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COMPARTMENTALIZATION TODAY

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Summary

For more than 30 years, the compartmentalization concept has helped tree care practitioners and land managers interpret patterns of decay in living trees. Understanding these patterns can help guide the selection of treatments that meet the needs of people and communities while respecting the underlying tree biology. At its simplest, compartmentalization resists the spread of infection in trees. The term most often refers to infections of wood decay fungi and associated organisms. Compartmentalization is a boundary-setting process that protects the vascular cambium from attack and that favors tree survival. Wood decay fungi and their associates exploit and create opportunities to breach or avoid these boundaries. The challenge for tree care is to favor and support the biology that contributes to safe, healthy, and beautiful trees while understanding that all trees die and that all wood rots.

Introduction

For many decades, researchers worldwide have noted aspects of the compartmentalization process. Compartmentalization resists the spread of pathogens in living trees (SHIGO 1984). The compartmentalization concept is most often applied to patterns of wood decay in living trees (SMITH and SHORTLE 1998). Compartmentalization is also used to describe the pathology of vascular wilt diseases and the response of bark to injury and infection. Arborists and land managers can improve tree care today by applying an understanding of the compartmentalization process. Compartmentalization is best understood by considering trees as organisms uniquely suited for long-term survival in a competitive, hostile world (LONSDALE 2004). Trees developed compartmentalization as members of ecological systems exposed to injury from many sources including periodic fire (SMITH and SUTHERLAND 1999, 2001) and storms (SHORTLE *et al*. 2003, SMITH and SHORTLE 2001). Trees in cities and towns face additional injuries as a consequence of

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human activity and treatments (DUJESIEFKEN and STOBBE 2002, LONSDALE 2004, SMITH and LEWIS 2005). Many more details of the interactions of trees and associated organisms remain to be discovered.

One measure of the power of a scientific idea is its ability to explain the patterns we see in nature. A second measure of the power of an idea is the depth and breadth of its acceptance by researchers and practitioners. Few ideas have had a greater effect on the understanding of tree biology, pathology, and treatment than the development of the compartmentalization concept (Manion 2003). Compartmentalization is used to describe the patterns of wound-initiated discoloration and decay in living trees in standard references (Harris *et al.* 1999, Fink 1999), specialized textbooks (Schwarze *et al*. 2000), and research reviews presented to applied practitioners (Pearce 2000). A quick search of the internet or library sources find thousands of references that use the concept in forest pathology and arboriculture. The fact that the term "compartmentalization" is so widely applied to the wood decay process in living trees testifies to the usefulness of the compartmentalization concept to arborists, foresters, and land managers.

This presentation, sketches out what compartmentalization is, how the initial concept has grown through criticism and research, and how the application of an understanding of the compartmentalization process improves tree care.

What is compartmentalization?

Mechanical wounding exposes wood to infection by fungi and bacteria. Some of these microorganisms cause disease (including decay) and are called pathogens. Tree wounding is part of normal development (such as the shedding of shaded branches), natural disturbance (storms, fire), human activities (pruning, road construction and maintenance), and direct pathogen activity (armillaria root disease). Microorganisms associated with the development of wood decay in living trees frequently spread in a succession with nondecay fungi and bacteria preceeding decay fungi (SHIGO 1967).

Compartmentalization involves both constitutive features and induced changes in tree anatomy and physiology. Compartmentalization 'walls off' infection and tends to resist the spread of the decay process into wood formed after wounding (BARRY *et al.* 2005, SHIGO 1984). Despite the high frequency of wounding and infection, the vascular cambium is usually protected by the compartmentalization process. The vascular cambium can then continue to produce new cells in new spatial positions. These new cells are essential to the tree for structural support, internal transport, storage, and defense. Because of effective compartmentalization, infected and decaying trees can live and contribute to the human landscape for many years (LONSDALE 2004).

Stages of Compartmentalization

The active compartmentalization process consists of two distinct stages of boundary-setting. The first stage of compartmentalization sets physiological boundaries in wood present at the time of injury. These changes can alter the anatomy of existing wood (BAUM *et al*. 2000) and result in the formation of a chemically distinct layer, integrated with the constitutive wood anatomy. These boundaries vary among tree species and have been referred to as reaction zones, marginal zones, column boundary layers, etc. Boundary formation in wood present at the time of wounding is integrated into constitutive features of tree anatomy such as protection wood at the base of branches, wood rays, the plugging of open cells that conduct water and induced shifts in metabolism in extant cells that resist water loss, colonization, and biodegradation.

The second stage of compartmentalization involves the formation of a barrier zone by the vascular cambium after wounding (SHIGO 1984). The barrier zone is distinctly different in anatomy and physiology from normal wood. Changes in anatomy and chemistry of xylem cells still undergoing differentiation at the time of wounding (FRANKENSTEIN 2006) should be included as part of the process of barrier zone formation. The barrier zone tends to resist the outward spread of wound-initiated discoloration and decay into wood formed after injury. Consequently, the wood decay process takes place generally in wood present at the time of injury.

Compartmentalization and the CODIT model

ALEX SHIGO with the help of many others introduced the compartmentalization concept to explain patterns of wood discoloration and decay and to distinguish changes in wood due to wounding from changes in wood due to heartwood formation (SHIGO and HILLIS 1973). SHORTLE (1979), SHIGO (1984 and 1991), SMITH (1989), and PEARCE (2000) reviewed additional supporting research.

Many people learned about compartmentalization through the publication of the CODIT (Compartmentalization of Decay in Trees) model developed by Shigo and packaged with the assistance of HAROLD G. MARX, a specialist in the presentation of applied research (SHIGO and MARX 1977). The aim of that publication was ‘to show how most columns of discolored and decayed wood associated with trunk wounds in trees are compartmentalized.’ The CODIT model ‘describes a system that makes it possible for forest managers to understand how most of these defects develop.’ Some criticisms of compartmentalization have come from researchers responding to this and other popular informational booklets rather than original scientific research and formal reviews. The CODIT model, its system of conceptual walls, and the attractive packaging were instrumental in educating a diverse public about the dynamic response of trees to injury and infection. However as with most simple analogies of complex biology, the descriptions of the inducible, moving, and partially discontinuous system of compartmentalization boundaries that are superimposed on constitutive anatomy conflicted with a simple understanding of ‘walls’. As the compartmentalization concept spread, some teachers and practitioners described the CODIT walls as if they were not conceptual but fixed elements like ‘bricks and mortar’. But this is more a limitation of the simplified CODIT model than a question of the validity of compartmentalization process itself. Some researchers find the CODIT model to be more useful if the letter “D” is used to represent ‘damage’ and ‘dysfunction’ as well as ‘decay’ (LIESE and DUJESIEFKEN 1996). SHIGO (1991) lists a series of problems, all beginning with the letter ‘D’, that lead to tree stress and strain (‘the demons of “D”’). Any adjustments to the model that are consistent with facts and that aid understanding should be welcomed. However, do not confuse the map with the territory! Do not confuse the limitations of the CODIT model with an understanding of compartmentalization itself!

Critical questions about compartmentalization

Of course, all researchers and practitioners do not unanimously accept the compartmentalization concept. Opposition does not make a concept untrue. Neither does consensus make a concept true or correct. Critical examination and testing of both new and established concepts are essential both for research and for the development of useful techniques for practitioners.

Here are some critical questions that have been raised about compartmentalization:

- **Can the boundaries that resist the spread of decay be said to be ‘for’ resistance to decay?**
  No, in science we must avoid purposeful or teleological arguments. An analogy is that most birds use wings to fly, but we cannot say that birds have wings so that they may fly! We may correctly say that most birds fly to find food and escape danger. Because of compartmentalization boundaries, the spread of pathogens is resisted. Slowing the spread of pathogens results in more wood being available for healthy functioning in energy storage, active defense, water conduction, and structural support. Slowing the spread of infection also favors the continued survival of the vascular cambium.

- **Can the patterns of infection be explained by the anatomy and the physiology of healthy wood?**
  Tree architecture and wood anatomy are indeed fundamental to the compartmentalization process (SHIGO 1984). One example of constitutive protection that contributes to compartmentalization is the protection wood formed at the base of branches (VON AUFSESS 1984). The initial, induced feature of compartmentalization is the plugging of the conducting elements in the xylem (SHIGO and HILLIS 1973). Is the primary effect of this plugging to resist the spread of infection or to resist the loss of moisture and the introduction of air (BODDY and RAYNER 1983)? The answer is 'both!' Contrary to the argument that the predominant function of compartmentalization boundaries is to resist water loss, some of the key fungitoxic phenolic compounds in reaction zones are produced in response to infection, not just injury (BARRY *et al*. 2002). Research on barrier zone and wound wood formation highlight the metabolic changes that result in the biosynthesis of specific chemicals that resist the spread of infection (EYLES *et al*. 2003). To say that these physiological changes are to resist water loss rather than to compartmentalize infection is to make the mistake of replacing one 'purposeful argument' with another!

- **Can the patterns of fungal succession be explained from the perspective of disturbance ecology rather than compartmentalization?**
  The wood exposed by wounding is available for infection by many microorganisms. Out of the many microorganisms that are available in the environment, a relatively small number actually do infect and spread into the wood from the exposed surface of the wound. These 'pioneer' fungi and bacteria can rapidly assimilate the nutrients from the wood cells killed by the injury. However, most pioneers are usually unable to degrade and digest the wood itself. Over time, the pioneer fungi spread further into the wood and are replaced by other microorganisms including other non-decay fungi in a loose series that eventually includes decay fungi (SHIGO 1967). Some decay fungi are specialists and can degrade only certain components of the wood cell wall and associated structural materials. Other decay fungi are generalists and can degrade most or all of the wood substance. This pattern of succession is not absolutely fixed and will vary from place-to-place and with circumstance. But a general tendency or trend in succession usually does occur. Few decay fungi effectively infect and spread from wounds without the activity of pioneers, but two exceptions are the serious pathogens that cause the annosum and armillaria decay diseases.

  Modern principles of disturbance ecology readily predict that pioneer microorganisms with high rates of cell division and efficient systems for the uptake of available nutrients proliferate first. After the 'easy' nutrients are exhausted, the pioneers are replaced by the wood decay fungi that obtain their nutrition from the more complex breakdown of wood cell walls. This simplistic view is complicated by the fact that the wood undergoing infection is itself changing in chemistry through the production of potentially toxic chemicals (for example, phenols and terpenes). Do the decay fungi replace the pioneers because the pioneers degrade the toxins or because the pioneers have exhausted the available nutrients? Both processes appear to occur at the same time. The principles of disturbance ecology can explain much about the succession of microorganisms as long as the dynamic changes in wood chemistry are considered as part of the environment within the wounded tree.

- **Can infections grow through or around compartmentalization boundaries?**
  The effectiveness of compartmentalization depends on tree species, individual genetics, cumulative stress, tree condition, and environmental factors such as the seasonal timing of injury (DUJESIEFKEN *et al*. 2005). The availability of stored energy is an important component of tree condition that affects compartmentalization (WARGO 1996). Trees low in energy reserves are less able to form effective boundaries. Compartmentalization boundaries can be breached by further mechanical injury. Some pathogens have developed strategies that overcome or outpace those boundaries (SCHWARZE and BAUM 2000, BAUM and SCHWARZE 2002, SCHWARZE and FERNER 2003, SMITH and HOUSTON 1994). Canker-rot fungi (e.g. *Inonotus obliquus* and *Phellinus pini*) evade compartmentalization boundaries by extending their infections into bark. The bark provides both a refuge and a base from which to initiate new wounds by wedging apart bark and wood with masses of mycelium. Some pioneer and wood decay fungi occur in apparently asymptomatic wood (BAUM *et al.* 2003). Whether these latent infections (CHAPELLA and BODDY 1988) are free-living endophytes or are restricted to compartments is not clear. The obvious is true: eventually all trees die and all wood rots. Some trees are more effective at compartmentalization than others, just as some trees are more effective at sprouting or enduring drought and flooding.

- **If compartmentalization is effective, why are there hollow, living trees?**
  A living hollow tree is ultimately an example of successful compartmentalization. From the point of view of the tree, ultimate success is continued tree survival. As long as the vascular cambium is moving outward and away from established infections by producing new wood, and the outward spread of decay is resisted, compartmentalization is successful.

Why should we care about compartmentalization?

Compartmentalization of wood decay in living trees is of more than academic interest to arborists and land managers. In a recent survey of arboriculture and urban forestry educators in the U.S. (ELMENDORF *et al.* 2005), 92% of the respondents identified the subject of "tree structure and decay identification" (including the topic of compartmentalization) as important or very important. Wood decay increases the cost of tree care in towns and cities. Although perhaps unpleasant to admit, many tree decay problems are caused by inadequate or improper tree care. Prevention or minimization of wounding that exposes wood to infection is the least expensive means to reduce the frequency and severity of decay problems.

- **Pruning**
  Probably the most commonly applied tree care practice is branch and stem pruning (DUJESIEFKEN and STOBBE 2002, SHIGO 1989). The compartmentalization process explains why the improper pruning of branches to be flush with the stem or the next higher order branch causes greater amounts of wood decay than with proper pruning. Proper placement of the pruning cut is immediately to the outside of the branch collar. This removes the branch without injuring the stem and does not leave a long branch stub. Long branch stubs interfere with closure of the pruning wound and provide a food base for decay organisms.

  After proper pruning, one of the constitutive boundaries that contribute to compartmentalization after branch pruning is the branch protection zone located at the base of the branch. The protection zone is encircled by the stem and contains constitutive chemicals that resist the spread of infection. In addition, the protection zone provides a framework for the induced formation of a reaction zone (PEARCE 2000) that further resists the spread of infection. Improper pruning by cutting a branch flush with the stem removes some or all of this protection wood, makes a larger wound overall, and injures the stem as well as the branch. Recent research shows that the presence of a pronounced branch collar is associated with effective compartmentalization following branch removal (EISNER *et al.* 2002).

- **Topping**
  Tree topping, the cutting of the main stem or stems at arbitrary positions along their length is a very damaging practice and should not be accepted for trees larger than saplings. Unlike the protection wood at the base of branches, branches and stems do not contain preformed boundaries along their length. Although column boundaries will form to resist axial spread, the open cellular structure and the potential for less responsive

heartwood in the core of the tree makes the extensive spread of decay likely. Boundaries will form within sapwood present at the time of wounding. Tree topping and flush cuts can cause branch and stem cracks that contribute more to a risk of tree failure than well-compartmentalized columns of decay. Similarly, compartmentalization is more effective in properly pollarded rather than topped trees (GILMAN and KNOX 2005). Compartmentalization is not aided or strengthened by the use of wound dressings (DUJESIEFKEN *et al.* 1999; HUDLER and JENSEN-TRACY 2002).

- **Hardware installation**
  The installation of hardware to support weak branch crotches and to reinforce cracked branches and stems has long been practiced. Individual trees that are in good condition and are of species that are naturally strong compartmentalizers effectively resist the loss of normal wood functioning and the spread of decay following the insertion of 'dead-end' screws and 'through bolts'. However, hardware installation can breach compartmentalization boundaries and release previously compartmentalized infections, resulting in the spread of decay (KANE and RYAN 2002). Consequently, the whole tree needs to be considered prior to the decision to install supporting hardware.

Future implications and applications of compartmentalization in the future

Effective compartmentalization leads to reduced spread of decay. Amounts of internal decay are assessed using a variety of techniques at a wide range of economic cost. Much of the impetus for technique development is due to increased social pressure for risk assessment and the assignment of liability for failure. Stress wave timing (LAWDAY and HODGES 2000), ultrasonic tomography (SOCCO *et al.* 2004), and magnetic resonance imaging (MÜLLER *et al.* 2001) are appealing due to their lack or low degree of invasiveness, but may not be sufficiently robust or economical for widespread use. Well-established techniques based on electrical resistance or resistivity (OSTROFSKY and SHORTLE 1989) can be difficult to interpret but are being refined (LARSSON *et al.* 2004). The relative merits of various simple drilling techniques are being tested with one recent finding that the condition of the drill hole may affect the spread of decay more than its diameter (KERSTEN and SCHWARZE 2005).

Further research will surely describe the physiological and anatomical components of compartmentalization in increasing detail. This research will require the full range of investigative techniques, from whole-tree autopsies to non-destructive imaging to detailed analysis of cell physiology and anatomy. Expanding the range of tree species and decay fungi studied in depth will likely find a broader array of mechanisms that resist the spread of decay pathogens.

Although there is much to learn, we know enough to respect the compartmentalization process and to avoid improper pruning, topping, and other mechanical injuries that aggravate existing problems and that create new ones. Researchers need to integrate across scientific disciplines to improve our understanding of trees and tree treatments as shown by SHIGO (1989, 1991), MATTHECK and BRELOER (1994), MATTHECK *et al*. (2006) and others. For arboriculture, the biggest challenges are to (1) determine the critical thresholds of tree condition that either favor compartmentalization or that predispose trees to greater frequency and severity of decay and (2) develop tools to teach the public about what keeps urban and community trees safe, healthy, and beautiful.

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