WOUND COMPARTMENTALIZATION IN TREE CULTIVARS: ADDENDUM

by Frank S. Santamour, Jr.

Abstract. Fourteen cultivars of *Acer* (maple), *Fraxinus* (ash), *Quercus* (oak), and *Tilia* (linden) that have been successfully propagated on a commercial scale by budding or grafting were found to be strong Wall 2 compartmentalizers of chisel wounds made in trunks. This confirms our earlier report of similar behavior in 20 other cultivars in 7 genera. The only exceptions to the strong compartmentalization response were in a *Zelkova* cultivar in which considerable wood discoloration was present at the time of wounding and in a sugar maple cultivar that became infected with a fungal canker organism in the wound area. Hybrid poplar clones have traditionally been propagated by cuttings, and both strong and weak compartmentalizers were found. There is a strong relationship between strong Wall 2 compartmentalization and the ability of the tree to restrict the amount of wood discoloration and decay following improper flush pruning of branches. Illustrations are also provided to show: (1) that trees that are inherently strong Wall 2 compartmentalizers will still give a strong response even when wounded outside previous wounds and (2) that Wall 2 does not necessarily form at an annual ring.

In an earlier paper (3), I reported that *all* of the 20 cultivars (in 7 genera) of landscape trees that I wounded by driving a chisel into the trunk sapwood exhibited strong Wall 2 (CODIT, 9) compartmentalization, thus limiting wood discoloration and potential decay to the wound zone. These observations led to the hypothesis that, since the methods of propagation of these cultivars (budding, grafting) involved rather severe wounding, only trees with a genetically controlled strong compartmentalization response could be propagated by these techniques on a commercial scale. Thus, all such cultivars would be strong compartmentalizers. As with most hypotheses, more data were needed.

In the following paragraphs, I will describe the methods and results of a series of "Experiments," not necessarily in the proper time sequence, made to (a) extend our observations to include more cultivars, including clones and cultivars traditionally propagated by cuttings, (b) attempt to relate Wall 2 compartmentalization response to chisel wounds in the trunk with the trunk wood discoloration that results from improper flush pruning of branches, and (c) clear up a few questions regarding Wall 2 formation and the stability of a strong Wall 2 response. "Flush" pruning cuts are improper cuts made *behind* the branch collar or branch bark ridge. For the reader, an understanding of the CODIT (Compartmentalization Of Decay In Trees) system (9), "Target Pruning" (6, 7), and the rationale for such pruning (8) would be most helpful, since there are many details that cannot be explained in this paper. Also, rather than use the various cultivar names in both the "Methods" and "Results" sections, they will only be given in "Results."

Materials and Methods

Experiment No. 1. Three cultivars of Norway maple (*Acer platanoides* L.) on the National Arboretum grounds had been trunk wounded with chisel cuts in June, 1983. These trees could not, for esthetic reasons, be cut down to examine the internal discoloration pattern. However, we have shown (3) that increment cores could be used as an accurate determinant of Wall 2 compartmentalization response, and these trees were bored, through the wounds, in October, 1985.

Experiment No. 2. Seventeen cultivars and selections of *Acer* (maple), *Fraxinus* (ash), *Quercus* (oak), *Tilia* (linden), and *Zelkova* were wounded at Princeton Nurseries, Allentown, New Jersey on February 24, 1984. Two trees of each cultivar were wounded by making 2 to 4 chisel cuts (1.8 cm wide and 0.2 to 0.5 cm deep) into the trunks at 1 m and 1.5 m above ground level. The wounded trees were cut down on December 13, 1984 and the trunk sections were sawn transversely through at both wounding heights in order to examine the compartmentalization response.

Experiment No. 3. The first report to suggest genetic control of the compartmentalization response dealt with hybrid poplars (10). Furthermore, the normal method of propagating hybrid poplars is by cuttings, rather than budding or grafting, thus eliminating the critical phase which, in our hypothesis, would lead to the inadvertent propagation of *only* strong compartmentalizers. We were able to wound 2 trees of each of 9 clones, of which 3 clones were also used by Shigo *et al.* (10) in the aforementioned study. The trees were part of a USDA Forest Service planting established at King's Men Tree Farms in Hampstead, Maryland in 1974. Each tree was wounded on June 1, 1983 with 2 sets of 4 chisel cuts 1.8 cm wide and 0.5 to 0.8 cm deep spaced around the trunk at 2 different heights. A rectangular piece of bark (25 × 14 mm) was removed around each chisel wound with a patch-budding tool. The wounded trees were harvested on February 13, 1984 and sawn transversely through the wound zones to examine the amount of wood discoloration caused by wounding.

Experiment No. 4. A number of young plants of maple cultivars rooted from stem cuttings, and supplied by J. Frank Schmidt & Son, Boring, Oregon, had been used in the previous studies on cultivar wounding (4) and juvenile wounding (3). By the spring of 1985, some of the sprouts from the young trees felled for the earlier study were 2 to 3 m tall with only a few well-developed lateral branches. On June 24, 1985, we pruned the branches on these trees. Since we already knew that the cultivars were strong Wall 2 compartmentalizers (3), most of the pruning wounds were flush cuts, made in an improper manner behind the branch bark ridge. Both proper and improper pruning cuts were also made on 5-year-old nursery seedlings of a progeny in which we suspected some variation in Wall 2 compartmentalization. Therefore, these seedlings were also chisel-wounded in the trunk to determine that response. The pruned and wounded young trees were harvested on October 30, 1985 and sawn transversely to determine Wall 2 compartmentalization or lengthwise to examine vertical discoloration patterns.

Experiment No. 5. What happens if a wounded, strong-compartmentalizing tree is wounded again near the previous wound? Will it once more exhibit strong compartmentalization? There are many unanswered questions of this nature that depend on some knowledge of how and of what material the "Wall" is built. We know that the "Walls" in maples are composed of 2 coumarino-lignan compounds that are virtually insoluble in water (1). Our own investigations indicate that the

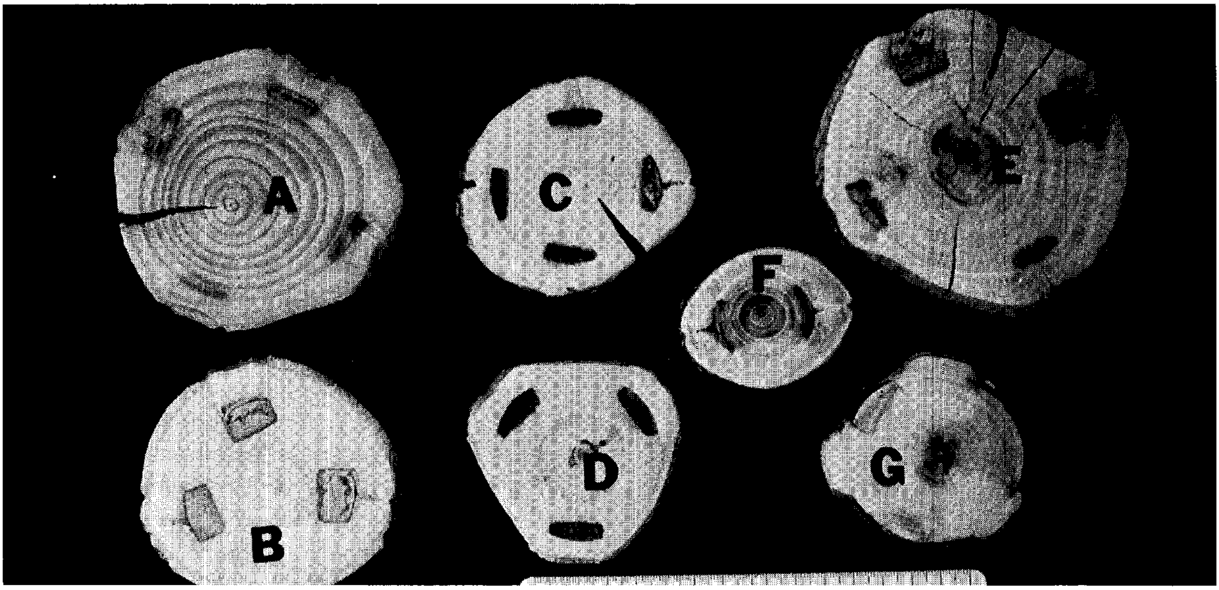

Fig. 1. Cross-sections of chisel-wounded trunks of cultivars: (A) 'Rosehill' white ash, (B) 'Redmond' American linden, (C) 'Green Mountain' sugar maple, (D) 'Summershade' Norway maple, (E) 'Crownright' pin oak, (F) 'Village Green' zelkova, (G) 'Bonfire' sugar maple.

wall-forming chemical compounds in poplar, elm, oak, honeylocust, linden, dogwood, magnolia, ash, and other genera are also water-insoluble. Two exceptions might be ailanthus and birch. However, these insoluble compounds must be synthesized from soluble substances present in parenchyma cells (largely in the wood rays) internal to the wound. And if more than 1 year's diameter growth has occurred after the first wounding, the tree should have the proper and sufficient raw materials which, under genetic control, can build a new wall after another injury. The mature maple trees used in our first study on the inheritance of compartmentalization (2) were first wounded on June 11, 1974. Some trees were wounded again on November 11, 1979. Another wounding was performed on July 11, 1981, making the chisel cuts close to, or literally on top of, previous wounds, Four trees, representing 2 each of the clonally propagated strong-compartmentalizing parent trees, were cut down and sawn transversely through at the site of wounding for examination of the discoloration pattern. Where does Wall 2 form? The language in the CODIT model (9) implies that Wall 2 is the boundary between annual rings. In fact, Wall 2 forms where the injury ends, even in the middle of an annual rings. This fact will be obvious in the illustrations that follow. A strong Wall 2, in most genera, is characterized by a narrow band of cells interior to the wound that is darker than uninjured sapwood and also darker than wood in the middle of the wound zone. Presumably this dark zone is the result of plugging of cells through the deposition of insoluble wall material.

Results and Discussion

Experiment No. 1. The Norway maple cultivars 'Almira', 'Chas. F. Irish', and 'Crimson King' were all strong Wall 2 compartmentalizers. The only discolored wood area in the increment core represented the cells killed at the time of wounding.

Experiment No. 2. All of the following chisel-wounded nursery cultivars showed strong Wall 2 compartmentalization: Norway maple 'Summershade' (Fig. 1D); sugar maple (*Acer saccharum* Marsh.) 'Green Mountain' (Fig. 1C); white ash (*Fraxinus americana* L.) 'Autumn Purple' and 'Rosehill' (Fig. 1A); green ash (*F. pennsylvanica* Marsh.) 'Summit'; pin oak (*Quercus palustris* Muenchh.) 'Crownright' (Fig. 1E) and 'Sovereign';

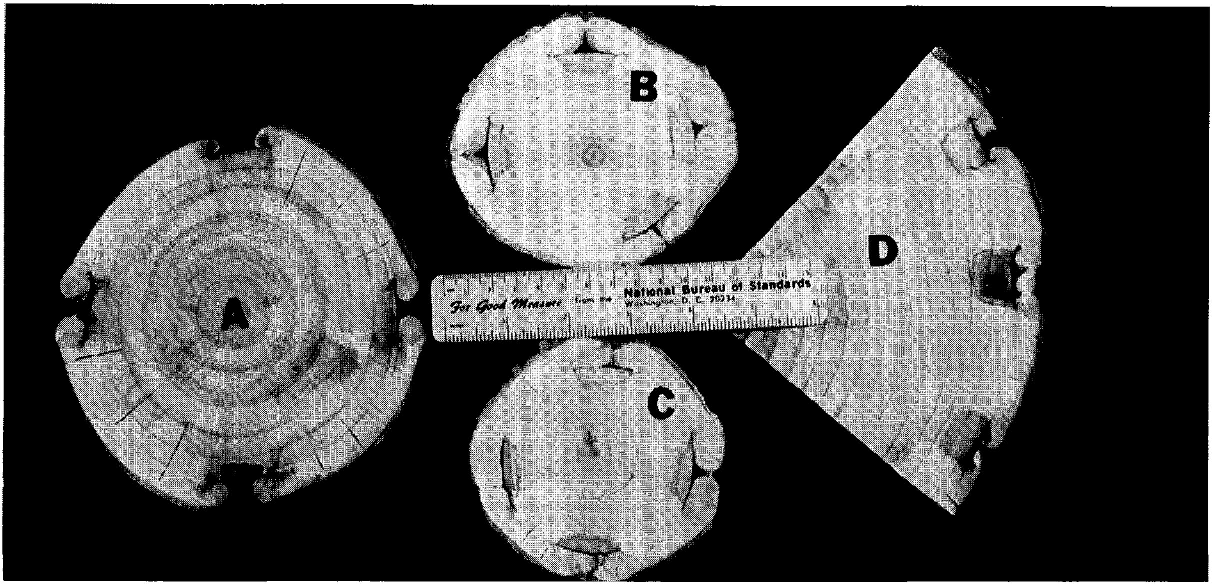

Fig. 2. Cross-sections of chisel-wounded trunks of hybrid poplars: (A) Clone NE-41 ('Androscoggin'), a weak compartmentalizer; (B) Clone NE-211, a strong compartmentalizer; (C) Clone NE-208, a weak compartmentalizer; (D) a strong compartmentalizing clone of unknown parentage. Note formation of Wall 2 between annual rings.

American linden (*Tilia americana* L.) 'Redmond' (Fig. 1B); littleleaf linden (*T. cordata* Mill.) 'De Groot', 'Greenspire', and 'Olympic'; *T.* X *flavescens* A. Br. 'Glenleven;' and a selection of silver linden (*T. tomentosa* Moench.) grown under the name "Princeton." In a few cultivars, the compartmentalization response could not be accurately determined. Trees of *Zelkova serrata* (Thunb.) Mak. 'Village Green' (Fig. 1F), and a selection grown under the name "Green Vase" showed what could have been interpreted as weak compartmentalizaon were it not for the central core of discolored wood (wetwood?) present at the time of wounding. The chisel wounds on these small trees nearly penetrated this discolored area and, perhaps because of disturbed physiology in this zone, no compartmentalization wall was formed. The other case of failure to observe a strong compartmentalization response was in 'Bonfire' sugar maple (Fig. 1G). In this cultivar, all of the wounds were infected with a canker-causing fungus, probably a *Cytospora.* Even though some of the wounds in this cultivar did not produce the typical wedge-shaped pattern of discoloration that is characteristic of a weak compartmentalization response, no interior boundary wall was formed.

It is important to note that the compartmentalization response we are studying is the ability of a tree to wall off potential decay organisma. When aggressive pathogens such as canker fungi are introduced at the time of wounding, the pathogen may succeed in invading the host tissue before an effective "wall" can be formed. This may be especially true if, as in this case, wounds are made during the dormant season, a period of low tree cell metabolic activity. Also the compartmentalization response is a response of *healthy* tissue. This discolored wood in *Zelkova* was indicative of invasion by other microorganisms (bacteria isolated) that might alter the normal cell metabolism in response to wounding.

Experiment No. 3. The following hybrid poplar clones were wounded: NE-41 (*Populus maximowiczii* Henry X *P. trichocarpa* Hook.); NE-47 (*P. maximowiczii* X *P.* 'Berolinensis'); NE-205, 208 and 211 (*P. deltoides* Marsh. X *P. trichocarpa*) and NE-225, 228, and 359 (*P. deltoides* X *P.* 'Caudina'). Clone NE-47 is the cultivar 'Oxford'

Fig. 3. Wood discoloration following flush pruning on, left to right; top row: 'Scarlet Sentinel', 'Scarlet Sentinel', 'Bowhall', 'Crimson King'; Bottom row: 'Silver Queen', 'Gerling'—with proper pruning wound on left side, 'October Glory'—flush pruned at fork. 'Crimson King' is Norway maple, 'Silver Queen' is silver maple, and all others are red maples. Note that discoloration does not extend vertically beyond the callus ridges that indicate the length of the pruning wound.

and NE-41 is 'Androscoggin' (5). Both cultivars have, unfortunately, been given other (and somewhat grandiose) epithets in irresponsible advertisements in the popular press. Both cultivars are also weak compartmentalizers (Fig. 2A).

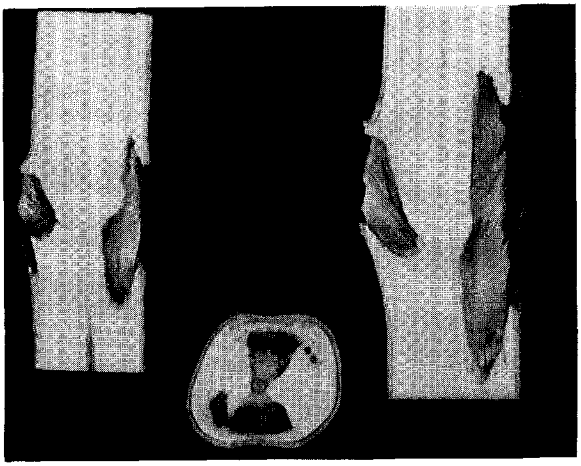

Fig. 4. Wood discoloration following proper (left side) and flush (right side) pruning of seedlings that showed weak Wall 2 compartmentalization of chisel wounds (cross-section). Note that discoloration in flush-pruned wounds extends beyond area wounded by the pruning cut.

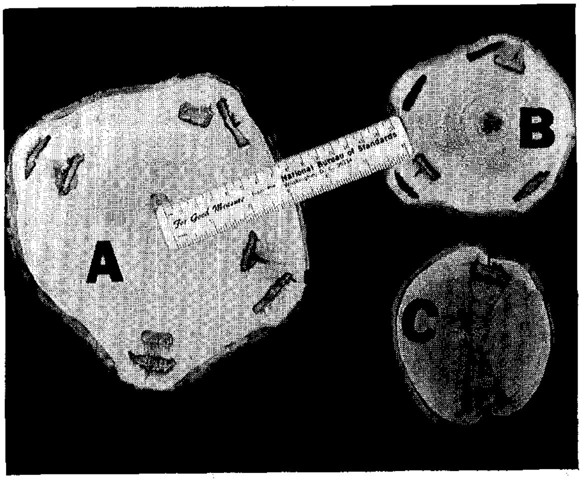

Fig. 5. Cross-sections of chisel-wounded *Acer rubrum: (A)* strong-compartmentalizing clone G-70, wounded twice in 1974, twice in 1979 and 4 times in 1981; (B) strong-compartmentalizing clone G-64, wounded twice in 1974 and 4 times in 1981; (C) typical discoloration pattern in weak-compartmentalizing trees. Note constancy on strong response even when later wounds were made close to earlier wounds.

Among the clones of identical parentage derived from controlled crosses, one clone of each group was a strong compartmentalizer and 2 clones were weak compartmentalizers. Thus, NE-359 was strong, while NE-225 and NE-228 were weak. Among the clones of the other group, NE-211 was strong (Fig. 2B) while NE-205 and NE-208 (Fig. 2C) were weak. These latter 3 clones had also been wounded by Shigo *et al.* (10) with deep drill wounds that approached or intruded into the central core of bacterial wetwood. Even though the data given in that paper for the proportion of discolored wood resulting from drill wounding are somewhat misleading since they include the wetwood present at the time of wounding, the 2 weak-compartmentalizing clones had a significantly greater amount of discolored wood that the strong clone. It is my opinion that great care should be taken when wounding trees suspected of having wetwood (elms, poplars) so the wetwood zone is not involved. Certainly, the illustrations (Figs. 2B, 2C) are far more convincing of the genetic potential for strong or weak compartmentalization response.

It was stated earlier that Wall 2 does not necessarily, if ever, form at the annual ring. Rather, it forms, or begins to develop, wherever the injury ends. This fact can be ascertained in many of the wounded trees pictured in Figs. 1 and 2, but nowhere more dramatically than in Fig. 2D.

Experiment No. 4. All of the flush-pruned young maple cultivars showed strong compartmentalization of pruning wounds in that vertical stem discoloration was limited to the portion of trunk injured at the time of pruning, visually bounded by the callus growth (Fig. 3). However, the amount of stem discoloration following flush pruning was always greater than when a proper pruning cut was made (Fig. 3—'Gerling'). These cultivars included Norway maple 'Crimson King' and 'Emerald Queen'; red maple (*Acer rubrum* L.) 'Bowhall'; 'Gerling', 'October Glory', 'Red Sunset', 'Scarlet Sentinel', and 'V. J. Drake'; and silver maple (*A. saccharinum* L.) 'Silver Queen'. Within the group of previously untested (for Wall 2 compartmentalization) seedlings, those that showed strong compartmentalization of chisel wounds likewise showed limited stem discoloration as a result of flush pruning. However, those that were weak Wall 2 compartmentalizers exhibited columns of stem discoloration that extended a considerable distance above and below the tissue wounded when making the flush cut (Fig. 4). Proper pruning of even these weak Wall 2 compartmentalizers produced the small amount of stem discoloration comparable to proper wounds on strong-compartmentalizing trees (Fig. 4).

Experiment No. 5. The results of multiple wounding of strong-compartmentalizing red maple clones are illustrated in Fig. 5. It would appear that the inherent capacity to "build walls" or compartmentalize a wound continues to be operational as long as any new wound does not breach the "wall" layed down, deposited, or built up as a result of an earlier wound. We are currently studying the chemical and physiological consequences of making holes in these walls.

It should not be surprising that the living cells of only a few years growth outside an old wound would have the physiological capacity to build a new wall. Indeed, in our studies on testing juvenile trees for compartmentalization response (4), some of the wounds penetrated almost to the boundary between the first and second growth ring, and the young plants were still able to compartmentalize the wound.

Summary

All of the landscape tree cultivars tested thus far, which have been propagated on a commercial scale by budding and grafting, are strong Wall 2 compartmentalizers of chisel wounds made in their trunks. These cultivars also respond more effectively than weak Wall 2 compartmentalizers (of seedling origin) in restricting the extent of wood discoloration following improper flush pruning of branches. This does not mean that we should exercise less care in the pruning of such cultivars; proper pruning is *always* best. What it does mean, however, is that nursery production techniques have, albeit inadvertently, provided arborists, horticulturists, and landscapers with many cultivars having the genetic capacity to endure the various wounds inflicted by men and his machines and still resist the spread of decay. All future cultivar introductions, regardless of how they are propagated, can and should be tested for this important characteristic.

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