

WOUNDING, COMPARTMENTALIZATION, AND TREATMENT TRADEOFFS¹

by Kevin T. Smith

Wounds damage trees. Tree care professionals routinely wound trees to apply fungicides, nutrients, and growth regulators. The practitioner knowingly makes the tradeoff of tree damage for the benefit expected to be gained by the chemical treatment. This paper is an overview of the effects of wounding on trees. It is directed to practitioners who make these tradeoff decisions of damage and benefit.

Trees are wounded throughout their lives, from broken branches, impacts and abrasions, animal damage, etc. Wounds large and small set into motion a cascade of events that may eventually lead to decayed, physically degraded wood. People who commonly work with trees know all of these things; what is not so well known is that the presence of decayed wood may not be the most harmful result of wounding trees. The practitioner must not get over-confident that his tradeoff of wounding for treatment is in the tree's benefit merely due to the absence of visibly decayed wood.

One riddle of tree biology is that the tree is threatened both by the failure and by the success of its own wound response system (4). This coordinated system that limits damage due to wounding is compartmentalization (3, 5, 11). The concept of compartmentalization is based upon the analytical dissections of many trees with natural or experimentally inflicted wounds. Compartmentalization explains the patterns of discoloration and decay seen in living trees.

Briefly, compartmentalization is a two-stage boundary-setting process. The first stage is to confine the effects of injury within boundaries that result in the smallest possible volume of affected wood. Some qualities that influence this process are built into the static architecture of the wood itself such as the cell types, sizes, and arrange-

ment. Other features of this stage are boundaries formed by tyloses, plugging materials, and toxic substances. The second stage of compartmentalization protects wood formed following wounding from the decay process initiated by that wound. This involves the formation by the cambium of anatomically distinct boundaries known as barrier zones. None of these boundaries is absolute. All boundaries may fail in time. Trees vary in their genetic ability to compartmentalize (7, 10). The patterns of decay that are frequently encountered such as central hollows and rotting branch stubs surrounded by sound collars are all accounted for by compartmentalization. One simplification of this complex process is the CODIT (**C**ompartmen**T**alization **O**f **D**ecay **I**n **T**rees) model that refers to these boundaries as "walls" (3). The term "wall" ought not to be taken too literally, as the boundaries of compartmentalization may change in shape and position over time.

To illustrate the compartmentalization process, consider a hardwood tree on a warm and sunny spring day at the time when the leaves are not yet fully expanded. Various layers of outer bark, impregnated with waterproofing and toxic chemicals, protect the living inner bark (phloem), vascular cambium, and sapwood from desiccation, mechanical damage, pests, and pathogens. Water is flowing up the outer rings of sapwood to replace water lost by transpiration and to provide the turgor necessary to unfold leaves. This flowing water is actually under tension, or is being "stretched" within the open, water-conducting vessels. Within the sapwood, there are orderly patterns of conducting vessels that move water and minerals up the tree. Ray cells arranged in incomplete sheets form the radial transport system throughout the sapwood. In the rays and interspersed with the vessels are living parenchyma

1. Presented at the Symposium on Systemic Chemical Treatments in Tree Culture at Michigan State University, East Lansing in October 1987.

The use of a trade, firm or corporation name does not constitute endorsement by the Forest Service or the U.S. Department of Agriculture.

cells, many of which store protective chemicals such as phenols as well as starch produced from photosynthesis of previous years.

Now introduce a drill wound into this ordered system. Similar consequences would occur with other types of injection and implantation wounds. As the drill is applied to the trunk surface, the waterproofed and chemically impregnated protective outer bark is cut and removed, followed by the removal of phloem that actively transports photosynthate from the leaves to growing tips and storage tissues. Continuing inward, the drill bit cuts into the vascular cambium, the tissue that grows new cells around the circumference of the stem and branches. Depending on the sharpness of the drill bit, the cambial cells are cleanly cut or ripped and torn beyond the perimeter of the drill. As the bit cuts into the sapwood, the water column (previously under tension) within each severed vessel snaps as air rushes in to equalize the pressure within the tree to the atmosphere. As the air rushes in, bacteria and fungal spores are also drawn into the vessels.

Shortly after wounding, the first stage of compartmentalization occurs. Water conduction in sapwood vessels above and below the wound is blocked with tyloses and other plugs. A tylosis is an outgrowth of the membrane from a specialized parenchyma cell into a vessel. As tyloses are formed, sapwood parenchyma shift their metabolism from normal energy-yielding metabolism to the production of poisoning phenolic and terpene substances. Some of these substances exist prior to wounding and following wounding are oxidized by shifts in enzyme activity in the presence of increasingly available oxygen. The oxidation products of phenols may be more toxic than their parent chemicals. Some of these poisoning materials cover or become incorporated into tyloses. This shift in metabolism accomplishes two complementary ends. First, as simple sugars and starch are consumed, they are no longer available as food for invading microorganisms. Secondly, the products of these metabolic shifts are broadly toxic or inhibitory to the microorganisms.

One consequence of these metabolic shifts is that the parenchyma cells die and the affected sapwood around the wound is essentially cut off

from the living network by the blockage of vessels, depletion of energy reserves, and death of cells. Although this affected sapwood is in physical contact with the rest of the stem, it is functionally outside of the dynamic, living tree. Within two months, dissection of wounded wood tissues reveals a tapered column of discoloration above and below the wound. Beyond the visible discoloration, wood is altered by increasing ionization that is detectable by electrical measurements and is associated with decreased decay resistance in conifer species (13). What ought to concern the tree care professional is not the discoloration itself, but that the discoloration indicates that the tissue is cut out of the living network.

The key to the second stage of compartmentalization is the activity of the vascular cambium. Sapwood damaged by wounding is never healed in the sense of being repaired or replaced. The vascular cambium produces new, fully functional sapwood capable of energy storage, active response, and water movement. If the drill bit is sharp, the cambium is minimally damaged by drilling. A dull bit can cause extensive damage, resulting in cambial dieback that could greatly lengthen the time necessary to form functional sapwood around the circumference of the stem. Cambial dieback also can occur if the cambium is split in the injection process.

A distinction must be made between this new, fully functional sapwood produced by the cambium and the production of callus (generally formed by outgrowth of ray cells) is a wholly separate process. Callus tissue is important for wound closure, but it does not fully function in the same sense that sapwood does. Callus lacks the precise organization necessary to efficiently conduct water, store starch, or respond to stimuli such as wounding. Strong callus production indicates that the tree is relatively vigorous, but is not related to a strong compartmentalization response.

Certain chemical treatments introduced through wounds hinder the compartmentalization process and are more damaging than the wound itself. Boundary-setting is forced further away from the wound site, resulting in a greater volume of affected tissue as was shown with injection of

Stemix in red maple and benzimidazole derivatives in American elm (1, 9). Of greater potential damage are those chemicals that induce cambial dieback as has been shown with Bidrin injected into red maple (9). This type of aggravated damage is especially serious as it delays barrier zone formation and greatly retards the production of new, functional sapwood.

Additional problems are posed by treatments requiring multiple wounds. In the case of annually administered multiple wounds, barrier zones formed within the current growth ring may coalesce, placing the tree's entire need for water conduction, starch storage, and wound response to a portion of a single growth ring (7). For American elms infected with Dutch elm disease, multiple wounding is especially serious as functional sapwood is lost both by the disease and by the treatment (8). Wounding for treatment every two or three years is comparatively advantageous in that more functional sapwood will be produced between wounding episodes to support the tree's physiological needs of growth, protection, and defense. However, this advantage only accrues if the tree is vigorously growing.

Increased attention is being given to wounds made parallel to the ground and angled obliquely away from the pith. Chemical materials such as growth inhibitors are taken up more quickly from oblique wounds than from strictly radial ones as a larger portion of the wound will occur in the conducting rings of the outer sapwood. These wounds may be especially damaging as they cut off a larger portion of the outer sapwood from the dynamic ray cell network, thus further reducing the sapwood available to the tree for healthy functioning.

Tree care workers have benefited from the development of systemic treatments applied through wounds. Individual trees have benefited from these treatments. Yet, there is a tradeoff of damage for expected benefit. The problem is that the damage is hidden. The development of decay from wounded tissues may pose a long-term problem. A more immediate concern is a tree's loss of functional sapwood as tissues respond to wounding. These responses are essential for tree survival, yet they make the tree more vulnerable by reducing the capacity to respond to future

demands.

The challenge to researchers is to develop new types of tree treatments that work in concert with the natural system of tree defense and protection as has been suggested for wound treatment (12). When the practitioner chooses chemical treatments to be applied through wounds, the guidelines presented by Shigo and Campana (6) and Shigo (2) should be followed:

Make clean-edged holes as shallow, narrow, and few in number as possible.

Place holes as low as possible on trunk ridges and not on roots or trunk depressions between roots.

Place multiple wounds of a single treatment in a spiral around the trunk circumference, avoiding apparent dead spots.

Before repeating injections in successive years, observe the previous wounds and do not wound an individual again if poor closure suggests low vigor.

And most of all, be aware that this type of treatment causes damage of its own that is not visible until the tree is felled and sectioned.

Literature Cited

1. Andersen, J.L., R.J. Campana, A.L. Shigo, and W.C. Shortle. 1985. *Wound response of Ulmus americana I: Results of chemical injection in attempts to control Dutch elm disease*. J. Arboric. 11:137-142.
2. Shigo, A.L. 1986. *A New Tree Biology*. Shigo and Trees, Associates, Durham NH. 595 pp.
3. Shigo, A.L. 1985a. *Compartmentalization of decay in trees*. Sci. Amer. 252:96-103.
4. Shigo, A.L. 1985b. *Wounded forests, starving trees*. J. Forestry 83:668-673.
5. Shigo, A.L. 1984. *Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves*. Ann. Rev. Phytopathol. 22:189-214.
6. Shigo, A.L. and R. Campana. 1977. *Discolored and decayed wood associated with injection wounds in American elm*. J. Arboric. 3:230-235.
7. Shigo, A.L., R. Campana, F. Hyland, and J. Andersen. 1980. *Anatomy of elms injected to control Dutch elm disease*. J. Arboric. 6:96-100.
8. Shigo, A.L., G.F. Gregory, R.J. Campana, K.R. Dudzik, and D.M. Zimel. 1986. *Patterns of starch reserves in healthy and diseased American elms*. Can. J. For. Res. 16:204-210.
9. Shigo, A.L., W.E. Money, and D.I. Dodds. 1977. *Some internal effects of Mauguet tree injections*. J. Arboric. 3:213-220.
10. Shigo, A.L., W.C. Shortle, and P. Garrett. 1977. *Compartmentalization of discolored and decayed wood associated with injection-type wounds in hybrid poplar*. J.

- Arboric. 3:114-118.
11. Shortle, W.C. 1984. *Biochemical mechanisms of discoloration, decay, and compartmentalisation of decay in trees*. Inter. Assoc. Wood Anat. Bull. n.s. 5:100-104.
 12. Smith, K.T., R.O. Blanchard, and W.C. Shortle. 1981. *Postulated mechanism of biological control of decay fungi in red maple wounds treated with Trichoderma harzianum*. Phytopathology 71:496-498.
 13. Smith, K.T. and W.C. Shortle. 1988. *Electrical*

resistance and wood decay by white rot fungi. Mycologia 80:124-126.

USDA Forest Service
 Northeastern Forest Experiment Station
 P.O. Box 640
 Durham, New Hampshire 03824

THERAPY FOR DUTCH ELM DISEASE¹

by Gerald N. Lanier

Abstract. An aggregate of 82 American elms in Syracuse New York and Washington D.C. naturally infected with Dutch elm disease were given therapy by pruning infected limbs, injection of benzimidazol fungicides, or combinations of these treatments. Pruning alone was applied only when there was a distance of 3 m or more from the last visible streak to the distal cut. Pruning without injection was successful in each of 10 current year infections, but in none of 3 residual infections. Fungicide injection without pruning succeeded in 76% of current year and 33% of residual infections. Fungicide injection plus pruning was successful therapy for 100% of the current year and 71% of the residual infections. Each of five "incurable" trees showed no further symptoms after fungicide was injected directly into infected wood in a large limb or the bole as well as into the root collars. Relatively massive injection of fungicide in trees with root graft-transmitted DED did not succeed.

Résumé. Un ensemble de 82 ormes américains à Syracuse, New York et à Washington, D. C., infectées

naturellement par la maladie hollandaise de l'orme, reçurent un traitement consistant en un élagage des branches infectées, une injection de fongicides à base de benzimidazol, ou une combinaison de ces traitements. L'élagage seul fut appliqué seulement lorsque qu'il y avait une distance de 3 m ou plus de la dernière strie visible à la coupe. L'élagage sans injection fut un succès pour chacune des 10 infections de l'année courante, mais pour aucune des 3 infections résiduelles. L'injection d'un fongicide sans élagage a réussi dans 76% des infections de l'année en cours et dans 33% des infections résiduelles. L'injection d'un fongicide avec un élagage fut un traitement efficace à 100% pour les infections de l'année en cours et à 71% pour les infections résiduelles. Cinq arbres "incurable" n'ont pas présenté d'autres symptômes après que le fongicide fut injecté dans le bois infecté dans une grosse branche ou dans de tronc, de même qu'à la base de l'arbre. Une injection massive de fongicides dans des arbres infectés par des greffes de racines n'a pas réussi.

1. Presented at the Symposium on Systemic Chemical Treatments in Tree Culture at Michigan State University, East Lansing in October 1987.