood formation commences at about 3 to 8 years tree age in walnut and at 3 to 9 years in cherry. No attempt was made to identify heartwood initiation in other portions of the stem. After heartwood formation has been initiated in a tree, various environmental and genetic factors impinge on the process as it continues during the life of the tree. As a result, number of sapwood rings and width of sapwood vary from tree to tree (table 1).

Table 1.—Sapwood characteristics at ground level

Species and number ¹	Age range	Number of rings						Sapwood width			
		Mean	Overall range	S ²	C.V.	Range for trees, age		Mean	Overall range	S ²	C.V.
						< 25 years	> 25 years				
	Yrs				Pct			Mm	Mm	Mm ²	Pct
Walnut (145)	5-77	13.0	3-23	14.9	29.8	3-13	6-23	34	4-80	262	47.4
Cherry (142)	5-80	13.6	3-34	27.2	38.4	3-11	6-34	22	4-44	76	39.1

¹Trees measured represented a variety of sizes and growth rates; all had some heartwood.

Limited information on variation between stands was obtained by comparing the mean number of sapwood rings of even-aged natural stands and plantations, all of a similar age (table 2, walnut; table 3, cherry).

An analysis of variance indicated significant differences between stand means for sapwood ring numbers in the walnut stands (table 2). (The Cedar Creek-22 stand was not included in this analysis because it was significantly younger than the other walnut stands.) Covariance analysis with adjustment for either tree age or recent rate of radial growth (average ring width for sapwood zone) as covariate gave the same result. Similar analysis indicated no significant differences between stand means for cherry (Kane-35 stand excluded from analysis).

A partition of total variation in number of sapwood rings revealed that in walnut, between-stand variation accounted for 43 percent of the total while the trees-within-stands component amounted to 57 percent. For cherry, the trees-within-stands component accounted for almost 100 percent of total variation. Cedar Creek-22 and Kane-35 stands were again excluded from the analysis.

Effect of Height in Tree

The limited data accumulated regarding the effect of height in stem on numbers of sapwood rings and sapwood width are presented in table 4. Higher positions in walnut stems typically exhibited narrower sapwood with fewer growth rings included in it than did the ground level portion of the same

Table 2—Correlations between recent radial growth rates and sapwood characteristics within even-aged natural stands and plantations of walnut (at ground level)

Stand	Age of stand	Number of trees sampled	Mean number sapwood rings	Range of recent radial ¹ growth rates	Relationship and \bar{r}^2 of recent radial growth rate versus	
					Sapwood rings	Sapwood width
	<u>Yr</u>			<u>Mm</u>		
Sinissippi (plantation, n. Illinois)	27	9	10.0	0.95-4.20	(+) 0.46 ns	(+) 0.93**
Cedar Creek-22 ³ (natural stand, s. Illinois)	22-26	8	—	3.50-7.00	(-) .44 ns	(+) .76**
Cedar Creek-30 ³ (natural stand, s. Illinois)	30-34	11	11.5	1.85-5.50	(-) .33 ns	(+) .29 ns
B-C Road (plantation, s. Indiana)	31	9	12.9	.55-2.65	(-) .12 ns	(+) .95**
Bryants Creek (plantation, s. Indiana)	32	16	14.2	.90-3.55	(-) .08 ns	(+) .95**
Goodman (plantation, s. Indiana)	34	17	14.3	.70-5.00	(-) .35*	(+) .84**

¹Recent radial growth rate = average ring width for annual growth rings in sapwood zone (mm).

\bar{r}^2 = coefficient of determination for linear regression between listed variables.

ns = not significant

* = significant at 95 pct level

** = significant at 99 pct level

³Cedar Creek-22 and -30 are actually 2 groups of trees within a single natural stand.

stem. Cherry had narrower sapwood at higher positions than at ground level. A t-test indicated that for walnut the differences between heights were significant at ≥ 99 percent level of probability for both number of rings in sapwood and sapwood width. In cherry the height effect was significant at the 99 percent level for sapwood width, but was nonsignificant for number of rings in sapwood. Between-position correlations within stems were moderately strong for both sapwood thickness and number of sapwood rings in both species.

Effect of Tree Age

Regression analysis was performed for the relationships between the sapwood measurements and tree age. The data in each regression included trees of a wide variety of sizes and growth rates. The raw data and regression curves for number of sapwood rings versus age are plotted in figure 1, and the results of the analysis are summarized in table 5.

For both species the number of sapwood

rings was positively correlated with tree age. The slightly curvilinear relationship was somewhat better approximated by using the logarithm of both number of rings and tree age. Sapwood width was not related to tree age for cherry and was only weakly related for walnut.

Effect of Tree Size

Regression analysis was also performed for the relationships between the sapwood measurements and tree diameter. The data included trees of a wide variety of ages and growth rates. The results are summarized in table 5.

The number of sapwood rings was related to tree diameter, but for neither species was the relationship as good as that between number of sapwood rings and tree age. Sapwood width on the other hand was more closely related to diameter than to age.

Although the effects of tree age and size on sapwood area and on the percentage of stem area in sapwood are of interest, regressions involving sapwood area and per-

Table 3—Correlations between recent radial growth rates and sapwood characteristics within even-aged natural stands of cherry (at ground level)

Stand	Age of stand	Number of trees sampled	Mean number sapwood rings	Range of recent radial ¹ growth rates	Relationship and $2r^2$ of recent radial growth rate versus	
					Sapwood rings	Sapwood width
	<u>Yr</u>			<u>Mm</u>		
Kane 138-47 (nw. Pennsylvania)	44-51	10	13.4	0.79-2.53	(-) 0.001 ns	(+) 0.91**
Kane RR-65 (nw. Pennsylvania)	57-63	13	15.5	.73-2.53	(-) .004 ns	(+) .92**
Kane-35 (nw. Pennsylvania)	30-36	13	—	1.23-5.50	(-) .66**	(+) .77**
Longhollow (nw. Pennsylvania)	51-55	10	14.0	.70-4.30	(-) .71**	(+) .78**
Mono.-Yellow (ne. West Virginia)	52-59	10	14.6	.42-2.82	(-) .68**	(+) .84**

¹Recent radial growth rate = average ring width for annual growth rings in sapwood zone.

$2r^2$ = coefficient of determination for linear regression between listed variables.

ns = not significant

** = significant at 99 pct level

centage area in sapwood are not presented since these variables are functionally related to sapwood width and tree diameter and hence add nothing to the information given above.

Effect of Growth Rate

Growth rate influences were investigated by sampling trees of a range of radial growth rates within even-aged stands and plantations, and performing regression analysis for

Table 4—Sapwood characteristics at two stem heights¹

Species and number	Age range	Diameter inside bark ground level	Height in stem	Number of sapwood rings ²	Sapwood width ³	⁴ r ² for upper vs. ground height values	
						Sapwood rings	Sapwood width
	Yr	Cm	M		Mm		
Walnut (12 logs and 2 increment cores)	27-76	27.4-66.0	Ground (0-0.23)	15.3	44	0.50	0.68
			Upper (1.89-3.66)	12.2	28		
Cherry (15 logs)	55-75	32.6-73.7	Ground (0-0.23)	10.9	33	.48	.67
			Upper (2.59-5.06)	10.5	27		

¹Measurements were made on the two ends of butt logs. For the two standing walnut trees, increment cores were obtained at one random position at each stem level.

²Average of counts at widest and narrowest portions.

³Average of measurements at widest and narrowest portions.

⁴r² = coefficient of determination. All r² significant at 99 pct level.

Table 5. Regressions¹ for sapwood characteristics versus tree age and diameter inside bark at ground level

Dependent variable	Independent variable	² r ²	
		Walnut	Cherry
Log sapwood rings	Log tree age	0.64	0.68
	Log tree diameter	.24	.41
Sapwood width	Tree age	.10	—
	Tree diameter	—	.23
Log sapwood width	Log tree age	—	.01 ns
	Log tree diameter	.52	—

¹3 models were tested for each regression; only the model giving highest r² is listed. N = 145 for walnut, 142 for cherry.

²r² = coefficient of determination. All r² significant at the 99 pct level, except for the one marked ns (not significant).

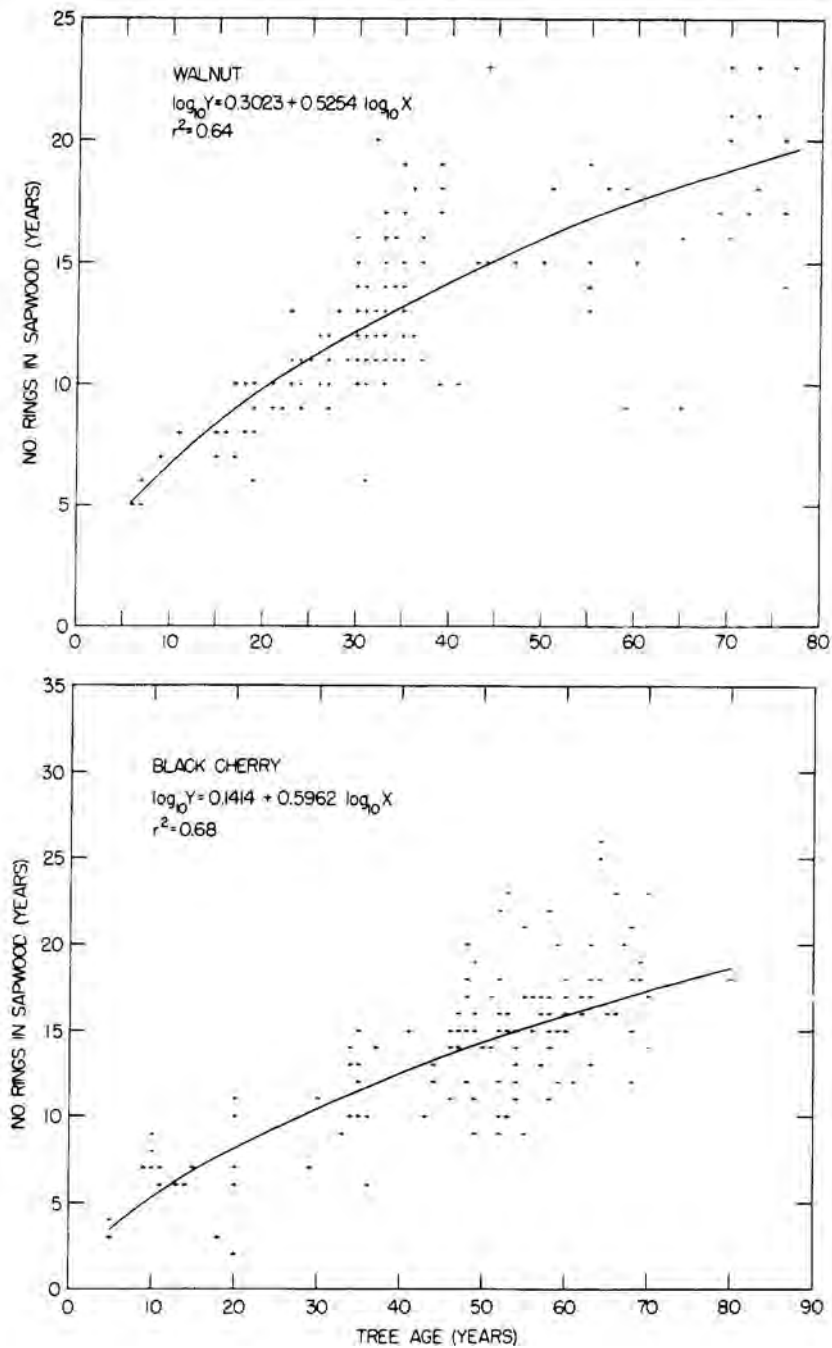


Figure 1.—Relationship between number of sapwood rings and tree age, at ground level. (Upper, walnut; lower, cherry)

M 143 673
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sapwood annual ring count and thickness in relation to recent radial growth rate within each stand (tables 2 and 3). Separate regressions were fitted for each stand to allow for possible stand x growth rate interactions.

In walnut, the correlation between recent growth rate and number of sapwood rings is weak and somewhat erratic, while the relationship between growth rate and

sapwood thickness is generally strong and consistent. In cherry, both relationships seem to hold in a relatively consistent manner; viz., all of the growth rate-ring number correlations are negative, and three out of five are statistically significant, while all of the growth rate-sapwood width correlations are positive and all significant.

DISCUSSION

It is interesting and somewhat surprising that heartwood formation can be initiated in walnut and cherry trees as young as 3 years. The literature on the subject has emphasized species of the *Eucalyptus* genus as being unusual in initiating heartwood at a similar early age (7). The age of the tree when heartwood formation is initiated may be a significant disease resistance consideration in the plantation culture of cherry and other hardwood species, and may warrant further investigation.⁴

The effects of stem height on heartwood-sapwood proportions found in this study parallel the data reported in an early study by Coile (6) on black walnut and in many studies of other species (e.g., 2,3,13,17,20).

The positive correlation between tree age and number of sapwood rings implies an unexpected advantage for the shorter rotations associated with intensive culture which helps to lessen the increases in sapwood width and percentage of stem area in sapwood due to faster growth and smaller tree diameters, respectively. The stability of the positive relationship between tree age and number of sapwood rings under the growth patterns of intensive culture is an important unknown factor.

One of the characteristic features of heartwood formation in woody species is the death of most of the parenchyma cells within the transition zone (11). Both axial and ray parenchyma are plentiful within the xylem of walnut. Axial parenchyma are usually absent from cherry xylem however, so that only ray parenchyma are involved in heartwood formation-associated death in that species. By definition, then, the control of heartwood-sapwood proportions through any means, genetic or cultural, proceeds through control of the life span of the xylem parenchyma cells.

An issue that is central to evaluating and eventually controlling a potential wide-sapwood problem is whether a species compensates for rapid radial growth by effecting a reduction⁵ in the number of annual rings present in its sapwood zone. A species or genotype that is genetically programmed for such a negative correlation between parenchyma cell life expectancy and growth rate can be considered to have strong spatial control over the senescence of its sapwood parenchyma cells. A species or genotype not exhibiting such homeostatic compensation

demonstrates only temporal control over parenchyma senescence. Spatial control in this case refers to the death of xylem parenchyma cells (heartwood formation) solely in response to an increase in the distance between them and the outer portions of the tree stem, cell age having no effect. This concept implies the existence of distance-associated stress as the effective control; e.g., translocation problems, aeration difficulties, and water deficits. Temporal control refers to the death of xylem parenchyma cells (heartwood formation) solely in response to the age of the cells, the distance between them and the outer portions of the tree stem having no effect.

The data for growth rate influences on sapwood width and number of rings in sapwood (tables 2 and 3) constitute preliminary evidence that walnut typically exhibits strong temporal control and weak spatial control over the senescence of its xylem parenchyma cells at a given tree age, while both types of control are important in cherry.

The differences between walnut and cherry with respect to temporal and spatial influences on heartwood formation result in important differences between the two species in the predicted severity of the wide-sapwood problem in fast-grown trees and in recommended methods of genetic selection for dealing with the problem.

The lack of spatial control in walnut means that a given walnut tree, and perhaps its progeny, will tend to have a certain number of annual rings in its sapwood region regardless of the rate of radial growth. Thus, any increase in radial growth rate for a group of walnut trees will potentially result in an equal increase in average sapwood width, presaging a serious wide-sapwood problem in intensively cultured walnut. This problem will be especially acute in smaller diameter logs because of the negative geometric relationship between area or volume proportion of sapwood and tree diameter for any given sapwood width.

⁴Campbell, W. A. 1937. Preliminary study of sprout decay hazard in northern hardwood stands in Pennsylvania. Unpubl. office memorandum, Div. For. Path., Bur. Plant Ind., USDA. 6 p.

⁵Reduction in sapwood ring number is the predicted usual form of spatial control. An increase in sapwood rings as a response to accelerated radial growth is the other possible form of spatial control, but would be expected to be less common.

Based on the data presented in this report for average number of sapwood rings and on radial growth rates expected for walnut under intensive culture, it is likely that sapwood thicknesses of 75 to 165 millimeters (3-6.5 in.) will be commonplace in such timber at harvest, unless genetic or silvicultural (or both) methods for stimulating heartwood formation are developed and implemented. For logs of average diameter inside bark of 381 millimeters (15 in.), these sapwood widths translate as 64-98 percent sapwood on an area basis. However, it is important to realize that the results for walnut do not include a significant number of trees with extremely high rates of radial growth (table 2) such as might be expected in many walnut stands of the near future. It is conceivable that diameter growth rates of 12 to 25 millimeters per annum might put sufficient stress on inner sapwood parenchyma to make spatial influences significant; viz., extremely rapid growth might cause a reduction in the number of sapwood rings, thereby lessening the size of the increase in sapwood width associated with the rapid growth.

Also requiring mention is an early study by Baker (1) which contains data contradicting the present findings. His results include a trend suggesting the presence of spatial influences on heartwood formation in walnut over a similar range of radial growth rates to those included here. However, it is impossible to judge the validity and significance of Baker's findings based on the information given in his paper.

The moderately strong spatial influences on heartwood formation that are present in cherry would reduce, but not prevent, increases in sapwood width due to accelerated growth. The additional presence in cherry of significant temporal control mechanism(s) over parenchyma senescence would guarantee some increase in sapwood width due to faster growth. Present data do not allow an evaluation of the magnitude and importance of the spatial "damping" effect in cherry under the growth rates accompanying intensive culture.

Between-tree variability in sapwood characteristics (table 1) appears to mirror the temporal-spatial control differences between walnut and cherry. The between-tree coefficients of variation (C.V.) for average ring width of annual rings in the sapwood zone (recent radial growth rate) for the populations represented in table 1 were 55.0 percent for walnut and 64.0 percent for cherry. Walnut exhibited greater tree-to-tree variability

in sapwood width than did cherry, in spite of the greater growth rate variability in the cherry population (compare C.V. values for sapwood width in table 1). This reflects the "damping" effect of the spatial control mechanism in cherry, and the absence, or only small presence, of such a spatial mechanism in walnut. Correspondingly, the presence of spatial influences in cherry may be the major reason for greater between-tree variability in the number of annual rings included in sapwood for that species than for walnut (compare C.V. values for number of rings in table 1).

Working criteria for genetic selection of parent trees that will ultimately produce progeny with acceptably reduced sapwood thicknesses can be proposed, based on the findings reported here, and should be applicable to selection from natural, plantation, provenance planting, and seed orchard-progeny test populations. For walnut, an efficient general selection criterion would be minimum number of sapwood rings within age classes (ignoring actual sapwood width and recent rate of radial growth); for cherry, minimum number of sapwood rings within age and recent radial growth rate classes.

The presence of age class in the criteria is a reflection of the role age plays in determining the number of rings in the sapwood. Recent radial growth rates are included for cherry, but not for walnut, because of the existence of spatial influences on heartwood formation in cherry and virtual nonexistence of the same in walnut. The existence of spatial control in cherry necessitates greater complexity and produces more uncertainty in genetic selection for reduced sapwood thickness. If later studies indicate that the magnitude of spatial effects in cherry is unimportant under conditions of intensive culture and accelerated growth, then the selection criterion for cherry can be identical with that listed for walnut, resulting in a simplified procedure. It should be noted that although radial growth rates can conveniently be ignored in the selection procedure for reduced sapwood width in walnut, in practice selection for increased growth rates would be part of any improvement program. Therefore, recent radial growth rates would only vary within an upper range for the trees selected for genetic evaluation and breeding.

It is fairly obvious that sapwood widths could be reduced in both walnut and cherry by reducing radial growth genetically or silviculturally, over the whole rotation or near the end of rotation. This is not, however,

likely to be feasible—economically or otherwise—and it is probably a better approach to attempt both increased growth and control of sapwood thickness simultaneously.

Some type of regression line (walnut) or regression plane (cherry) procedure with selection criteria as variables, would seem promising as an operational procedure for enforcing selection differentials for the suggested criteria.

The data on components of variance presented in this study for sapwood ring numbers (p.3) should also prove useful to geneticists in the initial design of efficient selection procedures for maximizing heartwood formation. According to that data, both stand-to-stand and individual tree (within stands) differences initially should be considered in superior tree selection for walnut. Individual tree variations would appear to be all important, and between-stand differences unimportant, in cherry. However, the problematical magnitude of the spatial control effect in cherry leaves some uncertainty in extrapolating that data to the design of actual selection procedures.

Accurate evaluation of the economic feasibility of altering heartwood-sapwood proportions in walnut and cherry through genetic tree improvement or cultural procedures awaits further study. The maximum difference in stand means of greater than four sapwood rings, for only five randomly selected stands of walnut (table 2), is an indication that it should be biologically possible to favorably affect sapwood thickness in that species through a combination of genetic and silvicultural manipulations.

Nicholls (15) and Nicholls and Brown (16) have provided the only heritability estimates available for heartwood-sapwood pro-

portions in any species. Nicholls and Brown report a narrow sense heritability estimate of 0.20 for area proportion of heartwood at breast height in *Pinus radiata* D. Don. Walnut trees within the restricted age class 30 to 40 years (71 trees) in the present study had a mean number of sapwood rings = 13.6 (at ground level). Selection intensities of approximately 0.01, 0.1, and 0.2 within the population would result in mean number of sapwood rings in selected parents (at ground level) of 6.0, 9.3, and 10.3, respectively; i.e., selection differentials of 7.6, 4.3, and 3.3 sapwood rings. Assuming a narrow sense heritability of 0.20, mass selection, sexual propagation, and open pollination, respective genetic gains (ΔG) would equal 1.5, 0.9, and 0.7 sapwood rings or 11.0, 6.6, and 5.1 percent.

The impact of such changes on actual sapwood width would, of course, depend on recent radial growth rates attained in the intensive cultural systems utilizing the improved genotypes. Economic feasibility of such alterations in sapwood width would then depend on a comparison of total costs involved versus improved value of the resulting stumpage and/or logs and/or products.

It should be emphasized that the heritability estimate assumed in these calculations could be significantly different than the actual range of heritabilities for sapwood ring number in walnut populations. Considerations beyond the scope of this paper suggest that narrow sense heritability for number of sapwood rings in walnut is greater than 0.20. The estimates of genetic gain given above should therefore be considered as conservative rough estimates only, of use primarily in deriving working hypotheses of tree improvement possibilities.

SUMMARY

Heartwood formation (at 0-0.23 m above ground level) commences at tree age 3-8 years in walnut (*Juglans nigra* L.) and 3-9 years in cherry (*Prunus serotina* Ehrh.). Five even-aged stands of walnut differed significantly in number of sapwood rings (range of stand averages = 10.0 to 14.3 rings) while four even-aged stands of cherry did not. In walnut, 43 percent of total variation in sapwood ring number was associated with a between-stand component and 57 percent with trees within stands. In cherry, these values were 0 percent for stands and 100 percent for the trees-within-stands component. Height in stem affected sapwood rings number and sapwood width in walnut, but only sapwood width in cherry. The number of annual growth rings in sapwood increased with tree age in both species.

Walnut shows little correlation between number of sapwood rings and recent rates of radial growth, while cherry exhibits a compensation for fast radial growth through a reduction in the number of sapwood rings. This suggests that temporal control of the senescence of sapwood parenchyma cells is strong and spatial control of the same is weak in walnut, while both temporal and

spatial controls are important in cherry. Consequently, in walnut, increases in radial growth can be expected to produce equal increases in sapwood thickness, and excessively wide sapwood is probable under intensive cultural conditions. In cherry, such increases in sapwood width due to accelerated growth will be less than the increase in growth. Sapwood widths of 75-165 millimeters (3-6.5 in.) can be commonly expected in intensively cultured walnut at harvest, assuming no genetic or silvicultural control of heartwood formation has been practiced.

The data suggest that genetic, and possibly silvicultural, control of heartwood-sapwood proportions is biologically feasible for walnut, without sacrificing growth rate. The results are equivocal with respect to biological control of heartwood formation in cherry. Tentative guidelines for genetic selection aimed at heartwood-sapwood control are proposed. Working estimates of genetic gain for reduced sapwood thickness in walnut are presented, based partially on heritability data from another species. Other variability data of direct use to hardwood geneticists and silviculturists are presented.

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