

ORIGINAL ARTICLE

An organismal view of dendrochronology

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Abstract

An organism is the most basic unit of independent life. The tree-ring record is defined by organismal processes. Dendrochronology contributes to investigations far removed from organismal biology, e.g., archeology, climatology, disturbance ecology, etc. The increasing integration of dendrochronology into a diverse research community suggests an opportunity for a brief review of the organismal basis of tree rings.

Trees are dynamic, competitive, and opportunistic organisms with diverse strategies for survival. As with all green plants, trees capture the energy in sunlight to make and break chemical bonds with the elements essential for life. These essential elements are taken from the atmosphere, water, and soil. The long tree-ring series of special interest to dendrochronology result from long-lived trees containing relatively little decayed wood. Both of those features result from organismal biology. While the tree-ring record tells us many things about local, regional, and even global environmental history, tree rings are first a record of tree survival.

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Introduction

Dendrochronology is a set of conceptual and practical tools that apply the tree-ring record as a tool to better understand the web of earth, ocean, atmosphere, life, and human society. Basic methods and the underlying rationale for tree-ring analysis are well established and continue to be refined (Fritts, 1976; Cook and Kairiukstis, 1990; Schweingruber, 1996). Analytical findings from dendrochronology can have an impact far from the living trees that produced the records.

As we use dendrochronology to understand the world at an increasing distance from trees, the danger is that we come to think of the tree-ring record as the output of another piece of environmental monitoring equipment, such as a seismograph or rain gauge. In this paper,

I suggest that however we manipulate the derived data, each tree-ring series is the record of an individual organism, the most basic unit of independent life. Each tree-ring series is initially rooted in time and space, with its own history and exposed to times of abundance and of stress.

Dendrochronology relies on annual increments of wood produced as part of tree growth. The annual periodicity of ring growth is most easily validated in trees of the temperate zone that have a distinct dormant season related to cold weather. However, some tree species may produce annual rings in response to a dry dormant season as in dry Mediterranean climates (Cherubini et al., 2003). Chemical signatures such as calcium enrichment may identify ring boundaries that are not visibly distinct in tropical trees exposed to strongly seasonal rainfall (Poussart et al., 2006).

As an artifact of typically being viewed in transverse section, these annual increments appear as a series of

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rings from bark to pith. The boundary between adjacent rings (Schweingruber, 1996) is usually determined visually. Both broadleaved and coniferous tree species are constructed on a common theme of an interconnected webwork of living cell contents (the symplast) in intimate association with the cell wall system and lumens of non-living conducting and support cells (the apoplast). Within this common theme is a range of diversity of cell types and dimensions from the comparatively simple wood structure of conifers with increasing variation through ring- and diffuse-porous broadleaved trees. Some of this variation reflects different survival strategies relating to the tradeoffs between safety and efficiency of water conduction (Hacke and Sperry, 2001).

Long tree-ring series are the result of (1) long-lived trees and (2) the absence of appreciable decay that degrades or destroys portions of the record. Both of these factors are based on the organismal biology of trees. The long-observed relationship of tree-ring characteristics to climate and disturbance reasonably suggests that external factors influence the process of organismal growth. Tree-ring records have been empirically related to trends in climate and forest stand maturation as well as to abrupt disturbances in climate, geology, and the outbreak of insect pests and disease. Although it seems intuitive that transient or persistent disturbances that directly or indirectly affect photosynthesis such as drought, canopy gap formation, repeated defoliation, etc., would affect ring series, the actual mechanisms that link the environment to fundamental processes of wood formation (xylogenesis) are not clear (e.g., Savidge, 2000).

Regulation of wood formation

Two basic approaches are used to investigate the regulation of wood formation. The intensive approach seeks to understand the fundamental mechanisms of xylogenesis using molecular genetics and cell physiology (Dengler, 2001; Mellerowicz et al., 2001; Li et al., 2006; Samuels et al., 2006). The extensive approach seeks to relate abrupt or gradual changes in the tree-ring record to changes in the environment using environmental observation and statistics (Cook and Kairiukstis, 1990; Schweingruber, 1996). At the risk of oversimplification, the former approach is a fundamental botanical science that seeks to determine the intrinsic factors of growth regulation while the latter approach is part of the applied science of dendrochronology used to investigate environmental events. The two approaches have synergistic potential, although crossing the scales of observation poses special problems. Identifying the physiological factors that alter tree-ring features may

present an opportunity to cross those scales. For example, white rings are visibly distinct growth rings that are more narrow, less dense, and contain fibers of smaller diameter with little thickening of the secondary cell wall than adjacent rings (Sutton and Tardif, 2005). White rings in *Populus tremuloides* (trembling aspen) are associated with defoliation from insect outbreaks (Hogg et al., 2002). White rings are also produced in *Betula alleghaniensis* (yellow birch) in response to crown loss from breakage during winter storms (Fig. 1).

The simplest description for xylogenesis and tree-ring formation is as the interaction of genetics and the environment (Savidge, 2000). Although this is true for ring formation and essentially all phenotypic expressions, applying that simple elegance requires the partitioning of the environmental factors into those elements that usually fluctuate within well-defined limits (e.g., year-to-year variation in temperature and moisture stress) as well as episodic disturbance (e.g., extreme drought or flooding, fire, gap formation, and pest outbreaks).

A conceptual model structured as a linear aggregation of factors was constructed to investigate dendroclimatic relationships for tree-ring patterns that are held in common among trees in a forest stand (Cook,

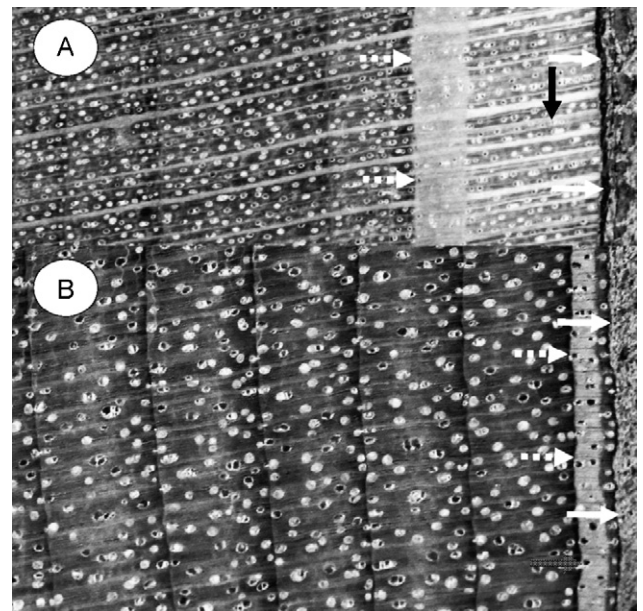


Fig. 1. White rings in *Betula alleghaniensis* (core collected after the 2000 growing season) associated with winter storm injury in 1998. The 1997/1998 ring boundaries (dotted white arrows) and the vascular cambium (white arrows) are marked. (A) Rapid recovery of growth after white ring formation in a tree that retained more than three-quarters of its live crown. The 1999–2000 ring boundary is marked (black arrow). (B) Little recovery of growth in a tree that retained less than one-quarter of its live crown. The white ring either contains both the 1998 and 1999 growth increments or one of those increments is locally absent.

1990). This model accounted for disturbance effects for individual trees and for the sampled stand as a whole in an effort to maximize the common climate signal and to remove noise (in this case, non-climatic variation). Widely used as a conceptual model in dendroclimatology, the model has also been used to identify and then remove the effect of climate in investigations of disturbance and other biological factors. A mechanistic model, TREERING, was also developed to simulate tree-ring structure from daily climatic data and the integration of tree water balance at daily time steps (Fritts et al., 1999). This type of model may provide a practical link between the intensive and extensive approaches to understand tree-ring formation.

Trees as organisms

An organism acts to maintain or extend the presence of the individual or species in time and space. Maintaining structure and activity against the natural tendency for disorder requires the continual supply of energy to the organism from its surroundings.

Trees are dynamic, competitive, and opportunistic organisms with a broad array of strategies for success. Successful trees maintain or extend their individual or community dominance within the limits of genetic capacity and environmental stability (or disturbance). Trees are intimately connected and responsive to their external environments. As photosynthesizing plants, trees use captured light energy to synthesize sugar from carbon dioxide and water. The sugar is then the feedstock for a host of cellular processes that support the overlapping needs for maintenance, reproduction, growth, constitutive protection, and induced defense of the organism.

Although some trees have a long lifespan, trees die throughout the development of a forest stand or community of trees (Franklin et al., 1987; Shortle et al., 2000). The greatest rates of mortality are for new seedlings, with continued mortality at all stages of tree and forest development. Although mortality rates can be expressed as a continuous function of stem diameter (Manion, 2003), mortality frequently occurs as episodic outbreaks mediated by storms, pests, pathogens, and fire.

There is no simple blueprint or strategy for long-term survival of individual trees. The two most famous long-lived species, *Pinus longaeva* (Great Basin bristlecone pine) and *Sequoiadendron giganteum* (giant sequoia) have markedly different habitats and strategies for survival (Lanner, 2002). Bristlecone pines have largely escaped competition by growing in a harsh environment with essentially unlimited sunlight and little competition from other tree species. Giant sequoia grows with other

large, competitive species in an amenable environment that is also prone to forest fire. Sequoia survive by avoiding injury from fire with a thick, fire-resistant bark and defensive chemicals that repel many insect pests (Lanner, 2002).

Growth

Trees grow by cell division or mitosis. In trees, most mitosis occurs in two dominant meristems. As with herbaceous higher plants, tree shoots and roots have apical meristems that produce primary growth that extends the length of shoots and roots from their tips. This extension growth increases the opportunity to intercept solar energy, water, and mineral elements. The pith of woody stems contains remnants of primary cells produced by the apical meristem.

Secondary growth provides the means for trees to grow upward and outward, into the sunlight, with the potential to escape or reduce competition from neighboring plants. Perennating growth provides a platform for new primary growth at the onset of the growing season. Growing taller improves competition for light resources yet imposes additional structural challenges. Trees accommodate to mechanical stress through the optimization of structural design. The unifying principle of ring growth as a biophysical construction is the axiom of uniform stress (Mattheck, 1998). The axiom states that the optimal design of the tree stem distributes mechanical stress uniformly across the stem, reducing or eliminating structural weakness while avoiding wasteful over-building. Both ring width and cellular structure are affected by unequal forces applied to a tree, resulting in the non-uniform distribution of mechanical stress. This is observed with “righting” phenomena and the formation of reaction wood (Constant et al., 2003; Almeras et al., 2005) and in response to flexure imposed by wind (Pruyn et al., 2000). Dynamic stresses from repeated stem flexure can stimulate radial growth and increase wood density, while maintaining hydraulic connectivity to the leaves (Kern et al., 2005). In addition to physical support of greater primary apical growth, the development of the wood stem and branch system introduces greater needs for hydraulic control, energy storage, and wound response.

Trees have one or more secondary meristems. The most important of these for wood production is the vascular cambium (Larson, 1994). Another secondary meristem, the phellogen or cork cambium, produces bark layers that protect the vascular cambium and living sapwood cells from desiccation and injury. In the absence of tree injury, the vascular cambium consists of a thin, continuous layer over the wood formed during previous growing seasons and beneath the bark. Mitoses

and subsequent differentiation of cells in the vascular cambium produces secondary xylem to the inside or pith side and secondary phloem to the outside or bark side. This phloem (“inner bark”) transports carbohydrate and other biomolecules such as growth regulators from their points of synthesis to their points of storage and utilization (van Bel and Hafke, 2005). Mature, lignified secondary xylem or wood provides the conduit for water and some essential mineral elements. Conceptually, meristematic growth is the basis for trees being generating rather than regenerating systems (Shigo, 1986). As a generating system, tree tissue that has been killed or seriously impaired is not replaced but functionality is restored and extended by new tissues produced in new spatial positions. That is, trees do not “heal” injured wood tissues; new wood is produced to replace the lost function of the killed cells.

“Annual growth” represents cell division and subsequent differentiation for a much briefer than a 1-year period. Although variable, the vascular cambial cells in temperate zone trees generally divide over a period of about 10–12 weeks. Wider growth rings may require a longer period of differentiation (Gričar et al., 2005) and consequently may be more affected by autumnal climate than more narrow rings. The timing of cambial activity and differentiation of cambial derivatives is affected by localized heating or cooling of the vascular cambium (Gričar et al., 2006). Ring width is the characteristic most often measured in tree-ring series, although other features such as latewood width (e.g., Drobyshev et al., 2004) and wood density can provide useful information and be a more sensitive recorder of climate than ring width.

The amount of annual growth depends in part on energy captured, carbon dioxide fixed, and carbohydrate stored during previous growing seasons. These factors also depend on the architecture of root and branches produced during still earlier periods of growth. Initial cambial divisions in the growing season are fueled from energy reserves held through the previous dormant season (Barbaroux and Bréda, 2002). Consequently, tree rings within a series vary in response to climatic and stress conditions during and prior to the current growing season. Although still a controversial concept, the relationship of tree-ring width to climate may not be as uniform through time as commonly assumed (Smith et al., 1999; Carrer and Urbinati, 2006).

Superimposed on traditional climatic factors such as temperature, precipitation, and soil moisture are changes in the chemical climate that may affect radial growth such as increased concentration of sulfur dioxide or tropospheric ozone that disrupts photosynthesis (Martin and Sutherland, 1990; Bartholomay et al., 1997), increased ambient concentration of carbon dioxide that may have a fertilizer effect and boost photosynthetic output (Berninger et al., 2004), and

increased deposition of airborne pollutants that affect soil fertility (Duchesne et al., 2002; Lawrence et al., 2005).

Cell division within portions of the vascular cambium can differ in the timing of seasonal onset, duration, and productivity. Characteristics of tree rings such as width, density, and chemistry are variable, periodic, and capable of abrupt change. Ring characteristics vary around the stem circumference and along the stem, branch, and root axis (Grabner and Wimmer, 2006; Lamlon and Savidge, 2006). This is the source of locally absent or axially incomplete rings (“missing rings”). Although still variable, tree-ring series collected from trees at breast height (1.4 m aboveground) minimizes the influences of the stem flare above the root junction (Mattheck, 1998) and the varying proximity to the base of the live crown (Bouriaud et al., 2005). This variability is a principal reason to measure ring series for at least two radii per tree. Observations along two radial vectors of wood formation may seem inadequate to capture the variability in ring characteristics within a tree. However, such dual observations can be sufficient to capture common patterns of response to growth influences across a forest stand or region.

For some applications, comparisons of index series derived from the high-frequency deviations from the growth trends of individual series can enable the comparison of series that widely differ in absolute values and facilitate climatic reconstruction. The variation of growth within and among trees that is not readily attributed to environmental qualities highlights the importance of variability in individual tree genetics and microsite conditions that affect growth. Despite some examples to the contrary, ring width tends to plateau and eventually decline in old, large trees. One explanation is that the volume of tree canopy exposed to sunlight and photosynthesis reaches a maximum extent. Similarly, the root system involved in water and essential element uptake may also reach a maximum extent. If energy allocation to wood formation remains constant, and a consistent amount of wood is formed each year, the width of new rings must decline due to the increase in stem girth. Alternatively, senescence of the vascular cambium may occur in the absence of resource limitation, decreasing mitotic activity and the production of wood cells.

Fundamental to dendrochronology is crossdating, the alignment of common patterns in tree-ring series to specific calendar years (Stokes and Smiley, 1968; Swetnam et al., 1985). Crossdating relies on the identification of patterns in common among the tree-ring series collected. The synchronizing influence is commonly climate or a recurring disturbance. Although crossdating is successful across many individual trees, species, and wide geographic areas, selection characteristics of desirable forest stands (located near their

ecological limit, sensitive species) and individual trees (healthy dominant or codominant individuals) greatly facilitate the detection of a common growth signal. Not all trees produce tree-ring series that can be crossdated.

Protection and responsiveness

Ring growth, although important for tree survival, generally has a relatively low priority for the allocation of internal resources (Savidge, 2000). Ring growth is also less sensitive than might be expected to partial defoliation as photosynthesis rates frequently increase in the remaining leaves (Hoogesteger and Karlsson, 1992). Ring growth can rapidly recover after growth rate depression caused by the loss of crown from storm breakage (Smith and Shortle, 2003). Rapid recovery from crown loss is associated with the building of a new crown from stem sprouts (Shortle et al., 2003).

In addition to different growth strategies, tree species vary in their investment in constitutive protection (Herms and Mattson, 1992). Much of this protection is oriented towards minimizing the effects of mechanical injury. Trees are wounded throughout their lives, from the natural shedding of branches and roots, storm injury, and numerous other causes. Protection may consist of thick bark to insulate the vascular cambium and living sapwood from lethal heating during forest fire (Harmon, 1984). Some trees constitutively deposit large quantities of protective phenols and terpenes in heartwood that reduce the rates of decay and insect infestation (Hillis, 1987). This impregnation of heartwood greatly contributes to the persistence of sound wood available for dendrochronological sampling both in the standing tree and in downed stems. This resistance to decay can be critical in the development of long tree-ring chronologies, such as was developed for *Lagarobrotos franklinii* (Huon pine) in Tasmania (Cook et al., 1991).

Tree-ring series record the response of trees to localized death of the vascular cambium caused by mechanical injury from fire, flooding, landslides, etc. Such cell death exposes the underlying sapwood to desiccation and infection by wood-destroying fungi and associated microorganisms. This exposure occurs whether or not the bark appears to be intact over the killed area. Wounds caused by fire or mechanical abrasion can be recognized by the frequently exposed wood and by the wider rings at the wound margins (Fig. 2). The locally wide rings can form pronounced ribs of woundwood that tend to eventually close over the wound (Shigo, 1986; Smith and Sutherland, 1999, 2001). This accelerated growth facilitates wound closure and reduces mechanical stress in the stem (Mattheck, 1998).

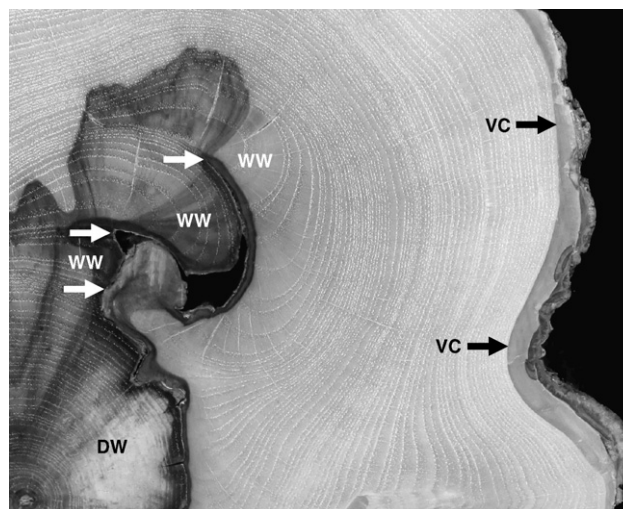


Fig. 2. Successful compartmentalization of infection in *Carya glabra* following multiple injuries due to fire. The circumferential limit of the killed vascular cambium is marked (white arrows). In each of the three wounding events, woundwood (WW) ribs were formed at the margins of the killed vascular cambium. At the time of tree harvest, the living vascular cambium (VC) was located well away from the decayed wood (DW).

The constitutive anatomy and induced responses that resist the spread of infection and loss of normal function in wood is the compartmentalization process (Shortle, 1979; Shigo, 1984; Schwarze et al., 2004; Smith, 2006). Compartmentalization occurs in both conifer and broadleaved trees, although the details of the process do differ across tree taxa. The primary goal of compartmentalization is to protect the vascular cambium from the twin adverse consequences of desiccation and infection. Although these consequences of mechanical injury seem separable as abiotic and biotic factors, they are inseparable in practice. Given the essential ubiquity of inoculum of wood-destroying fungi and their microbial associates, any abiotic breaching of intact living tissue immediately produces the opportunity for infection.

Compartmentalization is a boundary-setting process in two parts. In the first part of compartmentalization, boundary layers are formed by living sapwood that is present at the time of injury (Fig. 3). These layers can contain lipids, frequently in the form of terpenes in conifers and waxes such as suberin in broadleaved species, similar to those in bark that resist water loss and dessication. Metabolic shifts in living cells also produce antimicrobial resin acids or phenols (similar to those formed in heartwood) that tend to slow the spread of most wood decay fungi and their associates. These boundary layers are not absolutely effective and can be breached by wood decay pathogens (Schwarze et al., 2004). Given sufficient energy resources, the sapwood may form these boundaries repeatedly, as they are

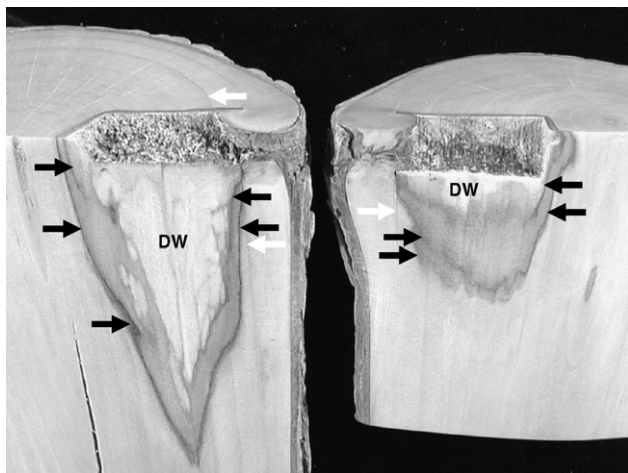


Fig. 3. Differential effectiveness of compartmentalization of half-sib *Liquidambar styraciflua* to borehole injury (Garrett et al., 1979). Multiple column boundary layers have formed in wood present at the time of injury (black arrows). The position of the barrier zone is marked (white arrows).

breached, at increasing distance from the wound. Comparisons of clones of *Liquidambar styraciflua* (sweetgum) (Fig. 3), *Populus deltoides* (eastern cottonwood), and *P. deltoides* × *P. trichocarpa* hybrids indicate a genetic component to compartmentalization effectiveness (Garrett et al., 1979; Smith and Shortle, 1993).

In the second part of the compartmentalization process, in both conifers and broadleaved trees, the vascular cambium produces a layer of anomalous, visibly distinct wood known as a barrier zone (Shigo, 1984, 1986; Deflorio, 2005). Barrier zones separate wood present at the time of injury from wood formed after injury (Fig. 4). Barrier zones are one source of “false rings” in dendrochronological analysis. Although barrier zone formation is most pronounced immediately adjacent to the injury, the barrier zone may extend axially and circumferentially for some distance away from the wound (Shigo and Dudzik, 1985). The position of the barrier zone within the growth ring can indicate the timing of the injury within the growing season. Barrier zone anatomy varies among tree species (Deflorio, 2005). In general, the conducting tracheids or vessels have thicker cell walls, are shorter in length, more variable in orientation, and contain a greater frequency of accompanying parenchyma. In species that produce them, traumatic resin canals are formed, frequently in one or more rows. Barrier zones protect the vascular cambium by resisting the outward spread of infection.

Both parts of compartmentalization give the vascular cambium time to move away from the area of infection and to produce new wood for structural support, storage of energy (usually in the form of starch), and for the potential to respond to later injury. Successful compartmentalization can result in the colonization and

degradation of wood by bacteria and fungi within the compartmentalization boundaries, even to the extent of producing cavities or voids within the central portions

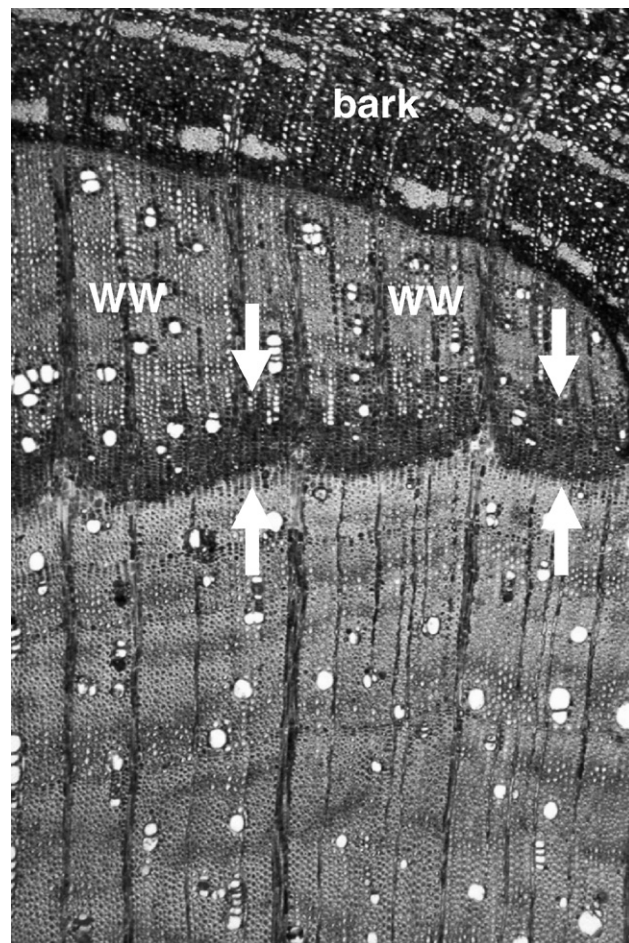


Fig. 4. Barrier zone (between opposing white arrows) in *Acer rubrum* separates woundwood (WW) formed after injury from wood present at the time of injury.

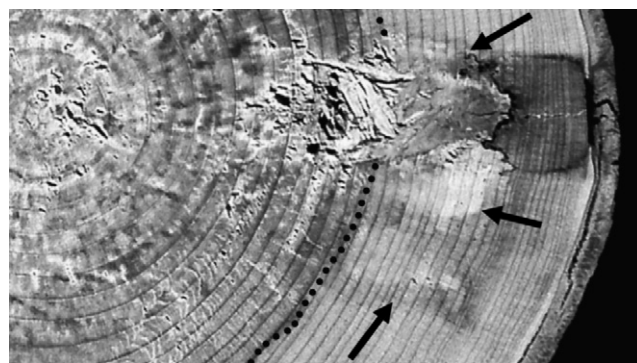


Fig. 5. Release of previously compartmentalized infection in *Acer rubrum*. One year after the breaching of the compartmentalization boundary (dotted line) with a borehole, the infection rapidly spread outward (black arrows) towards the vascular cambium. The borehole is about 1 cm below the plane of the sample.

of stems and branches, with little threat posed to the vascular cambium or tree survival. Mechanical breaching of a compartmentalized infection can result in the rapid spread of infection (Fig. 5), leading to the loss of structural integrity of the wood as well as threatening the vitality of the vascular cambium. The size and physical condition of the borehole or wound that penetrates the barrier zone affects the release of infection. Small-diameter holes packed with wood shavings appears to favor spread of pre-existing infection to a greater degree than the larger, open hole made by an increment borer (Kersten and Schwarze, 2005).

Conclusion

Tree rings record the allocation of energy and metabolites to secondary growth of the stem. That record can, in many instances, provide an environmental history. However, tree rings are first a record of tree survival. The simple presence of a living tree or wood fragments in place proves that conditions are or were at least minimally adequate to support tree growth. The presence of a sufficient record to be useful for dendrochronology is also likely a record of some combination of competition, pest and disease outbreaks, climate and geophysical disturbance, and human activity. An understanding of tree biology will likely assist the investigator to understand and to interpret the story contained in the tree-ring record.

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