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WOUND REACTIONS IN BAMBOO CULMS AND RHIZOMES*

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WEINER, G. & LIESE, W. 1997. Wound reactions in bamboo culms and rhizomes. Bamboo culms and rhizomes respond to wounds in order to protect the surrounding tissues against damaging influences through the wound surfaces. The defence arsenal consists of a number of cellular reactions such as closure of sieve tubes by callose, formation of slime and tyloses, phenolics, suberised wall layers, wall lignification and also septa development in fibres. These responses are similar to those in hardwoods, but due to lack of a secondary meristem, neither a barrier zone nor a callus for wound closing can be developed. There is also accumulation and mobilisation of starch around the wound, development of additional lamellae of the cell wall in parenchyma cells and fibres, and the formation of a suberin layer in vascular parenchyma cells. The spatial expansion of the wound reaction shows a distinct lateral boundary, but axially, it fades out gradually.

Key words: Bamboo - wound reactions - anatomy - culm - rhizome

WEINER, G. & LIESE, W. 1997. Reaksi kecederaan dalam rumpun dan rizom buluh. Rumpun buluh dan rizom buluh bertindakbalas terhadap kecederaan untuk melindungi tisu-tisu di sekelilingnya daripada pengaruh yang merosakkan melalui permukaan yang cedera. Ketahanan arsenal mengandungi sebilangan reaksi sel seperti penutupan tiub tapis oleh kalusa, pembentukan lendir dan tilosis, fenol, lapisan dinding bergabus, penligninan dinding dan juga perkembangan septa dalam gentian. Tindakbalas ini sama dengan yang terdapat dalam kayu keras, tetapi akibat kekurangan meristem sekunder, kedua-dua zon penghalang dan kalus bagi menutup kecederaan tidak dapat dikembangkan. Terdapat pengumpulan dan pergerakan kanji di sekeliling tempat yang cedera, perkembangan lamela tambahan dinding sel pada sel parenkima dan gentian, dan pembentukan lapisan gabus dalam sel parenkima vaskular. Pengembangan spatial bagi reaksi kecederaan menunjukkan batas sisi yang ketara, tetapi ia beransur-ansur hilang secara paksi.

Introduction

Plant organs have a natural protection against injury, like the bark for trees and the cortex for monocotyledons. If there is damage of the phloem and xylem, protective reactions restrict danger from invading air and micro-organisms. For dicotyledonous trees, defence mechanisms such as compartmentalisation and callus formation have been intensively investigated in recent years (e.g. Shigo & Marx 1977, Bauch *et al.* 1980, Shigo 1984,1994, Liese & Dujesiefken 1989, 1996, Bonsen & Kucera 1990, Schmitt & Liese 1990, Blanchette & Biggs 1992). The understanding of wound response was much enhanced by the CODIT Concept: Compartmentalisation of Decay in Trees (Shigo & Marx 1977).

**Dedicated to Professor Dr. Joseph Bauch on the occasion of his 60th birthday.*

Corresponding information about the reactions in monocotyledons is more meagre. El Hadidi (1969) investigated the wound healing process in some flowering plants, including monocotyledons. Wound responses were reported in the rhizome of bananas by Van der Molen *et al.* (1977) and in the stem of the royal palm *(Roystonea regia)* by Weiner and Liese (1995), but nothing is known about the defence mechanisms of bamboo. Its growth is completed within a few months, but the transport system has to function for a decade and longer. Although a bamboo culm appears rather resistant against physical damage due to its hard, siliceous cortex, insects can penetrate the culm wall to breed in the lacuna (Singh 1990, Kovacs & Azarae 1995). Moreover, a bamboo plant suffers seriously during the planting process. The common vegetative propagation by culm, branch or rhizome cuttings leads to considerable injuries. Rhizomes of leptomorph species are cut to limit growth. The upper crown of newly planted bamboos is often cut off to reduce respiration. In China the top part of the bamboo culms is removed as a routine operation to avoid snow breakage and to utilise additional material. Also injuries, as during harvesting, cannot be excluded. In each case, the transport of water and sap in the vascular bundles is interrupted. Bamboo as a monocotyledon cannot develop new cellular pathways or a callus for wound closure due to lack of a secondary meristem. Nevertheless, the damaging influence of the invading air must be efficiently blocked off to protect the surrounding tissue. Even branches must have such defence mechanisms to seal off a dying part from the remaining culm.

The reactions of bamboo were therefore investigated on artificial set wounds at the culm and rhizome of a number of species, and also at broken branches.

Material and methods

For this study , 380 bamboo samples belonging to 11 genera were examined (Table 1). The bamboo culms were of different ages and from two different climatic locations. Wounds of 2-4 mm^2 were set with a drilling machine in the middle of an internode, at a basal node and in the rhizome at different times of the year (Figure 1). The evaluation of response between wounding and sampling varied between one day and 360 days. Table 1 and Figure 1 present details of the wounding procedure. As a control, an unwounded culm from each species was prepared in the same way as the wounded material.

For light microscopy (LM) all wounded tissues with an adjoining part above and below were cut, fixed and stored in 4% formaldehyde at 4 °C. Longitudinal sections around a wound were cut with a sliding microtome. For general observations, the sections were double-stained with acridine/chrysoidine red and astra blue. For fluorochroming, an aqueous 0.1% solution of acridine orange was used. Suberin was tested with sudan III+IV, callose "plugs" with aniline blue and starch with Lugol's solution. Ruthenium red reacted with pectinophile substances, iron chloride (FeCrIII) with phenolic substances. Further, phloroglucin/HCL indicated lignified cell walls. All sections were embedded in glycerine and examined with an Olympus BH2 microscope equipped with fluorescence .

Table 1. Locations and preparation of the investigated material

Bamboo species	Location	Plant age (y)	Wound area	Season of sampling	Observation after wounding (days)	Method of investigation
Phyllostachys heteroclada *Pleioblastus maculatus* *Pseudosasa amabilis*	Nanjing/China	3 - 4	15. I	Oct. - Dec. 1992	3, 7, 14 21, 28 40, 51	LM, longitudinal
Semiarundinaria fastuosa *Phyllostachys viridiglaucescens*	Bot. Garden, HH	1 - 2	4. and 9. I.	May - June 1993	1, 3, 7, 10, 14 21, 29	LM, longitudinal
Arundinaria fastuosa *Chusquea quielea* *Fargesia muriela* *Phyllostachys decora* *Phyllostachys flexuosa* *Phyllostachys nigra* *Phyllostachys propinqua* *Phyllostachys quilio* *Phyllostachys rubromarginata* *Sasa palmata* *Semiarundinaria fastuosa* *Sinarundinaria nitida* *Thamnocalamus spathaceus*	Bot. Garden, HH	2 - 3	15. I.	June 1993	7, 14	LM, transverse
Chusquea quielea *Sasa palmata*	Bot. Garden, HH	Culm from 1993	2. N. and 15. I. 4. N. and 9. I.	Aug. - Sept. 1993	1, 3, 7, 10, 14, 21, 28	LM, longitudinal
Semiarundinaria fastuosa			2. N. and 9. I.			
Dendrocalamus spp.	Greenhouse, BFH	2 and 4	Upper 3. I.	June 1993	7, 14	
Sinarundinaria nitida	BFH	2 - 3	15. I.	July 1993	1, 3, 7, 10, 14, 21, 28	LM, longitudinal

(continued)

Table 1 (continued)

Chusquea quielea *Phyllostachys viridiglaucescens* *Semiarundinaria fastuosa*	Bot. Garden, HH	2 - 3	15. I. 9. I. 9. I.	June 93 - June 94	360	LM, longitudinal
Thamnocalamus spathaceus *Phyllostachys quilio*	Bot. Garden, HH	1	9. I.	May - Aug. 1994	Each 7 days up to 90 days	LM, longitudinal
Phyllostachys viridiglaucescens	Bot. Garden, HH	3 - 4	4. N. and 9. N.	May 1994	7, 14, 21	LM, longitudinal
Phyllostachys pubescens	Nanjing/China		Rhizome	Aug. - Sept. 94	1, 3, 7, 14 21, 28, 42	LM, transverse
Sinarundinaria nitida	BFH, HH	1	9. + 15. I.	April - May 1994	3, 7, 14, 21, 28	TEM, transverse and longitudinal
Phyllostachys viridiglaucescens	Bot. Garden, Greenhouse, HH	1 - 2	9. I. 9. I.	Dec. 94 - Jan. 95 Jan. - Feb. 95	7, 14, 21, 28	TEM, transverse TEM, transverse

BFH = Bundesforschungsanstalt für Forst - u. Holzwirtschaft, HH = Hamburg, I. = internode, N. = node, LM = light microscope, TEM = transmission electron microscope.

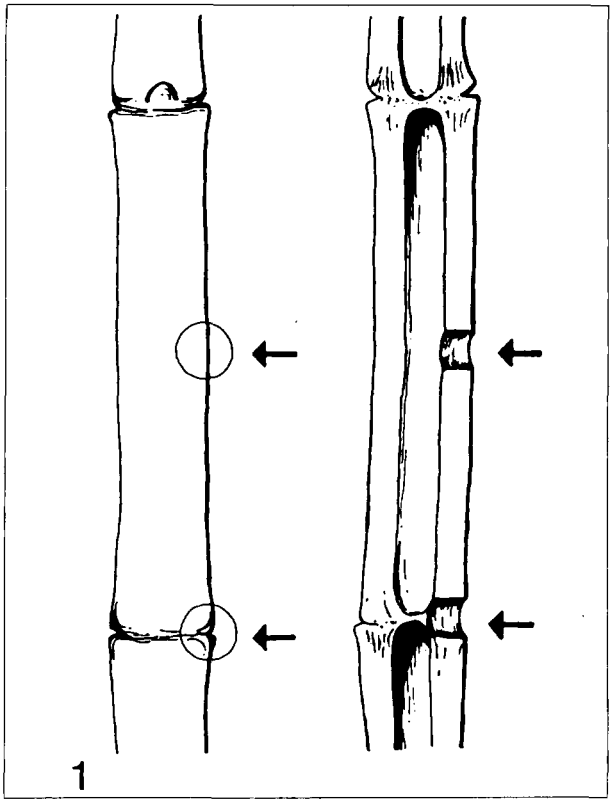

Figure 1. Wounding pattern in a bamboo culm at an internode and node

For transmission electron microscopy (TEM), small samples (1× 1 × 4 mm) around the wound area were processed. Samples were immersed for 3 days in Karnovsky's fixing solution (Karnovsky 1965), washed in 0.1M cacodylate buffer (pH 7.2), postfixed for 12 h in buffered 1% osmium tetroxide, washed again in buffer, dehydrated in a graded series of acetone, and embedded in Spurr's epoxy resin (Spurr 1969). Ultra-thin sections were poststained with uranyl acetate/lead citrate and examined with a Phillips CM12 transmission electron microscope.

Results

Macroscopy

After 7 days, all wounded culms showed a dark, narrow, round discoloration along the wound, both on the epidermis and more noticeably on the inner culm side. With time the discoloration expanded axially on the epidermis variably, e.g. in *Phyllostachys* as a short, thin strip and in *Chusquea* over the whole internode. In the lateral direction, the browning was often limited to only about 1.5 mm. Some species showed sporadically bleached spots. On the inner side of the culm, the discoloration increased with wounding time in all directions. After 360 days, the

whole inner surface of the wound internode from *Phyllostachys* and *Semiarundinaria* species was brown-black.

Light microscopy observations (LM)

An overview of reactions of individual cell types after wounding is given in Table 2.

Table 2. Wound reactions of the various cell types of a bamboo culm

Cell type	Wound reaction
Sieve tubes	Closing of sieve plates with 'plug' (callose) Formation of slime Lignification of sieve tubes Formation of phenolics
Metaxylem-vessels:	Formation of slime Partial formation of tyloses Formation of phenolics
Protoxylem-tracheids:	Formation of slime Formation of tyloses
Vascular bundle parenchyma	Accumulation of starch Formation of slime Partial formation of phenolics Formation of suberin Formation of additional cell wall layers
Ground parenchyma short cells	Lignification Formation of phenolics
Longitudinal cells	Accumulation of starch Formation of phenolics Formation of additional cell wall layers
Fibres	Fibres with starch Formation of septa Formation of additional cell wall layers

Internode

There were no significant intergeneric differences in wound response regardless of time of year. Leptomorph and pachymorph bamboos exhibited an identical response. General observations were as follows.

One day after wounding there were no tissue reactions. On the third day, all samples showed blockage formation ('plug') of their sieve plates (Figure 2). These reactions then expanded in the apical and basal directions.

After 7 days, a small slime layer was generally present in the parenchyma cells of the vascular bundle and in the metaxylem vessels for a distance of about 5 mm from the wound edge. In *Sasa* and *Semiarundinaria* this had developed after 3 days. In the ground parenchyma short cells became lignified at the wound edge. Longitudinal cells appeared brownish. At a distance of 3 mm increasing starch content was obvious in these cells in contrast to samples from the first and third days.

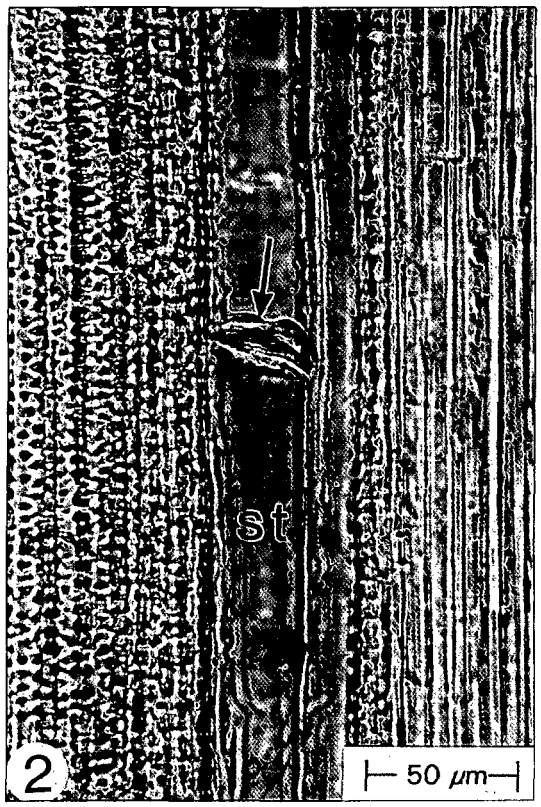

Figure 2. *Phyllostachys viridiglaucescens* culm, LM, longitudinal section, 3 days after wounding. Stained with acridin/ chrysoidine red and astra blue. Sieve tubes (st) with 'plugs' (arrow).

After 10 days, all cells at the wound edge were discolored, sieve tubes were lignified and vascular bundle parenchyma and metaxylem vessels were filled with pectinaceous slime (Figure 3). In some *Pleioblastus, Pseudosasa, Sasa, Semiarundinaria, Sinarundinaria* and *Thamnocalamus* spp., tyloses had also developed in the metaxylem vessels. The protoxylem tracheids, in contrast, showed tyloses in all specimens from all species and also in the controls.

After 14 days, phenolics were present as a thin layer in sieve tubes. The reactions of sieve tubes showed a distinct axial gradient from the wound edge: phenolics up to 5 mm, liginification up to 10 mm and 'plugs' in unlignified sieve tubes as far as 20-25 mm. In the ground parenchyma short and longitudinal cells had phenolics at the wound edge, further away short cells were lignified while longitudinal cells contained starch.

After 21 days, phenolics were concentrated up to 10 mm from the wound edge in sieve tubes, vascular bundle parenchyma and ground parenchyma cells. Short cells were completely filled up (Figure 4). Further away, at 20 mm, slime was present in vascular bundle parenchyma and metaxylem vessels, even in lignified sieve tubes

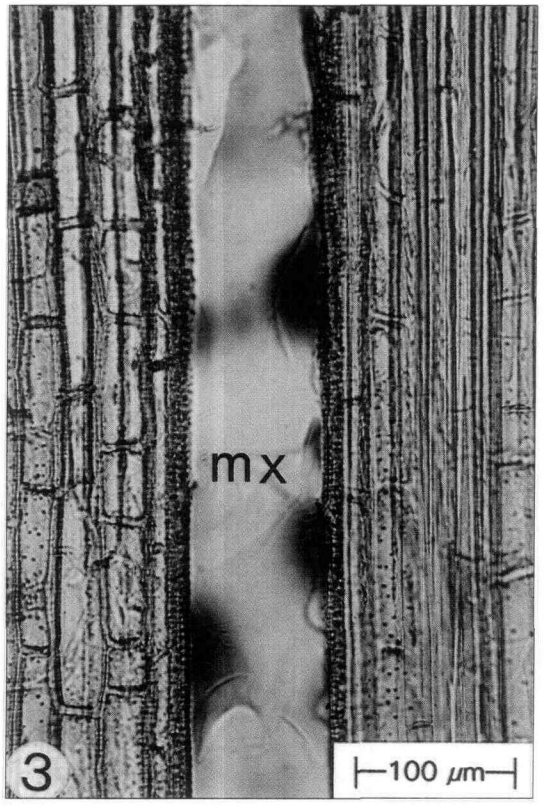

Figure 3. *Dendrocalamus* spp. culm, LM, longitudinal section, 3 days after wounding. Stained with astra blue. Metaxylem vessel (mx) with slime.

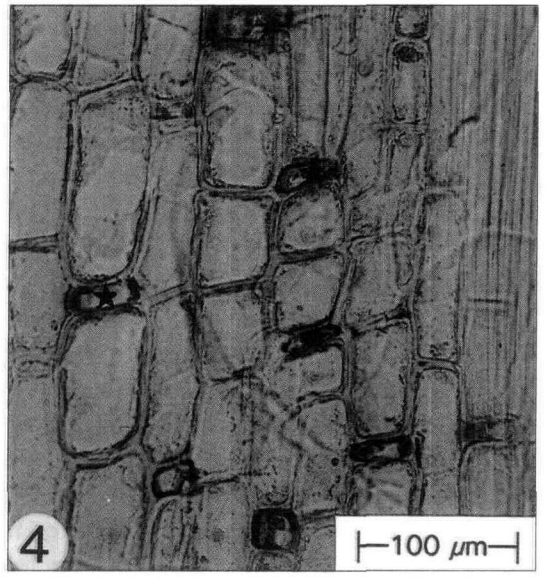

Figure 4. *Phyllostachys heteroclada* culm, LM, longitudinal section, 21 days after wounding. Stained with iron-chloride (FeCr III). Short cells of the ground parenchyma (*) with phenolic substances.

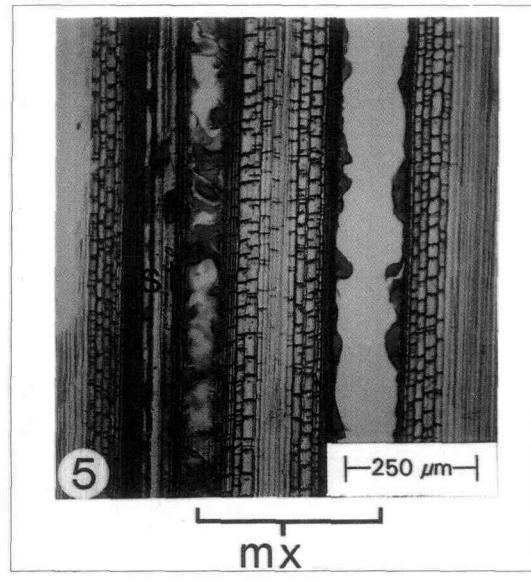

Figure 5. *Dendrocalamus* spp., culm, LM, longitudinal section, 21 days after wounding, 10-20 mm from the wound edge. Stained with acridin/chrysoidine red, astra blue and ruthenium red. Sieve tubes (st), vascular bundle parenchyma and metaxylem vessel (mx) with slime.

(Figure 5). The longitudinal parenchyma cells contained starch only in *Phyllostachys, Sasa, Semiarundinaria* and *Sinarundinaria* spp.

No additional wound reactions were found after 28 days, although lignification of sieve tubes and short parenchyma cells as well as slime in sieve tubes, vascular bundle parenchyma and metaxylem vessels extended further along the whole internode. However, in samples collected more than 56 days after wounding, a further reaction was observed. The longitudinal cells of the ground parenchyma in direct contact with vascular bundles formed additional cell wall layers (Figure 6). This reaction began about 5 mm from the wound edge, and exhibited the same intensity in basal and apical directions for about 50 mm over the entire cross section. These wall layers were unlignified at first but later lignified.

Observations of cellular reactions at broken branches (Figure 7) revealed similar results regarding 'plugs', slime, tyloses, phenolics and lignification. An additional reaction of parenchyma cells became obvious: at the break-off region the cells were brown discolored, whereas in a distance of 10 to 20 cells the nodal, isodiametrical parenchyma cells showed additional lignified wall layers. This extra thickening of parenchyma walls occurred over the whole cross section of a branch. In the longitudinal section a band of several cells across the branch could be distinguished (Figures 8a, b).

No structural reactions in the culm tissue due to wounding were noted in the samples taken after 90 days and 360 days. Suberin formation could not be detected by LM. No fungal hyphae were observed in the discolored area.

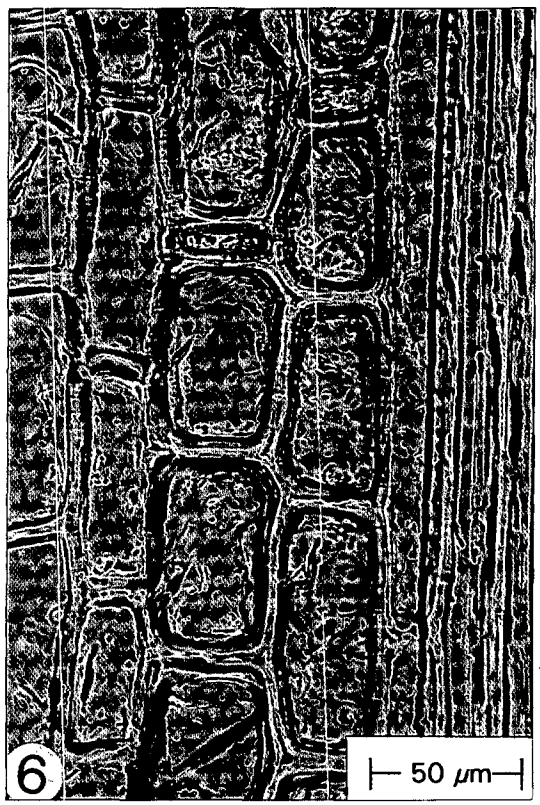

Figure 6. *Thamnocalamus spathaceus,* culm, LM, longitudinal section, 56 days after wounding. Stained with phloroglucin/HCl. Longitudinal cells of the ground parenchyma with additional lignified wall lamellae.

Node

The anatomical arrangement of the cells in a node is quite different from that in an internode (Ding & Liese 1995). Nevertheless, wounds in the node, nearby or in the diaphragm, caused similar tissue responses over the same time interval as for internode. Wound reactions were the same in the apical and basal directions, e.g. 21 days after wounding, *Phyllostachys* sieve tubes and metaxylem vessels contained slime in the internode above and below. The solid culm of *Chusquea* exhibited wound reactions over three internodes after 360 days.

Wound reactions were always strongly limited to injured tissue in the axial and lateral directions.

Rhizome

Wound reactions of the rhizome were investigated in *Phyllostachys pubescens* from China (Ding *et al.* 1997). Three days after wounding, slime was found in vascular bundle parenchyma and metaxylem vessels. Large intercellular spaces alongside

short parenchyma cells were filled with a brown-black substance, something which was not observed in the culm internode. After 7 days, a separation appeared in transverse section between 'wound modified' and 'undamaged' vascular bundles (Figure 9). In the former, sieve tubes and short parenchyma cells showed phenolics and became lignified and the metaxylem vessels occluded with slime. Around the 'undamaged' vascular bundles, short cells and sieve tubes remained unlignified, while the vessels were free of slime. Between 'wound modified' and 'undamaged' vascular bundles a zonation appeared, due to some longitudinal parenchyma cells developing additional wall layers. These new lamellae appeared partly unlignified. After 14 days, the demarcation zone was clear and consisted of longitudinal parenchyma cells with extra wall layers. Thus, wound-modified tissue became separated from uninjured ones. Also fibres evinced wall thickening as a wound reaction, especially that of vascular bundles in direct contact with the ground tissue. In the wound-modified zone, ground parenchyma cells had collapsed.

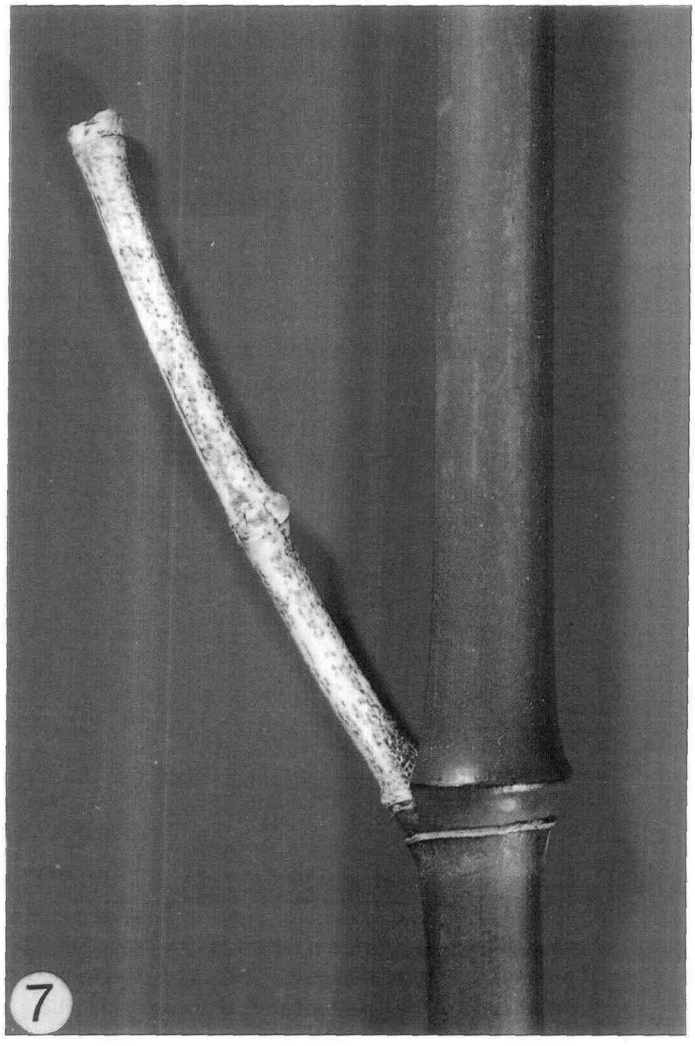

Figure 7. *Phyllostachys quilio* culm with dead branch

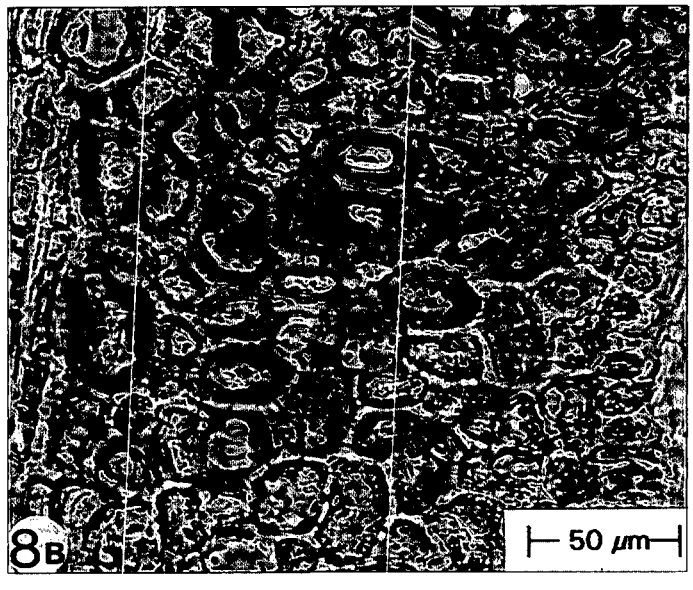

Figure 8. *Phyllostachys quilio*, LM. a) Longitudinal section: branch stub, parenchyma cells with additional lignified wall lamellae. b) Detail, stained with phloroglucin/HCl.

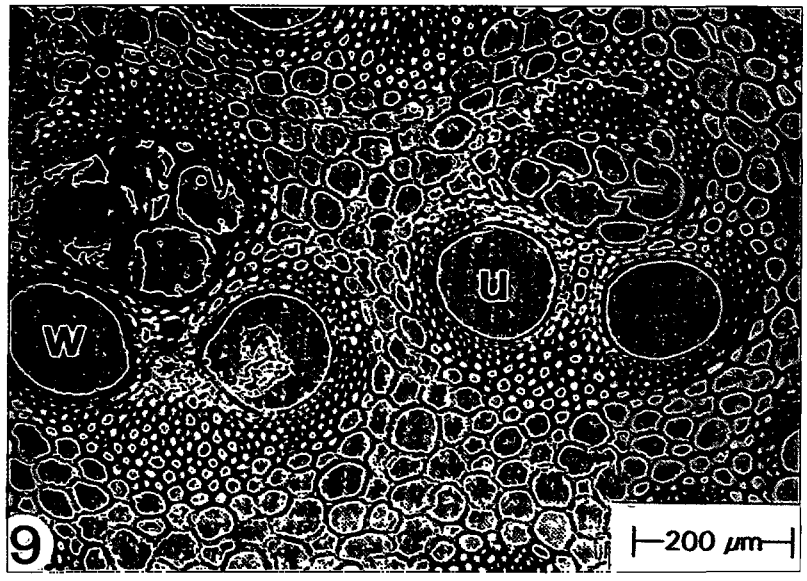

Figure 9. *Phyllostachys pubescens* rhizome, LM, transverse section, 7 days after wounding. Stained with acridin/chrysoidine red, astra blue and ruthenium red. 'Wound modified' (w) and 'undamaged' (u) vascular bundles.

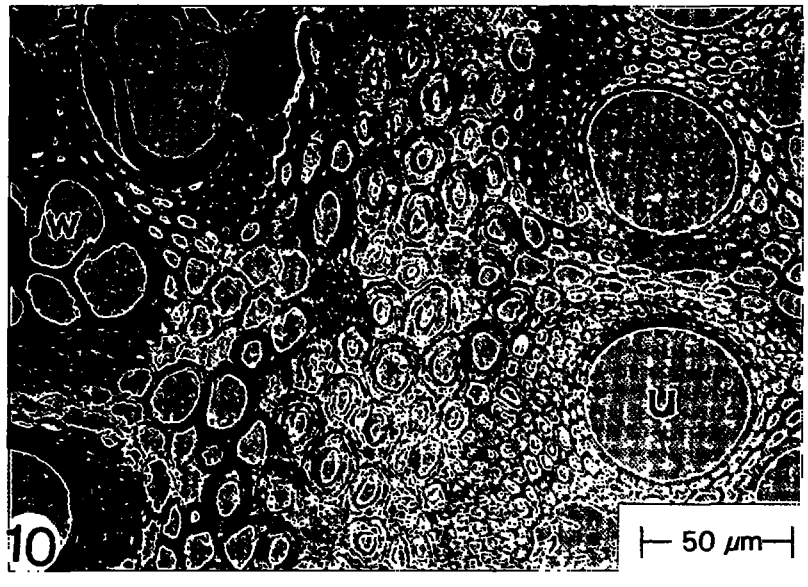

Figure 10. *Phyllostachys pubescens* rhizome, LM, transverse section, 14 days after wounding. Stained with acridin/chrysoidine red, astra blue and ruthenium red. Demarcation between 'wound modified' (w) and 'undamaged' (u) tissue formed by additional lignified cell walls in longitudinal parenchyma cells and fibres.

After 28 days, the longitudinal parenchyma cells showed a demarcation zone with thickened polylamellate cell walls, all of which were now lignified (Figure 10). The vascular bundles within this zone appeared inactive, sieve tubes were lignified and incrusted with phenolics, as also were vascular bundle parenchyma and metaxylem vessels. After 42 days, no further tissue reactions were obvious. As in the culms, no fungal hyphae were observed in the injured rhizomes .

Transmission electron microscopy observations (TEM)

Observations were undertaken with the TEM to obtain more insight into the additional cell wall thickening.

Samples from *Sinarundinaria* and *Phyllostachys* 7 days after wounding showed that all cells within 2 mm from the wound edge had collapsed. From 3 - 7 mm further away vascular bundle parenchyma had become filled with slime. These substances had extruded from parenchyma cells through pit membranes into adjacent metaxylem vessels (Figure 11). After 14 days, an additional cell wall layer

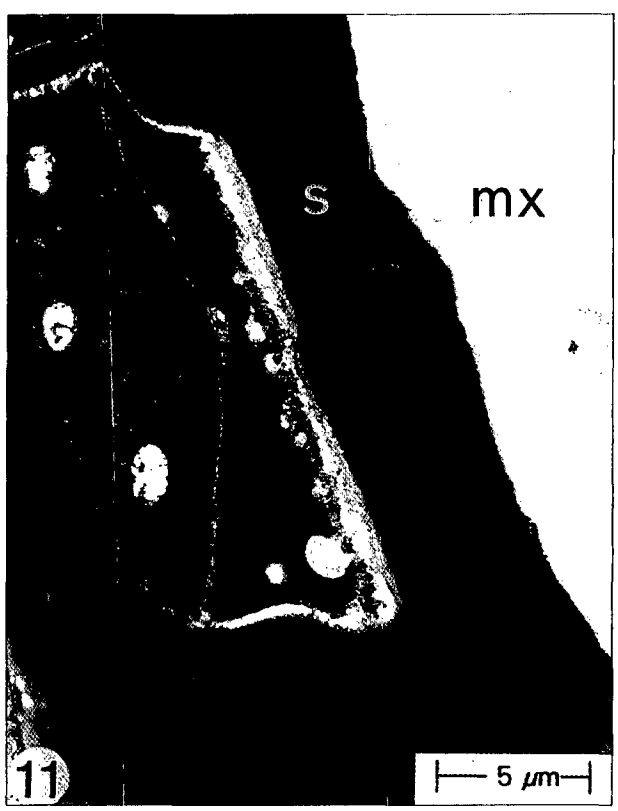

Figure 11. *Phyllostachys viridiglaucescens* culm, TEM, transverse section, 7 days after wounding. Contact parenchyma secretes slime (s) into metaxylem vessel (mx).

became apparent in the vascular bundle parenchyma. This layer appeared bright and laminated, characteristic of suberin (Figure 12). The suberin layer had a thickness of around 70 nm and adjoined the secondary cell wall beyond a thin dark contrasted intermediate layer. After 21 - 28 days, a further cell wall layer formed the suberin layer. Between these two layers – suberin and cell wall – again a thin intermediate layer was found (Figures 13a,b). The thickness of this additional unlignified wall layer was variable. The formation of such suberised wall layers was observed in the vascular bundle parenchyma and also in the longitudinal cells of the ground parenchyma. A peripheral cytoplasm indicates the viability of these cells.

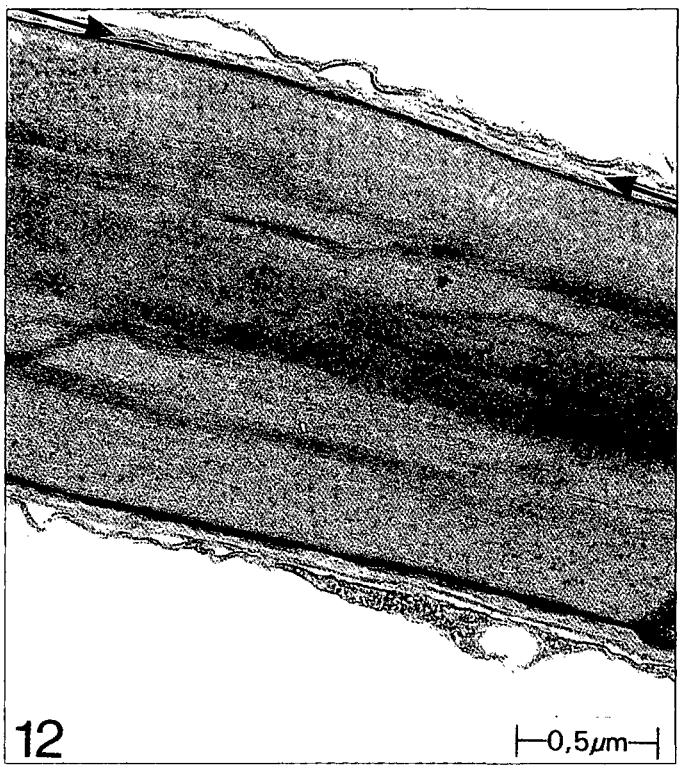

Figure 12. *Phyllostachys viridiglaucescens* culm, TEM, transverse section, 14 days after wounding. Contact parenchyma cell wall with suberin layer (arrow) and darker 'transition layer'.

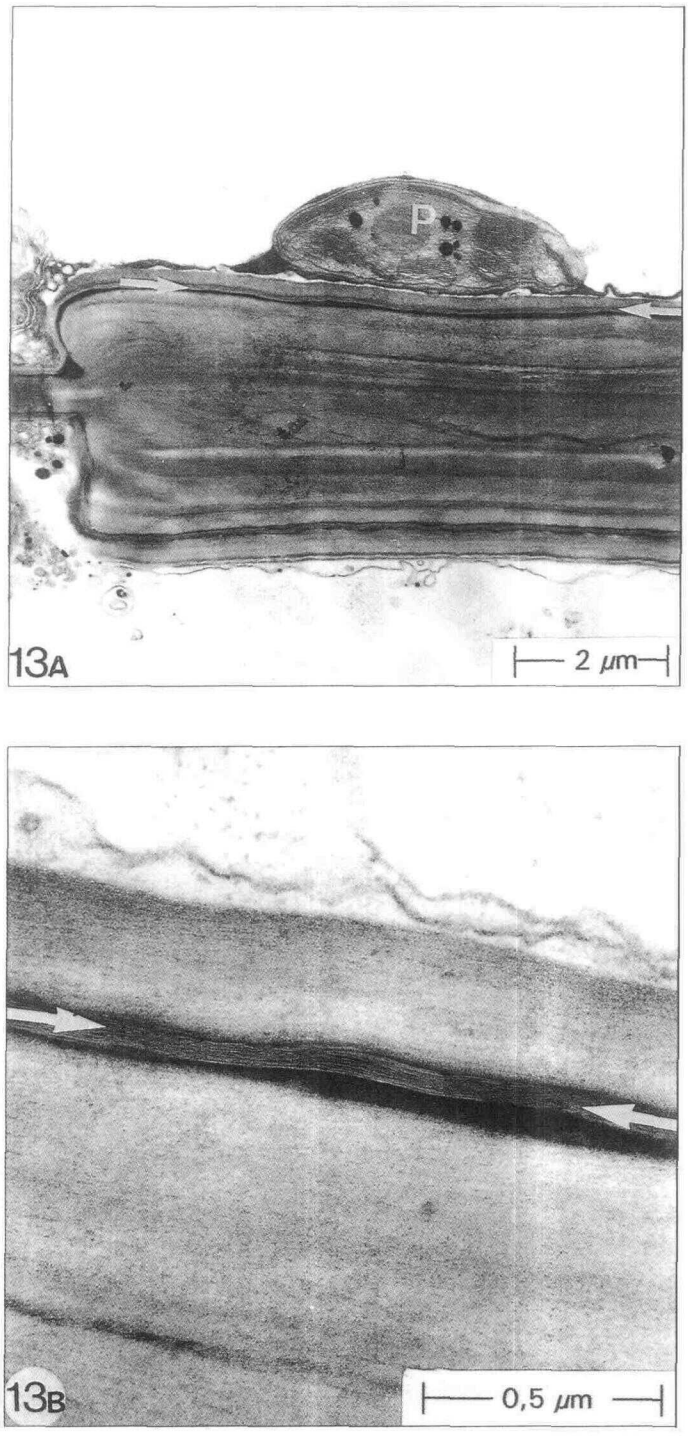

Figure 13. *Phyllostachys viridiglaucescens,* culm, TEM, transverse section, 21 days after wounding. a) Contact parenchyma cell with suberin (arrow) and additional cell wall lamellae and thin wall attached cytoplasm (p = plastid). b) Detail, wall with suberin layer (arrow) and additional wall lamellae.

Discussion

The results provide the first detailed analysis of wound reactions of bamboo. They may be general in monocotyledons. These were definite wound responses protecting functional tissue against air and micro-organism invasion. The defence arsenal consists of quite a number of cellular reactions, the closure of sieve tubes by callose, the formation of slime and tyloses, phenolics, suberised wall layers, wall lignification and also septa development in fibres. El Hadidi (1969) observed a healing reaction through the formation of lignified parenchyma. Beckmann (1969) and Van der Molen *et al.* (1977) described vascular pectinaceous gel formation in wilt-diseased banana roots The term 'gel' and our usage of the term 'slime' appear synonymous. A detailed analysis of wound reactions in a stem of the royal palm (*Roystonea regia*) also revealed slime, tyloses, phenolics and septa formation (Weiner & Liese 1995).

The responses observed in monocotyledons are similar to those of hardwood species (e.g. Pearce & Rutherford 1981, Dujesiefken *et al.* 1989, Trockenbrodt & Liese 1991, Blanchette & Biggs 1992, Schmitt & Liese 1993, 1995, Liese & Dujesiefken 1996). However, two additional phenomena were seen in the injured bamboos: starch granulae accumulated in parenchyma cells and also fibres. These were mobilised later. Furthermore, parenchyma as well as fibres showed cell wall thickening by developing additional lamellae, at first unlignified but later lignified. Suberinisation is a well known response in dicotyledons (Biggs 1987), but is hardly known in monocotyledons. Observations of bamboo here revealed the development of a suberin layer in vascular bundle parenchyma as well as in ground parenchyma. In hardwoods, however, this layer appears to be a final lamella before cell death (Schmitt & Liese 1993); in bamboo culms an additional wall layer is developed on the suberin layer and a pheripheral cytoplasm is present.

These reactions occurred in all the bamboos investigated, both leptomorph and pachymorph with minor modifications in time sequence. Only the formation of tyloses into the metaxylem vessels exhibited differences between species, since some such as *Chusquea quilea, Phyllostachys heteroclada* and *Dendrocalamus* spp. did not show these outgrowths from parenchyma into the metaxylem vessels. Also hardwoods do not develop tyloses in all their species, which has been attributed to the diameter of the pit aperture. Protoxylem tracheids always exhibited tyloses. This reaction cannot be considered a wound response because it is present even in controls.

Whereas the extension of wound response was much limited laterally, the axial extent increased with time. The latter could halt either in an internode, above a node or extend even through into the adjacent internodes.

The year-long observation time reported here showed that the extension of the wound reaction was efficiently stopped and that functional tissue was thus protected against further inactivation. A peculiar feature occurred in the rhizome, where living tissue was separated from the inactivated tissue by a layer of parenchyma cells with thickened walls. Such a demarcation was also observed in dying branches.

Due to the lack of a secondary meristem, bamboos, as all monocotyledons, cannot form a barrier zone by developing a callus to close a wound. In comparison with the CODIT-model of Shigo and Marx (1977), no given structural boundaries lead to wall 2 by ray cells or to wall 3 by growth rhythms or parenchyma. The term 'compartmentalisation' appears therefore not suitable for the defence system of bamboo, as shown also for the royal palm (Weiner & Liese 1995). The terms 'wall off' or 'seal off' were used by Shigo (1994) for observations on cross sections of the solitare palm (*Ptychosperma elegans*). Wounded bamboo culms also show a limitation of the wound response laterally, but not a defined axial blocking of the wound influence. These wound reactions resemble more a gradual 'fading out' of the cellular response.

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