DECAY DEVELOPMENT AND ITS RESTRICTION IN TREES

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Abstract. The major hypotheses that have been proposed to explain the patterns of decay development and its restriction in the wood (xylem) of living trees are outlined briefly. The current understanding of the biochemical and physiological events that contribute to the protection of pre-existing functional sapwood is reviewed, with particular reference to the formation of reaction zones at the host-pathogen interface in *Acer* species, especially the European sycamore maple (*Acer pseudoplatanus*) in which the interactions between wood-inhabiting fungi and sapwood have been extensively investigated. Studies using conventional anatomical and biochemical approaches have been integrated with the application of advanced physical techniques (nuclear magnetic resonance [NMR] imaging, proton induced X-ray emission [PIXE] microanalysis and mapping, and electron paramagnetic resonance [EPR] spectroscopy), allowing a model describing the development and function of reaction zones in this species to be proposed. Results from other woody angiosperms indicate that in some (e.g., European beech [*Fagus sylvatica*]) reaction zones may be essentially similar but that in others there may be significant differences. The implications of our developing understanding of antimicrobial defense in trees on the practice of arboriculture is discussed briefly.

Key Words. Antimicrobial defense; decay; compartmentalization; reaction zones; *Acer pseudoplatanus*; *Fagus sylvatica*.

Four principal models have been proposed to describe the development and restriction of decay in living trees. Until the 1970s, the heartrot concept was widely accepted (Boyce 1961; Peace 1962); decay was regarded as an essentially saprotrophic process, fungi entering through wounds or dead organs that exposed the nonliving heartwood, which was subsequently invaded, with little or no attack on the functional, living, sapwood. This was recognized as insufficient to account for the patterns of colonization observed behind many wounds and the occurrence of morphological and chemical changes at the margin between decay lesions and living sapwood (xylem), which have been interpreted as protective barriers that restrict the spread of infection.

Boundaries formed at the interface between infected xylem and pre-existing sapwood were interpreted as dynamic defenses, retreating ahead of the advancing infection front, and have been termed reaction zones (Shain 1967, 1971, 1979), column boundary layers (Shortle and Smith 1990) or CBL reaction zones (Pearce 1996). Subsequent studies in a number of broad-leaved trees have refined this model, indicating that reaction zones form essentially static lesion boundaries that can retain their function for an extended time. When these lesions expand, a volume of wood may become colonized with little or no expression of host responses, before a new reaction zone boundary is established (Pearce 1987, 1991; Boddy 1992).

On the basis of patterns of discoloration and decay observed behind wounds, the compartmentalization of decay in trees (CODIT) model was proposed (Shigo and Marx 1977; Shigo 1979, 1984). According to this model, lesions in functional sapwood are bounded by 4 walls laid down in the wood, envisaged as essentially static barriers preventing the spread of infection. Walls 1 to 3, formed in wood present at the time of wounding are equivalent to reaction zones, but wall 4 is distinct, comprising a tissue laid down de novo by the cambium in the vicinity of wounds, and is the most durable of the compartmentalization walls.

Both the reaction zone and CODIT models imply that lesion development is restricted by active host defenses. As an alternative, it has been suggested that changes in the internal microenvironment of trees, consequent upon wounding and associated xylem dysfunction, could determine lesion development without any need for active host responses. The high water content, and consequent low availability of oxygen, in functional sapwood would itself inhibit fungal growth. Lesion morphology determined by the drying and oxygenation of compromised xylem would be closely similar to that associated with the compartmentalization model

(Boddy and Rayner 1983; Rayner 1986; Rayner and Boddy 1988; Boddy 1992).

These different models are in no way mutually incompatible, and elements of all may function in concert to protect the living tree. Compartmentalization and reaction zone barriers may have the dual functions of protecting against fungal attack directly, and helping to prevent aeration and to maintain the functional integrity of the healthy xylem adjacent to a wound or infection site.

Although a substantial body of information on the various mechanisms that may contribute to protection in the xylem of living trees has been acquired in recent years (Kemp and Burden 1986; Pearce 1987; 1996; Blanchette and Biggs 1992), our understanding of the physiology and biochemistry of decay restriction in the wood of living trees is still fragmentary. However, an improved understanding of these processes would be valuable to both arboriculture and forestry because it could contribute to the better and more informed management of decay and other disease problems in amenity and crop trees.

The European sycamore maple (*Acer pseudoplatanus*) is a convenient tree in which to study antimicrobial defense. Endogenous defenses commonly appear effective in restricting the spread of decay, and the green-colored reaction zones formed by this species are easy to recognize when trees are dissected. Juvenile trees are easily grown for experimental use, and the absence of formation of a differentiated heartwood can simplify the analysis of host-pathogen interactions. Further, a number of studies on other *Acer* species (e.g., Sharon 1974; Green et al. 1981; Pearce and Woodward 1986; Shortle and Smith 1990) have contributed a background of knowledge on defense in this genus.

MATERIALS AND METHODS
Experimental Systems
Reaction zone responses in sycamore maple (*Acer pseudoplatanus*) were investigated in field-grown trees naturally infected with *Cryptostroma corticale* (sooty bark disease) and in juvenile trees 3 to 6 years old grown in 170-mm (7-in.) diameter plastic pots (*cf.* Pearce et al. 1997a). Alternatively, excised stem lengths could be maintained for periods of up to 1 month *in vitro*, to provide a convenient model sys-

tem for use in short-term studies of defense elicitation and lesion development (Pearce et al. 1994). Xylem tissues of young plants and stem lengths exposed by wounding were inoculated with cultures of the aggressive pathogen *Chondrostereum purpureum* or the weakly invasive decay fungi *Ustulina deusta* or *Ganoderma adspersum* grown on 3% malt agar (Pearce et al. 1994; Pearce et al. 1997a).

RESULTS AND DISCUSSION
Reaction Zone Anatomy
Reaction zones in sycamore were seen as green regions, typically 0.5 to 2 mm (0.02 to 0.08 in.) wide at the interface between healthy and infected sapwood (Figure 1). Apparently healthy wood adjacent to this was normally strongly fluorescent to a depth of approximately 2 mm (0.08 in.) (*cf.* Grime and Pearce 1995). In the green-stained regions the lumens of vessels, fibers, and some parenchyma cells were occluded with green or brownish insoluble "gummy" polymeric deposits, which appeared to infiltrate adjacent cell walls also (Figure 2). Fungal hyphae were present in decaying wood adjacent to the reaction zone but were generally absent from the reaction zone itself (Figure 3). These altered tissues exhibited increased resistance to degradation by wood decay fungi (Pearce et al. 1997b).
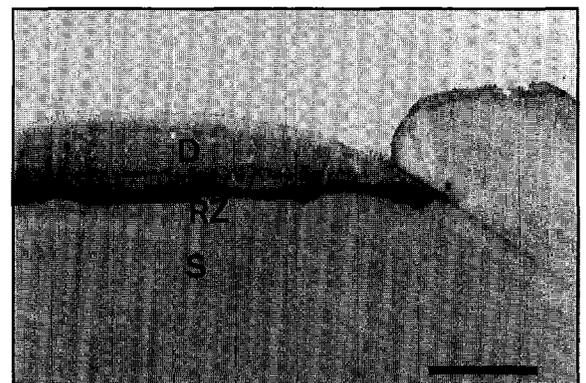
Figure 1. Reaction zone behind a wound that has destroyed the bark of a sycamore (*Acer pseudoplatanus*) tree. A green reaction zone [RZ] has formed between the decaying, exposed wood [D], and the healthy, underlying sapwood [S]. Scale bar = 20 mm (0.8 in.)

Figure 2. Radial longitudinal section through a reaction zone in sycamore (*Acer pseudoplatanus*), showing colored polymeric deposits occluding the lumens of vessels and xylem fibers, and infiltrating the wood cell walls in this region. Scale bar = 100 μm.

Figure 3. Radial longitudinal section through the margin of a decay lesion in sycamore (*Acer pseudoplatanus*), stained using a nitro blue tetrazolium method (Shain 1967; Pearce et al. 1994). Dark-staining hyphae [H] are present in the decaying wood but are not seen in the reaction zone tissues, where characteristic coloured polymeric deposits [P] fill many of the cells. Scale bar = 100 μm.

Non-Invasive Imaging of Reaction Zone Development

As reaction zones are formed within the xylem, their development and dynamics are difficult to investigate using conventional approaches, especially because their functional environment would be disturbed by the wounding required to gain access to the host-pathogen interface. However, noninvasive techniques, such as nuclear magnetic resonance (NMR) imaging, allow studies of the formation of reaction zones *in situ* without the disruption caused by destructive sampling methods.

NMR images revealed lesion anatomy in both naturally infected and experimentally inoculated trees (Pearce et al. 1994, 1997a). Reaction zones exhibited high contrast in spin-echo images (Pearce et al. 1994, 1997a). Image contrast can reflect either differences in the total number of protons giving rise to the signal (imageable proton density, M_0), or changes in the proton relaxation times (T_1, T_2). Analysis of image data sets revealed that contrast in reaction zones was attributable to an increase in M_0, rather than to altered relaxation times. This indicated that the water content had increased in reaction zone tissues compared to normal, healthy sapwood (Pearce et al. 1994, 1997a, 1997b) (Figure 4). Gravimetric determinations of the water content of xylem tissues excised from naturally occurring lesions or experimental inoculation sites revealed an increase in tissue water content of 1.1 to 1.7 times in reaction zones compared to healthy wood. This has been shown to have resulted from the infusion of water into the normally gas-filled lumens of the xylem fibers in the wetter tissues (Pearce et al. 1997a).

Sequential imaging of the same plane through developing lesions in stem lengths inoculated with *U. deusta* revealed that following initial drying behind the wounds made by cutting the stems, water accumulated in reaction zones developing close to the inoculation site. The location of these remained essentially static for the duration of the experiment. In
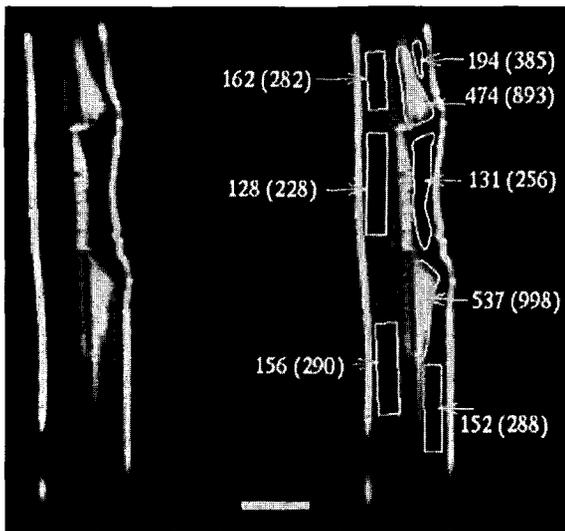
Figure 4. Spin-echo NMR image of a radial longitudinal slice through a juvenile sycamore stem 17 months after wounding and inoculation with the weakly aggressive decay fungus *Ganoderma adspersum*. Experimental details and full explanation are given in Pearce et al. (1997a). High-contrast cones of reaction zone tissue extend above (474) and below (537) the wound (131), which has become occluded with healing callus. Imageable proton densities (M_0), essentially reflecting tissue water content, are increased in the reaction zones compared to healthy sapwood or callus tissue. Mean pixel information densities for the delineated areas are indicated, calculated from T_1 (nonparenthesized)- or T_2-weighted image data sets. T_2-weighted values are given in parentheses. Scale bar = 10 mm (0.4 in.)

contrast, in stem lengths inoculated with the aggressive pathogen *C. purpureum*, a spreading necrotic lesion developed rapidly, with no early accumulation of water at its margin (Pearce et al. 1994). Similar results have been obtained using rooted juvenile trees imaged over a more extended period of time (Pearce, unpublished data).

Elemental Changes at Lesion Margins
Proton-induced X-ray emission (PIXE) microanalysis and mapping of elements at lesion margins in sycamore xylem has revealed that concentrations of potassium and manganese increase in reaction zones, and potassium and calcium in the lesion tissues immedi-

Table 1. Potassium concentration, measured by flame photometry, and osmotic pressure, determined using a dew-point osmometer, of fluids extracted by centrifugation from the wood of a sycamore (*Acer pseudoplatanus*) tree naturally infected with *Cryptostroma corticale*.

	[K⁺] (mM)	Osmotic pressure (bar)
Healthy wood	5.8	1.5
Stained wood		
(equivalent to reaction zone)	118.0	4.8

ately adjacent to the reaction zone (Grime and Pearce 1995). Potassium concentrations, measured by flame photometry, were similarly elevated in the fluids extracted by centrifugation from the wetter, reaction zone-like, stained tissues of *Cryptostroma corticale* lesions and could account for the elevated osmotic pressure of these fluids (Table 1). Similar elemental changes have been reported in reaction zones from other species (Shain 1971, 1979; Tattar et al. 1972; Safford et al. 1974; Shevenell and Shortle 1986; Smith and Houston 1994).

Accumulation of Phytoalexin-Like Compounds
Phytoalexin-like compounds have been reported from the reaction zones of many woody species (Kemp and Burden 1986; Pearce 1996), including *Acer* spp. (Manville and Levitin 1974; Pearce and Woodward 1986; Pearce et al. 1994; Pearce 1996). In *A. pseudoplatanus* the principal compounds accumulating were the coumarins scopoletin and (transiently) fraxetin, the glucosides of these compounds, scopolin and fraxin, and at least three coumarinolignans (Manville and Levitin 1974; Pearce 1996; Pearce, unpublished data). Following wounding and inoculation, fluorescent compounds started to accumulate around infection sites within 24 hr. of challenge (Pearce 1996). Initially scopolin and scopoletin increased, the latter reaching a peak, fungitoxic, concentration in the wood about 3 days after inoculation and declining thereafter. Accumulation of fraxin and the coumarinolignans occurred more slowly, but concentrations remained high in fully developed reaction zones. This paralleled the deposition of the colored polymeric material, which commenced a few days after the initial response (Pearce, unpublished data).

While scopletin inhibits fungal growth in bioassay at concentrations reached in challenged sapwood, the other phytoalexin-like compounds do not exhibit strong antifungal activity at physiological concentrations under standard bioassay conditions on thin layer chromatography plates (*cf.* Woodward and Pearce 1985) or in liquid medium (*cf.* Woodward and Pearce 1988) (Pearce, unpublished data).

Free Radicals in Reaction Zones

An oxidative burst, generating free radicals, occurs as an important component of the hypersensitive response in many plant species. This response, resulting in cell death, the accumulation of phytoalexins and, commonly, brown polyphenolic materials (Goodman and Novacky 1994), shares a number of features in common with reaction zone formation. Free radicals may also be generated during the activation of many phytoalexins, enhancing their antimicrobial activity (Downum 1992).

Examination of sycamore maple reaction zone material using electron spin (paramagnetic) resonance (ESR) spectroscopy revealed the presence of high concentrations (typically up to 0.5 mM) of unusually long-lived free radicals in the reaction zones (Pearce et al. 1997b). These radicals had a g-value (analogous to the chemical shift in NMR) of 2.0046, close to the free electron spin value of 2.0023, characteristic of organic free radicals (Pearce et al. 1997b). The insolubility and stability of these radicals, both intrinsic and in the presence of free radical scavengers, together with their apparent lack of effect on proton NMR relaxation times, indicated that they probably comprised a component of the lignin-like polymeric material deposited in reaction zones. Delocalization of the radical electron and steric hindrance would tend to stabilize radicals sequestered in such an environment (Pearce et al. 1997b).

White and brown rot fungi generate free radicals that are thought to have a primary role in the depolymerization of wood cell wall material (lignocelluose) (Rayner and Boddy 1988; Hirano et al. 1997). Free radicals in a reaction zone could themselves scavenge these degradative free radicals produced by wood decay fungi. By specifically inactivating the principal cell wall degrading systems of many decay fungi in this way, the long-lived free radical-rich polymers laid down in reaction zones could protect adjacent wood

from fungal attack, conferring a barrier function on the altered tissues.

A Model for Reaction Zone Formation in *Acer pseudoplatanus*

On the basis of the studies reviewed above, a model describing the formation of reaction zones as durable barriers to the spread of wood-inhabiting (decay) fungi can be proposed.

Following wounding and infection of sapwood, metabolic changes occur rapidly in the vasicentric parenchyma cells of the xylem. Biosynthetic pathways are induced, leading to the formation and accumulation of secondary metabolites. Phytoalexin-like compounds (coumarins) start to accumulate in the vicinity of inoculation sites within 24 hours of wounding and reach inhibitory concentrations within 3 days. Fungal elicitation appears important in this process because this accumulation occurs more slowly behind uninoculated wounds (Pearce, unpublished data). These compounds may function as a first line of induced defense, inhibiting the initial establishment of potential pathogens or slowing their invasion into the sapwood.

Within 5 to 7 days, the xylem compromised by the wound, which initially dried as the water columns in the vessels retracted under xylem tension, starts to re-wet, and a region corresponding to the site of formation of the colored reaction zone becomes wetter than the adjacent healthy wood. In this region, water occupies the lumens of the xylem fibers, which are normally gas-filled in functional sapwood. Concentrations of certain cations, especially potassium, increase in the vicinity of reaction zones. This accumulation of ions may allow the movement of water to the lesion margins, against the forces of xylem tension, through an osmotic mechanism. This water may carry secondary metabolites produced by elicited xylem parenchyma cells to the developing reaction zone and would permit their accumulation in the nonliving cells of the differentiated wood. This impregnation process would be necessary for the formation of a structurally continuous defensive barrier; an induced defense response restricted to the metabolically active parenchyma cells alone would be structurally discontinuous and readily circumvented by a pathogen adapted to growth in wood, rather than being capable of providing durable pro-

tection against decay. Further, the increased water in these lesion margin tissues may itself confer protection against fungal attack by creating a microenvironment inimical to fungal growth, by restricting oxygen availability in these tissues (*cf.* Boddy and Rayner 1983; Rayner 1986; Rayner and Boddy 1988; Boddy 1992).

Although potentially effective as an initial, short-term, defense, it is likely that continuing fungal activity could eventually erode a barrier solely dependent on the maintenance of a high tissue water content. Similarly, soluble inhibitory compounds may not be best suited to conferring durable protection in sapwood because of their potential mobility. In *Acer* spp. (and in many other woody species) insoluble polymeric materials are deposited in the lumens of vessels and cells, and infusing cell walls. In *A. pseudoplatanus*, long-lived free radicals are associated with this polymeric material. These may have a key role in the mechanism of protection against wood decay, scavenging degradative radicals generated by the lignolytic and cellulolytic enzyme systems of the wood-rotting fungi, thus terminating the depolymerization chain reaction and protecting adjacent cell wall material from decay.

The deposition of such material in a physically continuous reaction zone could confer relatively durable protection. Eventually the concentration of protective radicals would fall by attrition as they were used in the capture of pathogen-produced radicals; lesion extension might then proceed with the eventual breaching of the reaction zone boundary (*cf.* Schwarze and Fink, 1997) and the initiation of a further phase of colonization. Alternatively, the reaction zone may be reinforced, for a time at least, by the formation of new polymeric material. The narrow zone of fluorescent wood between the reaction zone and healthy sapwood, possibly to be considered equivalent to a transition zone (Shain 1979), may act as a source of the coumarin glucoside fraxin, which, as its aglycone fraxetin, is possibly a precursor of the free radical-rich polymer (Pearce, unpublished data). *De novo* free radical formation, apparently stimulated by oxygenation, can be observed in excised reaction zone tissues (Pearce et al. 1997b).

Reaction Zones in Other Tree Species

Although comparably detailed studies have not yet been completed in other species, analysis of the fragmentary evidence available indicates both similarities and significant differences. Brown or colored polyphenolic materials are commonly deposited in reaction zones (Pearce 1990), and long-lived free radicals have been detected in reaction zones in the 3 other species of temperate hardwoods examined to date. A range of phytoalexin-like compounds has been reported from reaction zones in various woody species (Kemp and Burden 1986). Preliminary NMR imaging studies of naturally occurring infections in beech (*Fagus sylvatica*) show high contrast in the reaction zones (Figure 5), suggesting water accumulation in this region, while PIXE microanalysis and mapping has indicated the presence of various ions, including potassium, calcium, and manganese, at elevated concentrations in beech reaction zones (Figure 6; Table 2), as occurs also in *A. pseudoplatanus* (Grime and Pearce 1995).

In many tree species, but not *A. pseudoplatanus*, xylem suberization responses are expressed in reaction zones (Pearce 1990). These may also contribute
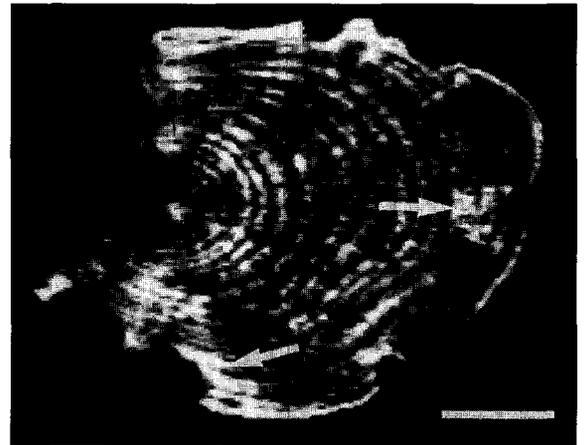
Figure 5. Spin-echo NMR image of a transverse slice through a naturally infected beech (*Fagus sylvatica*) stem with local bark necrosis and staining and incipient decay of the underlying wood. Reaction zones (arrowed) at the margin of these xylem lesions are higher contrast than the healthy wood, suggesting that the water content of reaction zones is elevated in this species also. Scale bar = 10 mm (0.4 in.)
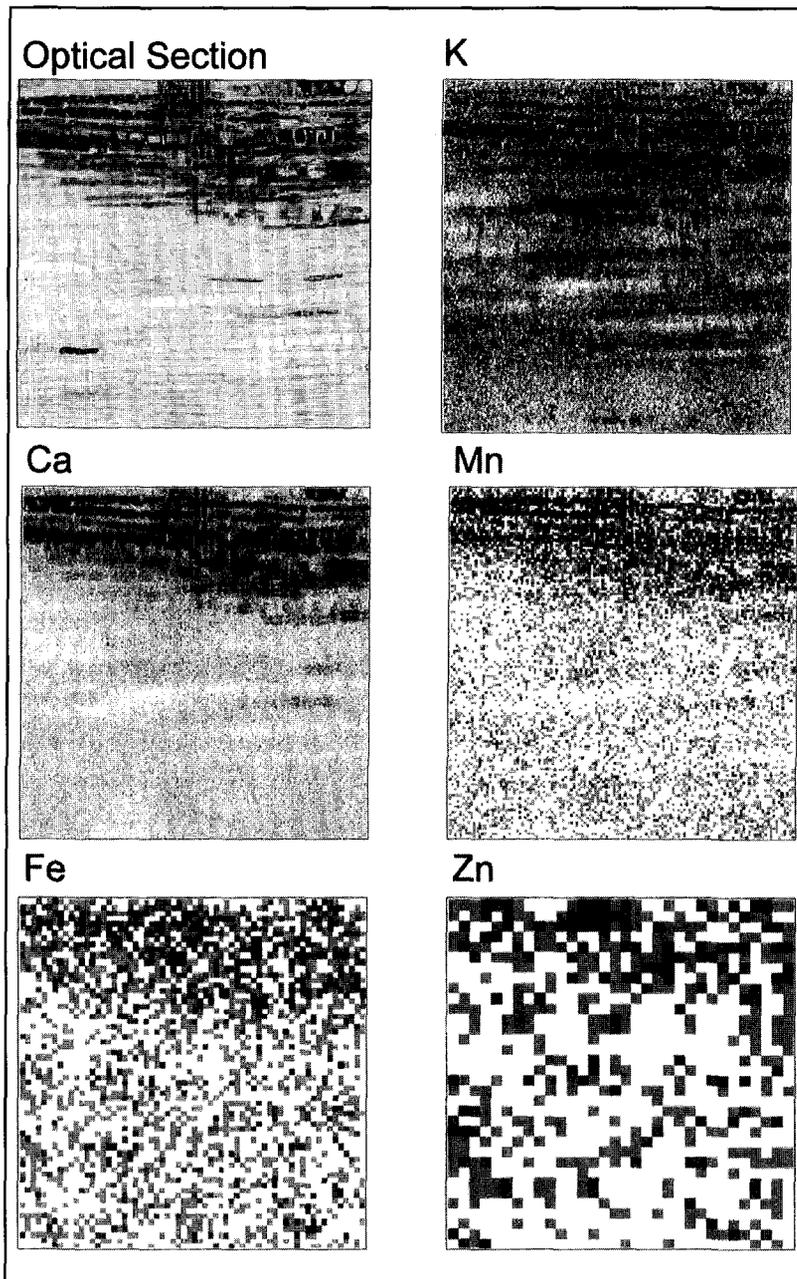
Figure 6. Elemental distribution in a reaction zone in beech (*Fagus sylvatica*), formed in the branch collar region at the base of a small branch that had died naturally. Elements were mapped using PIXE, essentially as described by Kramer et al. (1997), from a radial longitudinal section (15 μm thick) that included a fully developed reaction zone characterised by insoluble, brown, polymeric deposits, an intermediate region in which reaction zone responses were not fully developed, and healthy wood (see optical section). PIXE maps of potassium (K), calcium (Ca), manganese (Mn), iron (Fe), and zinc (Zn) show the accumulation of these elements in the discolored reaction zone. Potassium concentrations are also elevated in the intermediate tissues. Field = 750 μm.

Table 2. Elemental concentrations measured using PIXE (Kramer et al. 1997) from a branch collar reaction zone in beech (*Fagus sylvatica*). Mean elemental concentrations were calculated from the delineated areas (below) from the mapping data sets illustrated in Figure 6.

Region[*]	Elemental concentration (ppm)									
	Ca	K	Mn	Fe	Zn	Mg	Na	Cl	P	S
Healthy wood	1272	1218	192	32	<14	906	3220	3360	155	259
Reaction zone	7784	3090	852	65	88	3065	3679	3893	182	393

*Diagrammatic representation of data acquisition areas from PIXE maps shown in Figure 6.

to barrier function by resisting degradation by wood decay fungi (Pearce and Rutherford 1981; Pearce 1989) or by acting as a hydraulic seal, but cannot alone form a continuous reaction zone barrier because the suberin polymer is only deposited from living cells. It occurs as tyloses or vessel-lining material, where it may block fungal spread along vessels, which provide channels for the rapid axial extension of lesions, or may be deposited on the walls of living parenchyma cells. Once fully differentiated, nonliving cell types such as xylem fibers do not become suberized, although if compromised before differentiation is complete, they may undergo this response (Biggs 1987; Pearce 1990). A zone of morphologically continuous suberization is, however, formed at the compartmentalization wall 4 barrier, where a circumferential sheet of axial parenchyma cells is laid down following a major wound and may suberize to form an exceptionally durable barrier to the outwards spread of decay (Pearce and Rutherford 1981; Pearce 1987, 1996). In reaction zones of suberizing species such as beech, phenolic polymers are commonly present also and may fulfill a defensive function by protecting those cell walls that cannot be reinforced by suberization.

In contrast, preliminary data from *Eucalyptus nitens* suggest that although tylosis formation and xylem suberization occur, many of the events characteristic of reaction zone formation in *A. pseudoplatanus* are poorly developed (Barry et al. 1998). Although much further work is required, it is clear that the process of reaction zone formation is not essentially identical in all woody species, and that in certain species such factors as microenvironmental conditions (*cf.* Boddy and Rayner 1983; Rayner 1986; Rayner and Boddy 1988; Boddy 1992) may have a primary role in protecting functional sapwood, with reduced involvement of active defense,

at least during the initial stages of the tree-pathogen interaction.

ARBORICULTURAL IMPLICATIONS

Our developing understanding of the interactions between trees and decay fungi does not yet allow us to prescribe the optimal strategy to prevent the ingress and development of decay in trees. However, the results confirm the wisdom of many currently recommended practices for pruning and the management of decay that seek to avoid compromising the trees' endogenous defenses. The identification of mechanisms by which reaction zones could protect healthy sapwood and act as barriers to the spread of decay fungi supports the interpretation that they have a protective function and indicates that breaching any such barriers during tree management adds to the risk of further decay development in the tree.

In *A. pseudoplatanus*, the process of reaction zone formation is initiated soon after wounding and fungal inoculation (an essentially inevitable accompaniment of wounding in nature), even if visually recognizable reaction zones are not formed until days or weeks later. Much of the risk of sapwood infection may, therefore, be determined within the first few days after wounding, and protective treatments that accelerate or stimulate tree responses have the potential to reduce the establishment of infection in sapwood. However, nonliving heartwood, which cannot respond actively to infection, is always likely to be vulnerable to the entry of decay when exposed by wounds.

A better understanding of the nature and dynamics of defensive responses in different species may provide pointers towards the durability of the protection conferred and the likely progress of decay in those species. Similarly, temporal analysis of the tree's defense responses may identify favorable times for tree management operations, or unfavorable times that are more likely to allow the ingress of infection. Seasonal differences in susceptibility to fungal attack (Spiers et al. 1998) may be attributable, in part at least, to alterations in the efficacy of endogenous defense. Such changes could arise from seasonal alterations in the availability of starch reserves

or changes in a tree's internal microenvironment, which may influence the ability of the plant to establish durable defensive barriers. Some of the effects of stress on tree health may prove to be similarly explicable; for example drought stress might impair the ability of compromised xylem to re-wet—apparently an important stage in the formation of a structurally continuous reaction zone barrier.

An understanding of the defense processes in trees may also facilitate the development of accelerated methods for screening trees for disease resistance for use in tree improvement programs and may contribute to the development of chemical or biological treatments for boosting a tree's ability to protect itself against the entry of pathogens following pruning or other wounding. Similarly, an understanding of the physiological and biochemical basis of resistance will be a prerequisite if genetic engineering is ever used to enhance the disease resistance of plantation or amenity trees.

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—Editor

Résumé. Les hypothèses majeures qui ont été proposées pour expliquer les patrons de développement de la carie et sa restriction dans le bois (xylème) des arbres vivants sont présentées brièvement. La compréhension courante des événements biochimiques et physiologiques qui contribuent à la protection du bois d'aubier fonctionnel déjà existant est revue, et ce avec une référence particulière à la formation des zones de réaction sur l'interface hôte-pathogène des espèces d'Acer, plus spécialement avec l'érable sycomore (*Acer pseudoplatanus*) dans lequel les interactions entre le bois infecté et l'aubier ont été analysés intensivement. Des études employant des approches anatomiques et biochimiques conventionnelles ont été intégrées avec l'application de techniques physiques avancées (imagerie par résonance magnétique nucléaire, émission protonique induite par rayons X, micro-analyse et cartographie, spectroscopie par résonance électronique paramagnétique), permettant ainsi de proposer un modèle descriptif de développement et de fonctionnement des zones de réaction chez cette espèce. Les résultats d'autres espèces d'angiospermes indiquent que certaines des zones de réactions sont essentiellement similaires, mais que pour d'autres espèces il peut y avoir des différences significatives. Les implications du développement de notre compréhension des défenses antimicrobiennes des arbres sur la pratique de l'arboriculture sont discutées brièvement.

Zusammenfassung. Hier werden die Hauptthesen zur Entwicklung von Fäulnis in lebenden Bäumen und die Begrenzung im Xylem kurz dargestellt. Das gegenwärtige Verständnis der biochemischen und physiologischen Vorgänge, die zum Schutz des bereits existierenden saftleitenden Holzez beitragen, wird hier mit Referenz auf die Bildung von Reaktionszonen an infizierten Acer-Arten, insbesondere des Bergahorns (*Acer pseudoplatanus*), bei dem die Interaktionen zwischen holzzerstörenden Pilzen und des Splintholzes genau untersucht wurde, vorgestellt. Studien, die mit konventionellen anatonischen und biochemischen Methoden arbeiten, wurden mit neuartigen physikalischen Methoden (Nuklear Magnetic Resonanz (NMR) Darstellung, Mikroanalyse und Aufzeichnung von protoneninduzierter Röntgenstrahlen-emission (PIXE) und eine Spektroskopie der Elektron Paramagnetic Resonanz (EPR) integriert, um ein Modell zu entwickeln, welches die Entwicklung und Funktion von Reaktionszonen bei dieser Baumart aufzeigt. Die Ergebnisse von anderen Angiospermata zeigen, daß bei einigen (z.B. Europ. Buche) die Reaktionszonen grundsätzlich gleich sind, aber daß bei anderen auch deutliche Unterschiede bestehen. Die Auswirkungen unseres wachsenden Verständnisses von mikrobiellen Verteidigungssystemen bei Bäumen auf die praktische Arbeit von Arboristen wurde hier kurz diskutiert.

Resumen. Son esbozadas brevemente las hipótesis principales que han sido propuestas para explicar los patrones de desarrollo del decaimiento y su restricción en la madera (xilema) de árboles vivos. Es revisada la comprensión actual de los eventos bioquímicos y fisiológicos que contribuyen a la protección del xilema funcional preexistente, con particular referencia en la formación de las zonas de reacción en la interfase hospedero-patógeno en especies de Acer, especialmente el sicomoro europeo (*Acer pseudoplatanus*) en el cual las interacciones entre madera-hongos y albura han sido investigadas extensivamente. Los estudios que integran aproximaciones anatómicas y bioquímicas han sido integrados con la aplicación de avanzadas técnicas físicas (resonancia magnética nuclear (NMR), microanálisis y mapeo de emisión de protones de rayos X inducidos (PIXE) y espectroscopía de resonancia electrónica paramagnética (EPR), seguidos de un modelo que describe el desarrollo y función de las zonas de reacción en las especies propuestas. Los resultados de otras angiospermas leñosas indican que algunas zonas de reacción pueden ser esencialmente similares, pero que en otras especies pueden haber diferencias significativas. Son discutidas brevemente las implicaciones en la práctica de la arboricultura sobre nuestro conocimiento