Wounding and Decay in Trees

Frank Fogliati

Have you ever cut up a tree or branch and observed colors, hollows, wedge-shaped discoloration, rings or gum or kino, ring shakes or ray shakes? If you haven't, then perhaps you need to look more closely at trees and timber. The history of trees is locked up inside them and phenomena such as the above tell us about it.

Trees, during their often long lives, may be wounded many times both naturally (branch-shedding, storm damage, insect attack) or by people (vandalism, mechanical injury, pruning). Yes, pruning is wounding! Trees and animals differ radically both in their anatomy and in their response to wounding. Animals heal; that is, they repair or replace cells. Trees don't heal by repairing cells; they defend themselves from the effects of injury and infection by walling off the damage, a process known as compartmentalization. A principal researcher into this area has been Dr. Alex Shigo, who spent over 25 years wounding, dissecting, and analyzing more than 15,000 trees.

The Tree's Response to Wounding

When a tree is wounded, two things occur: the tree responds and many microorganisms colonize the wound surface

Compartmentalization in trees is a defense mechanism wherein boundaries form to contain injuries to tissues and to resist the spread of pathogens. The capacity of a tree to compartmentalize appears to be under strong genetic control; that is, some species react more readily and more successfully than other species. Sometimes the defense response is so successful that too much infected tissue can be walled off and the tree starves; this is the case in *Ulmus* spp. resisting Dutch Elm disease. (Magnoliaceae as a family exhibits an average response).

The whole process of the tree's response to wounding is an interaction between the tree and the microorganisms and pathogens that may have invaded it. It is one of nature's battlefields. Survival of the tree after injury and infection depends greatly on its ability to compartmentalize pathogens. This process requires energy. Survival of the pathogens after injury and infection depends greatly on their ability to occupy as much tissue as possible before they are compartmentalized. If the tree's responses are stronger than those of the pathogen, then the spread of the pathogen is resisted. If the pathogens are very aggressive, they may spread rapidly and the tree may decay.

The genetic makeup of the host and the invaders play an important role in the interactions, as do environmental conditions at the time of wounding; the tree's history of wounding; the age, health, and vigor of the tree; and the amount of energy reserves. Clearly this has implications when choosing the best time to prune.

Compartmentalization of Decay in Trees (CODIT)

Compartmentalization is a three-dimensional concept that occurs in two stages:

- At the time of wounding the tree attempts to confine the pathogen to a small compartment (localization). If this is unsuccessful, the pathogen may eventually spread through and digest all the tissues present at the time of wounding until a cavity forms. A cavity indicates that some boundary must separate the tissues present at the time of wounding from new tissues that continue to form. At one extreme, this first stage may be a localization process or, at the other extreme, a complete breakdown of all boundaries.
- After wounding, the tree forms a barrier zone that usually localizes the compartment for the first stage and protects the cambium. Closure of the wounds by callus takes place after wounding as new cells are generated in new spatial positions. (Callus is new phloem, xylem, and other tissues produced by the cambium but not arranged in an organized way as is "natural" growth.)

Stage 1

This occurs at the time of wounding. When a wound occurs, parenchyma cells in the phloem, cambium and/or xylem are broken and their contents are exposed to the air. Oxygen combines with a number of cell contents, some of which react to produce compounds that break down living materials, and their cells may die. In nearby living, but injured, cells some energy reserves are converted to phenols. These phenols either oxidize or combine with proteins. The products of these reactions become antimicrobial substances, or at least resist microbial breakdown. Ions accumulate in the injured cells and the pH of the cells changes. All of these chemical processes are part of the tree's response to rapidly convert energy reserves into antimicrobial products and into products that cannot be used as food by the microorganisms.

During this stage, to localize the injury, the tree produces three "walls." (The term wall relates to the CODIT model and not an actual anatomical structure; see Figure 1). Wall 1 resists vertical spread. It is formed after injury by plugging of xylem vessels. It is the weakest wall.

Wall 2 resists inward spread and is moderately strong. After each flush of growth or each season's growth, sets of highly lignified cells are formed. Most microorganisms do not have the enzymes to digest lignin, hence Wall 2 is already in place in the tree. When shallow wounds kill the cambium, Wall 2 resists inward spread of pathogens behind the wound. As deeper wounds are inflicted, the injuries approach older

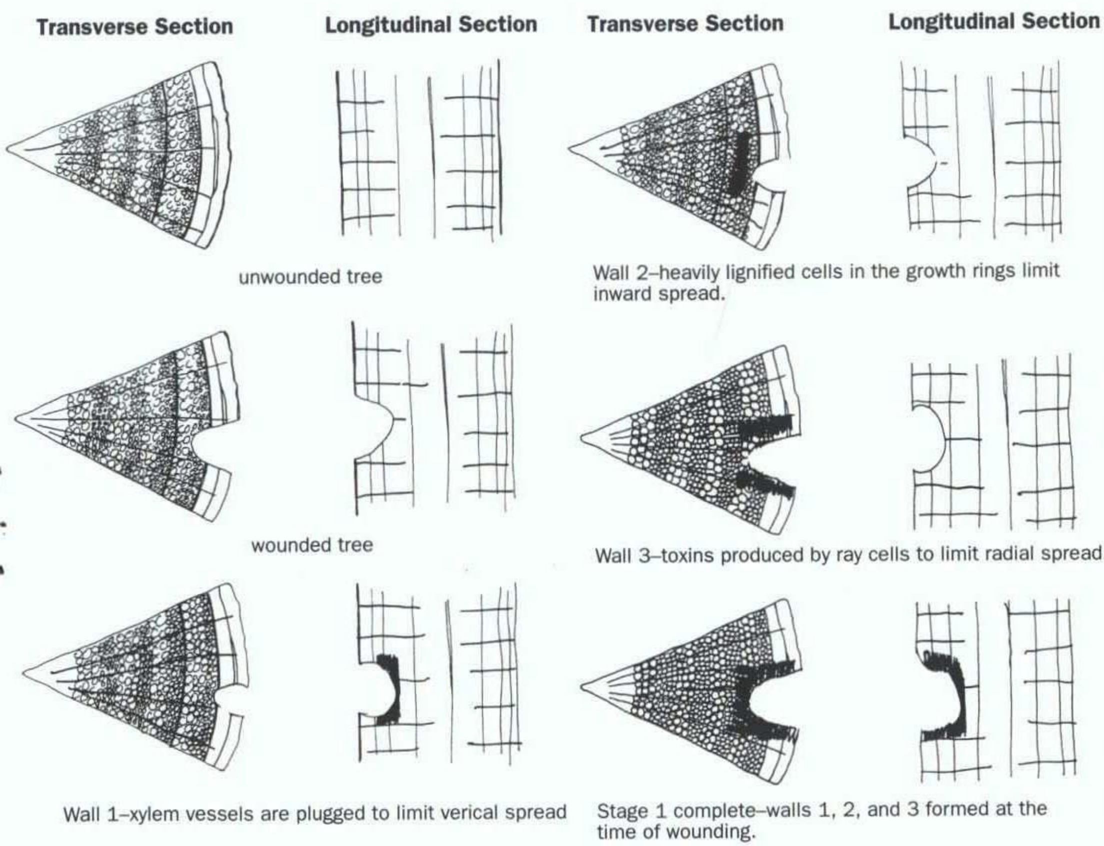

Figure 1a. This figure illustrates Stage 1 of compartmentalization. Figure 1b illustrates Stage 2.

sheaths of xylem and the resisting power of Wall 2 diminishes. When Wall 2 fails to the pith, inward spread ends.

Wall 3 resists lateral spread and is the strongest wall produced at the time of wounding. Wedge-shaped sections defined by ray cells provide a living cell communication between the older, inner xylem and the newer, outer xylem and phloem. The rays form a screen of small groups of living cells that are capable of a short-term response to invasion. This response includes many of the chemical reactions already mentioned; that is, the production of oxidized phenols and other antimicrobial substances. Because they maintain a living connection with the cambium of a vigorous tree, the rays may be continually re-supplied with energy reserves for extended response and containment of invasion by decay fungi. Hollows or cavities will form if this wall fails over time and the boundaries open as a fan.

While the walls are operating or failing in Stage 1, the undamaged cambium is generating new cells in new positions: that is, the rest of the tree continues to grow. These new cells are protected from the infected

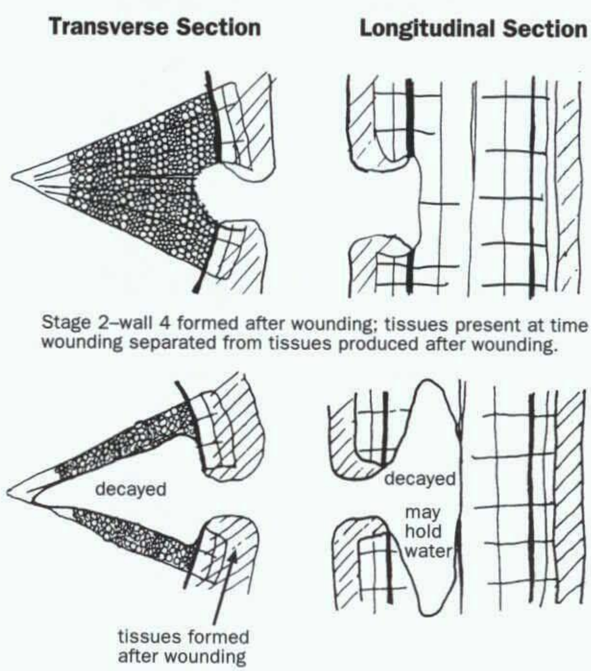

Figure 1b. This figures illustrates the formation of Wall 4 after wounding, but here, Walls 1, 2, and 3 are failing and a cavity has developed. Wall 4 is separating tissues present at the time of wound from those produced after wounding.

tissues in the second part of the process of compartmentalization. In the CODIT model, only Stage 1 is present at the time of wounding. Stage 2 may not begin to form for many months, depending upon the time of wounding in relation to the next surge of cambial activity.

Stage 2

This occurs after the wounding (see Figure 1b). Wall 4, also known as the barrier zone, is formed. This is a protective tissue or boundary that is formed by living cambium in response to mechanical wounding and infection. It serves to isolate or separate the infected wood from the healthy wood that continues to form after the zone is completed. After wounding, the cambium produces cells that differentiate to form a protective boundary. Some of the cells convert their contents to antimicrobial substances.

The barrier zone is usually non-conducting and, in some trees (*Quercus*), suberin is present in the cell walls of such tissue. In some species of trees, the cambial zone responds to wounding by producing ducts of defensive materials. For example, *Eucalyptus* spp. produce kino which is a polyphenol; conifers produce resin ducts; and *Liquidambar* spp. produce storax veins. The barrier zone may be extensive and encircle the stem or it may be only localized. Factors affecting the extent of barrier zone formation are poorly understood.

Wall 4 is produced by trees when the cambium is active, so a tree wounded during a dormant period will not form a barrier zone until after growth resumes in spring. (Have you ever cut and split firewood and noticed that sometimes the timber falls out in rings, or that the wood is most easily split around a ring? If you have, then you have observed a characteristic of Wall 4.) The barrier zone is a very strong protective boundary against pathogens, but a very weak structural boundary. As wood dries, or after felling, cracks often start along the barrier zone; if they are around the tree they are usually referred to as ring shakes. Ray shakes—separations along the rays that radiate outwards—usually start from a ring shake and hence originate from old wounds. They may also form where new callus begins to roll inward from the sides of the wound.

One final point while we are discussing fractures in trees. Shallow vertical cracks, often referred to as growth splits, may also form in the bark as a result of rapid growth. These do not affect the growth of the tree and require no treatment.

Summary of the CODIT Model

Refer to Figure 2 for an illustration of the summary of the CODIT model.

Stage 1: At the time of wounding

Wall 1. Xylem vessels are plugged to resist vertical spread of microorganisms—this is the weakest wall.

Wall 2. Heavily lignified cells in the growth rings resist inward spread.

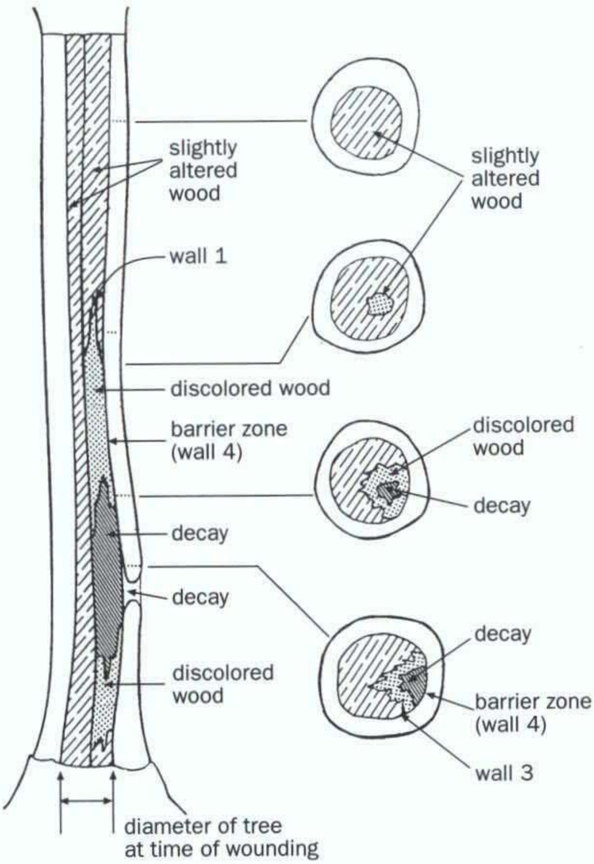

Figure 2. Summary of compartmentalization. Depending on the severity of the wound, there will be varying degrees of alteration, discoloration, and decay. Compartmentalization is not always effective; sometimes micro-organisms kill the tree before compartmentalization commences. Some individual trees are more effective in implementing this process than others.

Wall 3. Toxins produced by living ray cells resist lateral spread—this is the strongest wall produced at the time of wounding.

Stage 2: After wounding

Wall 4. A barrier zone is produced by the cambium which separates tissues present at the time of wounding from tissues produced after wounding—this is the strongest of all walls and the tree's best defense mechanism.

Remember, the tree's success in compartmentalizing wounded tissue depends on many tree factors (genetics, age, vigor, and history) and on the type and number of colonizing microorganisms. Trees are not always successful in compartmentalizing.

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References

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In the next issue, Mr. Fogliati will discuss the practical implications of compartmentalization: pruning; cavity treatment (filling, draining); other treatments (injection, cabling, bracing); preventing decay; and measurement of decay. Not surprisingly, many of these traditional practices are counter-productive to a tree's longevity.