XYLEM MORPHOLOGY AND DISCOLORATION IN BIGTOOTH ASPEN *(POPULUS GRANDIDENTATA)*[1]

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ABSTRACT.--Bigtooth aspen *(Populus grandidentata* Michx.) stem wood from seventeen trees was studied to explore relationships between discoloration due to stem wounding and xylem variables. Vessel grouping and the percentage of growth ring broken by vessels groups were correlated with discoloration. These characters may have potential for indirect selection in this species.

INTRODUCTION

Discoloration and decay cause major annual loss of timber yield (Schmitt et al., 1978). Response to decay organisms in living trees has been modeled according to a compartmentalization concept (Shigo and Marx 1977) which can help explain patterns of discoloration and decay in hardwoods. The model conceptualizes four "walls" which are based on various anatomy and physiological responses of cells to decay fungi and their pioneers (Shortie 1979a). When microorganisms invade through wounds, living parenchyma cells produce phenols that can limit spread of microorganisms colonizing discolored wood (Shortie 1979b). Furthermore, wood formed after wounding is seldom infected unless new wounds have been inflicted. A barrier zone which has smaller vessels (Mulhern al. 1979) and higher concentration of phenols (Skene 1965) is formed by the cambium. This barrier zone constitutes a distinct tissue (Sharon 1973) and restricts infection to wood present at time of wounding.

Hybrid poplars were found to differ in their ability to compartmentalize discoloration (Garrett et 1976, and Shigo *et al.* 1977). These authors also presented evidence for genetic control of compartmentalization ability for those hybrids. Genetic control of discoloration response has also been reported for sweetgum *(Liquidambar styraciflua* L.) and Eastern cottonwood *(P. deltoides* Marsh.) (Garrett *et al.* 1979).

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The relationship of compartmentalization success with anatomical differences was examined by Eckstein _et al_., (1979). It was reported that strong compartmental izers generally had fewer and smaller vessels with fewer connections to other vessels than weak compartmentalizing trees. Bigtooth aspen (_Populus grandidentata_ Michx.) xylem was examined in this study to investigate the relationship of xylem morphology to compartmentalization success.

MATERIALS AND METHODS

In autumn of 1979, twenty-one bigtooth aspen trees were wounded, each receiving four wounds 1.4 m above ground, 4 cm deep and 2 cm in diameter. Seven trees were located on the East Foss Farm and seven on the West Foss Farm in Durham, New Hampshire. The remaining seven were growing at the Kingman Farm in Madbury, N.H.

The aspens were felled in October of 1980. One tree had died during winter, one of the wounded trees was a trembling aspen (_Populus tremuloides_ Mich.) and two others were excluded because the growth rings were too large to be sectioned by the equipment used, leaving seventeen trees in the analysis. Width of discoloration measured approximately 5 cm above the coring wound and averaged for each tree was used as the measure of discoloration for data analysis.

Three 1 cm x 1 cm x 3 cm blocks were cut from clear wood near the wounds so that the 1 cm^2 face was cross sectional. Three longitudinal sections of 20 mm thickness were cut and the outer two rings on each section were examined. Eight variables, most of which were used by Eckstein _et al_., (1979), were taken from each ring. There were 18 repeated sets of measures per tree, as follows:

1. Proportion of vessels per 101 diagonal points. A micrometer was located in the microscope eyepiece. This scale was oriented diagonally across the ring and the number of times the end of each point on the scale touched a vessel group was counted.

2. Proportion of fibers per 101 diagonal points. As above, counting fibers instead of vessels.

3. Proportion of parenchyma cells per 101 diagonal points. As above, counting radial parenchyma cells.

4. Width of growth ring.

5. Vessel grouping. The number of vessels were counted in each of 150 groups in each ring and this total number of vessels divided by the number of groups (150) gave the average number of vessels per group, or vessel grouping.

6. Radially oriented vessel groups bridging growth ring. The number of vessel groups that broke the growth ring (longitudianl parenchyma) over a 1 mm distance were counted.

7. Percent of the terminal parenchyma broken by vessel groups bridging it. Over the 1 mm segment in the above measure, the width of each vessel group bridging the growth ring was measured and summed.

8. Compartment openness. The cross sectional area of each vessel group within a compartment was summed so that the total vessel area for the compartment was achieved. This number was then divided by the area of the compartment (distance between two rays multiplied by the ring width), giving the percent of the compartment area taken up by vessels, or the compartment openness (Walter Shortie, personal communication). We defined a compartment as the cross-sectional area between two rays and two zones of summerwood.

The above eight variables and discoloration response were analyzed using nested ANOVA with three replications (sample tree locations). Relationships between the above eight variables and discoloration response were analyzed with correlation and regression analyses. Discoloration response was divided into two categories: stronger compartmentalizers with discoloration extending 3.5 cm or less beyond the coring width, and weaker compartmentalizers with discoloration extending 4.0 cm or more beyond the coring width. Mean values of the eight variables were tested with a two tailed t test of mean differences. Finally, relationships among variables, except discoloration response, were explored using discriminant function analysis with 17 trees such that each tree was considered one group. All analyses were done with SPSS routines or Fortran program written for specific problems.

RESULTS AND DISCUSSION

Significant variation ($P \leq .01$) was detected among trees for all eight anatomical variables and width of discoloration using nested ANOVA. Among site variation was not significant ($P < .05$) except for annual ring width which was different ($P \leq .01$) at the three sites.

Multiple linear regression of eight mean anatomical values and discoloration response accounted for 77 percent of the variation observed in discoloration response ($R = .88$, $P \leq .05$, df = 10). Using simple linear regression, the best single predictor of discoloration was percent of the terminal parenchyma broken by vessels group, variable number 7 ($R = .619$, $P \leq .01$, df = 15).

Three xylem anatomical variables of bigtooth aspen with wounding response discoloration of 4 cm or more were significantly different from those with less than 3.5 cm of discoloration for three xylem anatomical variables and annual ring width (Table 1). The stronger compartmentalizing trees (discoloration less than 3.5 cm) had fewer and smaller breaks in the annual rings and fewer vessels per group. Correlation analysis based on sample tree means resulted in significant positive correlation ($P \leq .01$) between width of discoloration and the percent of the growth terminal parenchyma broken and the number of vessels in each group of vessels ($P \leq .05$) (Table 2).

A relationship between compartmentalization of decay in hybrid poplars and the vessel system was reported by Eckstein _et al_. (1979) and has also been observed by Wittberg and Eckert (unpublished data). Sinclair _et al._ (1972) indicated that mean vessel diameter could be useful for rapid assessment of potential Dutch elm disease resistance in American elm. Elgersma (1967) earlier theorized that cross connections between vessels (vessel grouping) was important in the tangential spread of spores in Dutch elm disease.

Table 1. Comparison of anatomical variable means in strong and weak compartmentalizing bigtooth aspens.

	Discoloration below 3.5 cm	Discoloration 4.0 cm and above
average discoloration width 5 cm above wound	3.350	4.293
number of trees	5	6
proportion of vessels per 101 diagonal points across growth ring	0.3175	0.3183
proportion of fibers per 101 diagonal points across growth ring	0.6174	0.6134
proportion of radial parenchyma cells per 101 diagonal points across growth ring	0.0751	0.0789
average annual ring width	1.81 mm	1.46 mm[a]
vessel grouping, average number of vessels per group	1.72	1.92[a]
number of vessel groups bridging terminal parenchyma per mm	1.6	2.2[a]
percent of terminal parenchyma broken by vessel groups	3.2	4.8[a]
compartment openness, ratio of summed vessel area within a compartment area	0.38	0.392

a. Significant at .91 level of significance

Eckstein _et al_. (1979) also reported that strong compartmentalizers in hybrid poplar had fewer vessel groups bridging terminal parenchyma in growth rings than did weak compartmentalizers. In the current study, one of the strongest relationships observed was the positive correlation between increasing discoloration and percent of the terminal parenchyma broken by vessel groups (Table 2). In the compartmentalization framework, these breaks in marginal parenchyma are "holes" through Wall 2 (Shigo and Marx, 1977).

To investigate the relationship annual ring width has with xylem variables, discriminant function analysis with individual trees as groups was utilized. The proportion of vessels was dropped from the analysis since it has a strong inverse correlation (-0.95) with proportion of fibers and represents approximately the same information. Since eighteen observations were made per tree, among group discrimination is artifically inflated and significance levels for discrimination among groups (trees) are not presented. However, the analysis is appropriate for examination of relationships among variables

Table 2. Simple correlations between anatomy variables and average discoloration width 5 cm above wound midpoint

Variable	Correlation with discoloration
proportion of vessels per 101 diagonal points across growth ring	-0.309
proportion of fibers per 101 diagonal points across growth ring	0.328
proportion of radial parenchyma per 101 diagonal points across growth ring	-0.373
average annual ring width	0.027
vessel grouping, average number of vessels per group	0.482a
number of vessel groups bridging terminal parenchyma per mm	-0.394
percent of terminal parenchyma broken by vessel groups	0.619b
compartment openness, ratio of summed vessel area within a compartment to compartment area	0.422

a. $P<.05$
b. $P<.01$

Discriminant analysis resulted in four functions (Table 3) which accounted for 98 percent of the variation in the data. Function 1 accounted for 70 percent of the variation, which was essentially due to annual ring width. Variation due to xylem variables was accounted for by the three remaining functions which accounted for 28 percent of the variation. Each discriminant function is orthogonal from the others so that a variable with a high weight on one function, and low weights on the others can be said to be independent of variables which have high weights on other functions. Following this rationale, annual ring width accounts for a major portion of the total variation but is independent of xylem anatomy variables in the 17 study trees (Table 3). Vessel grouping (Function 2) accounts for about 19 percent of the total variation and is relatively independent of the other xylem variables. Thu number of vessel groups bridging the growth ring is the major component of Function 3 which only accounts for 5 percent of the variation. The percent of ring broken, highly correlated with discoloration, is not a strong source of variation in the xylem anatomy data since it is a minor component of Function 3. Function 4 is difficult to interpret because it accounts for only 3 percent of the variation, however it represents compartment openness more than any other variable.

Compartment openness, which we hoped would reflect xylem anatomy characteristics important in determining, discoloration response was not significantly related to discoloration response in our analyses and represented a minor component of variation represented by Function 4. This measure does not seem useful for relating xylem anatomy and discoloration response.

Table 3. Standardized canonical discriminant function coefficients for discriminant analysis among seventeen bigtooth aspen trees.a

Variable	Func 1	Func 2	Func 3	Func 4
proportion of fibers per 101 diagonal points across growth ring	-0.142	0.204	-0.322	-0.489
proportion of parenchyma per 101 diagonal points across growth ring	0.208	-0.172	0.491	-0.431
annual ring width	<u>0.994</u>[b]	0.072	-0.091	0.038
vessel grouping, average no. of vessels per group	0.138	<u>-0.856</u>	-0.485	0.011
number of vessel groups that bridge terminal parenchyma per mm	0.052	-0.107	<u>0.758</u>	-0.444
percent of terminal parenchyma broken by vessel groups	-0.095	-0.200	-0.375	-0.151
compartment openness, ratio of summed vessel area within a compartment to compartment area	0.102	-0.084	0.452	<u>0.667</u>

a. Percent of variance explained by functions 1, 2, 3 and 4 respectively: 70%, 19.6%, 5.3% and 2.9%.

b. Underlined weights indicate the variable most characterized by the function.

CONCLUSIONS

Two xylem variables, percent of ring broken by vessel groups and vessel grouping are correlated with discoloration response to wounding in our bigtooth aspen sample. Percent of ring broken by vessel groups was the most important variable in prediction of discoloration response in the 17 study trees. These variables should be studied in other samples of this species since they may have potential as correlated characters useful for indirect selection or screening for individual trees with high compartmentalization potential.

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