# INHERITANCE OF WOUND COMPARTMENTALIZATION IN SOFT MAPLES

## by Frank S. Santamour, Jr.

**Abstract:** Compartmentalization of discolored wood associated with stem wounds of soft maple is genetically controlled. Silver maple is apparently a stronger compartmentalizer than red maple, and red X silver maple hybrids are generally superior to red maples. Compartmentalization varies widely among red maples, but there are significant differences in general and specific combining abilities for strong compartmentalization. Thus, in breeding programs designed to produce trees with strong compartmentalization, care must be taken not only to parental selection but also to progeny testing.

All trees are subject to wounding. Forest trees in natural areas may be injured by fire, weather, or animals. Landscape trees may be intentionally wounded above ground level by pruning operations for esthetic purposes and during line clearance operations. Other intentional wounds are inflicted when various chemicals are introduced into the tree trunk to combat disease and insect pests or to correct mineral nutritional deficiencies. Vandalism is another source of intentional wounding. The wide variety of accidental wounds to trees is limited only by the possible or seemingly impossible activities of man and his machines.

Until recently, tree wounds and the wood discoloration and decay brought about by wounding were considered to be a "fact of life" that the arborist would just have to live with. In speaking to various groups about the potential of genetic improvement of landscape trees, I have often stated that we could breed and select for resistance of tolerance to all urban stresses except automobiles. Today, even though the smaller compact cars still represent a formidable danger to curbside trees, we may have the opportunity to develop trees "resistant" to injury.

Shigo (1974a) introduced the concept of "compartmentalization" of wood discoloration and decay resulting from wounding. Later, Shigo and Marx (1977) provided excellent pictorial illustrations of the systems of compartmentalization operating within a tree. Evidence that such com-

partmentalization may be under genetic control was first given by Shigo et al (1977a). Other recent papers (Shigo 1977, Garrett and Shigo 1978, Schmitt et al 1978) have strengthened this contention, but more data are needed, in many genera, before we can incorporate wound compartmentalization into breeding and selection programs with some assurance of success.

The present study, on soft maples of known genetic background, was undertaken to provide additional data on the genetic contribution to wound compartmentalization.

## Materials and Methods

The trees used in this study were included in test plantations GP-3-46 and GP-4-46 of the USDA Forest Service in Beltsville, Maryland. The Forest Service had abandoned these plantings a number of years ago but had given me permission to use the trees for research. The area in which the plantations are located is now under the control of the U.S. Secret Service.

The plantings included control-pollinated intra- and interspecific hybrids between selected parent trees of red maple (*Acer rubrum* L.) and silver maple (*A. saccharinum* L.), and plants grown from rooted cuttings of several of the parents. The crosses had been made in 1940 and 1941 in New Haven, Connecticut but, because of World War II, remained in nursery rows until outplanted in 1946. In one planting, the progenies were merely planted in rows, according to parentage, while in the other planting, each progeny was represented by a 36-tree block. There was no conscious attempt at statistical design in the row plantings. A second replicate of the block plantings was destroyed for construction prior to 1974. A few hybrid combinations were planted in both the row and existing block plantings, but they do not represent true replication. Spacing between trees in both plantings was 8 feet.

The last systematic evaluation of these plan-

tings was made in 1958, and some growth data were presented at the field sessions of the Sixth Northeastern Forest Tree Improvement Conference (Anon. 1959). Cytological studies of certain parents and progenies have also been reported (Santamour 1965).

On June 11 and 12, 1974, 470 trees were wounded and inoculated with spore and mycelial suspensions of the Verticillium wilt fungus. Each tree was wounded twice at about 1.4 m above ground by pounding a 1.9 cm-wide chisel into the trunk, on opposite sites, to a depth of about 0.5 cm. About 2 ml of inoculum was introduced into each wound and no further protection of the wound area was attempted. A few trees were wounded and inoculated with water to serve as controls.

This particular method of Verticillium inoculation on these 35- to 36-year-old maples proved to be almost totally useless. Only two trees of one of the parent clones showed any wilt symptoms during 1974. The technique was effective (with smaller wounds) on 3-year-old seedlings of tuliptree (*Liriodendron tulipifera* L.) and American elm (*Ulmus americana* L.), indicating that the fungal inoculum was potentially pathogenic.

Thus, the inoculation experiment on maples was considered a failure and the trees grew on and were used for other (morphological and biochemical) studies. In 1978, however, as a result of the publications cited above and conversations with Dr. Shigo, it occurred to me that the wounding of 1974 might be significant. Felling and observation of a few trees convinced me (and Dr. Shigo) that it was!

**Measurements.** During November and December of 1978 we felled, sawed, and made measurements and calculations on 135 trees. Five trees from each of 22 progenies were felled for the major analyses. Most of the parent clones were represented by only one of two living trees, although three clones had more than five trees. At least one tree of each of the available parent clones was cut, and two trees where possible. A few additional trees of several pogenies were felled to check on the wound response on different sites (200 m apart) or to replace original selected trees that contained discoloration or rot not

associated with our wounding. Each tree was severed at 30 cm below the wound area. The length of the vertical column of discoloration, above and below the wound, was determined in the field by making successive cuts at 30 cm intervals and noting the presence or absence of discoloration extending from each wound. A 60 cm-long section of trunk, 30 cm above and below the wound area, was brought into the laboratory for further analysis.

The trunk sections were cut into disks with a band saw, first directly through the wound area, and then at 5 cm intervals in both directions from the wound. The upper surface of the first section above the wound area was selected for detailed calculations of the extent of internal discoloration.

A piece of acetate film (0.005 inches thick) was placed on the surface of the cut section and the discolored areas were outlined with indelible ink. These areas were cut out and weighed on an analytical balance. The weight of each discolored area was divided by the weight of a rectangle 1.9 cm wide (the width of the chisel) and a length equal to the distance from the outside of the chisel wound to the pith. This method of calculation proved accurate to within 3%.

Analyses of variance were performed on actual or arcsin-transformed data and means compared using Duncan's multiple range test. Correlation analyses utilized the least squares method.

## Results and Discussion

Our "control" wounds were few in number and did not cover a wide range of progenies or clones. However, it was evident that the extent of internal discoloration was *not* dependent on Verticillium inoculation. Shigo (1974b) reported similar observations on red maples inoculated (with controls) in chisel wounds with other fungi. Also, even though our "replications" of certain progenies were not statistically designed, the internal discoloration patterns observed in progenies planted in two different areas did not differ significantly. External wound closure, or "healing" was not correlated with internal compartmentalization of discolored tissue (Fig. 1A,D). Previous studies (Shigo et al 1977a,b) have reported this lack of correlation.

The internal discoloration patterns tended to be

of two basic types: "crescent" — in which the discolored area was only slightly more extensive than the original wound (Fig. 1B), and "wedge" — when the discolored region extended to the pith (Fig. 1C).
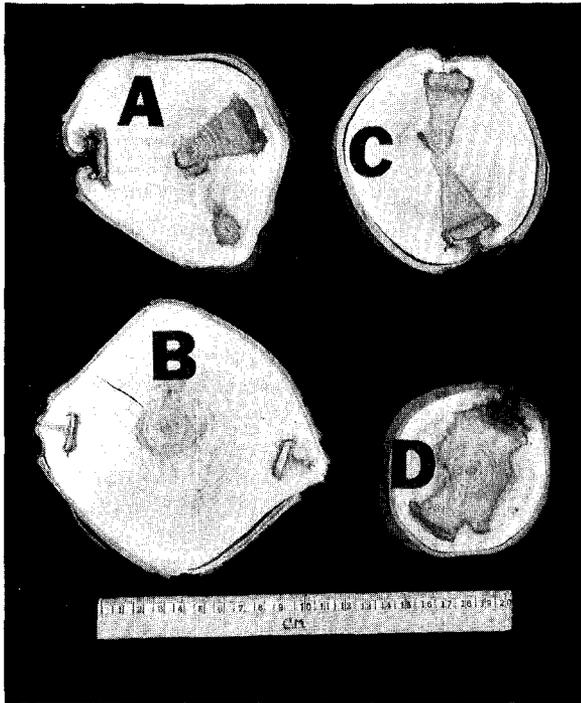


**Figure 1. Wood discoloration patterns in wounded red maples (A) strong compartmentalization of one wound that has not "healed", but weak compartmentalization in the other "healed" wound; (B) both wounds showing weak compartmentalization; (C) both wounds showing strong compartmentalization; (D) very weak compartmentalization breaching the radial "walls" set up along ray cells.**

The varying strengths of the compartment "walls," as explained by Shigo and Marx (1977-p. 12-13), were borne out in this study. The tops and bottoms of the compartments (Wall 1) were the weakest. The inner wall (Wall 2) was next weakest, as evidenced by the frequent extension of discoloration to the pith. The side walls (Wall 3) formed by the ray cells were somewhat stronger, as shown in the regularity of the sides of some "wedge" discoloration patterns. Occasionally, even these walls were breached (Fig. 1D). The strongest wall (Wall 4) was the outer wall formed by the cambium. We did not find any discoloration

in the new wood formed since wounding.

The length of the discolored column below the wound only varied from 20 cm to 35 cm among all trees, and there were no significant differences between parents or progenies. There was, however, great variation in the vertical extension of discoloration above the wound (Table 1). The length of the discolored column was not correlated with "wedge" or "crescent" patterns of discoloration. It is obvious from Table 1 that vertical compartmentalization in red X silver maple hybrids was significantly superior to that in red maples. Among red maples, the progenies of G-64 showed significantly stronger vertical compartmentalization than those of G-70, as would be expected from the data for the parent clones. Average lengths of discoloration, calculated from the six common comparable control-pollinated progenies were 112 cm for G-64 and 163 cm for G-70. These figures compare well with the averages of 113 cm and 184 cm found in open-pollinated progenies of G-64 and G-70 respectively. Among the progenies of G-64, it is obvious that G-64 X G-60 and G-64 X G-61 were significantly superior to all others. Among male parents, the progenies of G-303 exhibited the weakest compartmentalization, even though the differences were not significant in all comparisons.

**Table 1.** Length of vertical discolored column (cm) above wounds in maple parents and progenies (five trees per progeny).

| Male Parents | Female Parents | | | | |
| | Red Maple | | Silver Maple | | |
| | G-64 (53)[1] | G-70 (154) | G-58 (25) | G-201 (?) | G-202 (?) |
|---|---|---|---|---|---|
| *Red Maple* | | | | | |
| G-28 (35) | — | 88 | — | — | — |
| G-60 (30) | 60 | 170 | — | — | 42 |
| G-61 (25) | 67 | 177 | — | 48 | 47 |
| G-62 (25) | 119 | 128 | 48 | — | 51 |
| G-63 (?) | 102 | 154 | — | — | — |
| G-75 (83) | 145 | 162 | — | — | — |
| G-303 (?) | 180 | 216 | — | — | 75 |
| OP[2] | 116 | 184 | — | — | — |
| *Silver Maple* | | | | | |
| G-58 (25) | — | 60 | — | — | — |
| G-201 (?) | — | 84 | — | — | — |

[1]Parental averages based on two trees in G-64, G-70, and G-58; one tree in all others.

[2]OP = open-pollination.

The area occupied by discolored wood became progressively reduced with increased vertical distance above and below the wound zone. "Wedge" patterns were reduced in width before any reduction in wound-to-pith extension was found, demonstrating once again the relative strengths of Wall 2 and Wall 3. At the upper and lower limits of vertical discoloration, the only discoloration found was directly associated with the original wound zone.

The extent of wound-associated discoloration calculated from stem cross-sections is given in Table 2. Our method of calculation (described above) included the original wound zone (roughly 1.9 X 0.5 cm) in the discolored area. The percent discoloration, even if it were strictly confined to the original wound zone, would be 6.4% in a 6-inch (15.4 cm) diameter tree and 12.8% in a 3-inch (7.7 cm) diameter tree. Based on the distribution of discoloration percentages, we selected 25% as the upper limit for strong compartmentalization. Significant differences among progenies tended to follow a pattern similar to discolored column lengths. The correlation between cross-sectional area and column length was high (r=0..93), but there were notable exceptions. The progeny of G-64 X G-303 had a high column length (180 cm) but showed good cross-sectional compartmentalization (16.9%). Still, the data indicate that, in general, strong vertical compartmentalization is highly correlated with strong cross-sectional compartmentalization.

However, in the breeding and development of trees with superior compartmentalization (injury "resistance"), we should be more concerned with the numbers of good trees derived from the various crosses.

The number of trees and wounds showing strong compartmentalization are given in Table 3. As before, the red X silver maple progenies showed stronger compartmentalization than the red maples. Thirty-eight of the 40 trees sampled from the 8 interspecific hybrid progenies exhibited strong compartmentalization of both test wounds. The red maple progenies derived from G-64 were superior to those of G-70. In the six common and comparable control-pollinated progenies, 22 of 30 trees derived from G-64 showed

strong compartmentalization compared to only 9 of 30 trees of the G-70 progenies.

**Table 2.** Cross-sectional discolored areas 5 cm above wounds in maple parents and progenies (five trees per progeny), in percentages.

| | Female Parents | | | | |
| | Red Maple | | Silver Maple | | |
| Male Parents | G-64 (15.4)[1] | G-70 (17.4) | G-58 (11.5) | G-201 (?) | G-202 (?) |
|---|---|---|---|---|---|
| Red Maple | | | | | |
| G-28 (9.4) | — | 44.7 | — | — | — |
| G-60 (37.8) | 23.3 | 70.9 | — | — | 12.0 |
| G-61 (9.8) | 10.4 | 38.9 | — | 11.7 | 11.2 |
| G-62 (56.6) | 20.9 | 27.3 | 16.7 | — | 9.3 |
| G-65 (?) | 52.6 | 52.5 | — | — | — |
| G-75 (14.0) | 58.9 | 45.6 | — | — | — |
| G-303 (?) | 16.9 | 88.9 | — | — | 11.7 |
| OP[2] | 23.6 | 47.5 | — | — | — |
| Silver Maple | | | | | |
| G-58 (11.5) | — | 17.0 | — | — | — |
| G-201 (?) | — | 12.3 | — | — | — |

[1] Parental averages based on two trees in G-64, G-70, and G-58; one tree in all others.
[2] OP = open-pollination.

**Table 3.** Numbers of trees and wounds showing strong compartmentalization (less than 25% discoloration) in maple parents and progenies.

| | Female Parents | | | | |
| | Red Maple | | Silver Maple | | |
| Male Parents | G-64 (4/4)[1] | G-70 (4/4) | G-58 (4/4) | G-201 (?) | G-202 (?) |
|---|---|---|---|---|---|
| Red Maple | | | | | |
| G-28(2/2)[1] | — | 3/5 7/10 | — | — | — |
| G-60 (1/2) | 5/5[3] 10/10 | 0/5 1/10 | — | — | 5/5 10/10 |
| G-61 (2/2) | 5/5 10/10 | 4/5 8/10 | — | 5/5 10/10 | 5/5 10/10 |
| G-62 (1/2) | 4/5 9/10 | 2/5 5/10 | 4/5 9/10 | — | 5/5 10/10 |
| G-65 (?) | 2/5 4/10 | 1/5 3/10 | — | — | — |
| G-75 (2/2) | 1/5 2/10 | 1/5 3/10 | — | — | — |
| G-303 (?) | 5/5 10/10 | 1/5 2/10 | — | — | 5/5 10/10 |
| OP[2] (?) | 3/5 6/10 | 2/5 5/10 | — | — | — |
| Silver Maple | | | | | |
| G-58 (4/4) | — | 4/5 9/10 | — | — | — |
| G-201 (?) | — | 5/5 10/10 | — | — | — |

[1] Parental fraction is number of wounds (of 2 or 4) showing good compartmentalization.
[2] OP = open-pollination
[3] Upper fraction refers to number of trees (of 5) in which both wounds were well compartmentalized.
Lower fraction refers to number of wounds (of 10) showing good compartmentalization.

**Cytological Implications.** Cytological studies on trees in these plantations (Santamour 1965 and unpublished data) showed that all silver maples were tetraploid with 2n=52 chromosomes. The red maples used most frequently as female parents, G-64 and G-70, were both octoploids with 2n=104 chromosomes. Among the red maple male parents; G-60, G-61, and G-65 were octoploids, G-62 was a septaploid with 2n=91 chromosomes, and G-75 was a hexaploid with 2n=78 chromosomes. Both G-28 and G-303 were determined to be octoploids with irregular meiosis that led to production of both diploid and tetraploid pollen grains. In the combinations G-70 X G-28 and G-70 X G-303, the diploid pollen grains were functional and the resulting progenies were hexaploid with 2n=78 chromosomes. No investigation of the crosses G-64 X G-28 and G-64 X G-303 have been made.

It would appear that chromosome number, *per se*, is not a major factor in determining wood discoloration patterns. Among the parents, wedge-shaped patterns indicating weak compartmentalization were found in octoploids and septaploids (G-62). The septaploid progenies derived from crossing with G-75 (hexaploid) included trees with strong and weak compartmentalization. Known octoploid progenies exhibited wide variation in the distribution and extent of compartmentalization.

**Inheritance Patterns.** The compartmentalization of wood discoloration and decay associated with wounding is a complex process. Chemical, physical (anatomical), and physiological responses of the host to wounding and a succession of invading microorganisms may all play a part. Thus, it is tempting, and perhaps valid, to suggest that compartmentalization is under the control of many genes, even though we may have no direct evidence of gene number or gene action. The polyploid nature of the maple species and hybrids investigated in this study is a further complication to understanding the genetics of the wounding response.

Still, there are some potentially important conclusions to be drawn from this study that may have a significant bearing on future studies dealing with breeding and selection for strong compartmentalization. First, there appear to be significant differences between species. Even though we directly sampled only one silver maple parent, the compartmentalization exhibited by its interspecific hybrids, and other interspecific hybrids involving different silver maple parents, further suggests that the strong compartmentalization of silver maple is inherited as a "dominant" characteristic.

It would have been desirable to include other silver maple parents and the progenies of controlled crosses between these parents in our study. They would have been included — if they had survived up until the time of wounding. The plantations had originally contained rooted cuttings of another silver maple parent (G-201), open-pollinated progenies of all three parents, control-pollinated intraspecific progenies involving all three parents, and selfed progenies of G-58 and G-201. The selfed progenies and G-201 clone had almost completely died out by 1958 (Anon. 1959). The other silver maple progenies died between 1958 and 1974, from unknown causes.

There is considerable variation in compartmentalization potential among red maples. Furthermore, if we can (perhaps improperly) regard compartmentalization as a single characteristic, red maples may vary in "combining ability" for strong compartmentalization. Combining ability refers to the ability of a plant to transmit the desired trait, in this case strong compartmentalization, to its offspring. Our data show that G-64 is superior to G-70 in "general" combining ability. Comparisons between open-pollinated progenies and the averages of six comparable controlled crosses indicate that the progeny of G-64 have shorter and less extensive areas of discoloration and include a higher proportion of trees and wounds with strong compartmentalization. One-parent progeny tests would be ideal for selecting potential parents with good general combining ability.

However, the vast differences in *specific* combining ability may offset any breeding advantage that might be gained by such parental selection. Thus the combination G-64 X G-75, both strong compartmentalizers, produced a progeny in which only one of five trees showed strong compartmen-

talization. In contrast, the cross of G-64 with the weak-compartmentalizing G-60 resulted in progeny in which all trees were strong compartmentalizers. Other comparisons can be made using the data in the tables.

Still, in selecting parents for proposed controlled crosses or for parental stock in open-pollinated seed orchards, the selections should probably be limited to trees exhibiting strong compartmentalization. If, as will often be the case, the primary selection criteria will be for other characteristics (such as disease resistance), the inclusion of some weak-compartmentalizing trees might not be a major problem. Progeny tests would be necessary in any event.

As stated above, the polyploid nature of the species used in this study may have complicated the genetic picture. Studies with diploid species may, therefore, produce either different or similar results.

One other problem, that will occur in any selection or breeding program involving compartmentalization, is the size, type, timing, and number of wounds necessary to determine whether a tree is a weak or strong compartmentalizer. In many situations, only a single tree will be available for this determination, and not several members of a clone or cultivar. An accurate assessment of the compartmentalization potential of parent trees is absolutely necessary before valid judgments on inheritance can be made. It is possible that some of the trees classified as strong compartmentalizers in the present study, would, with more or different wounds, have demonstrated the capacity for weak compartmentalization.

### Conclusions

The heritability of wound compartmentalization has now been demonstrated in a number of species. Landscape tree cultivars presently in the trade should be tested for this important survival

trait. Breeding and selection programs to develop superior new cultivars should include wound compartmentalization among the selection criteria.

### Literature Cited

Anonymous. 1959. Field Sessions. Northeast. Forest Tree Impr. Conf. Proc. 6: 33-34 (1958).

Garrett, D.W. and A.L. Shigo. 1978. Selecting trees for their response to wounding. Metro. Tree Impr. Alliance (METRIA) Proc. 1: 69-72.

Santamour, Frank S., Jr. 1965. *Cytological studies in red and silver maples and their hybrids.* Bull. Torrey Bot. Club 92: 127-134.

Schmitt, Dan, Peter W. Garrett, and Alex L. Shigo. 1978. *Decay resistant hardwoods? You bet!* Northern Logger and Timber Processor 27(3): 20-21, 30-31.

Shigo, Alex L. 1974a. *A new look at decay in trees.* Northern Logger and Timber Processor 23(4): 10-11, 38-39.

Shigo, Alex L. 1974b. *Relative abilities of Phialophora melinii, Fomes connatus, and F. igniarius to invade freshly wounded tissues of Acer rubrum.* Phytopathology 64: 708-710.

Shigo, Alex. 1977. *Superior tree production fights tree wound fatalities.* Amer. Nurseryman 146(12): 10-11

Shigo, Alex L. and Harold G. Marx. 1977. Compartmentalization of decay in trees. USDA Forest Service Agric. Inform. Bull. 405, 73p., illus.

Shigo, Alex L., Walter C. Shortle, and Peter W. Garrett. 1977a. *Genetic control suggested in compartmentalization of discolored wood associated with tree wounds.* Forest Sci. 23: 179-182.

Shigo, Alex L., Walter Shortle, and Peter Garrett. 1977b. *Compartmentalization of discolored and decayed wood associated with injection-type wounds in hybrid poplar.* Jour. Arboriculture 3: 114-118.

*Research Geneticist*
*U.S. National Arboretum*
*USDA, SEA*
*Washington, D.C.*