MECHANICAL STRESS AS STIMULUS FOR STRUCTURALLY AND CHEMICALLY ALTERED WALLS IN WOOD XYLEM CELLS

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SUMMARY

Cell walls in woody tissues affected by mechanical stress often display structural and chemical modifications. Electron microscopy and UV-microspectrophotometry were used to study modifications in the secondary xylem tissues caused by wounding and exposure to extreme wind. Wounding of hardwoods initiates wall modifications in already differentiated as well as differentiating xylem. Modifications include atypical wall architecture, increase in lignin content, and partial incorporation of phenolic compounds. In spruce trees, exposure to extreme wind often leads to the formation of so called "Wulstholz" on the compression side of bent trees. Walls of "Wulstholz" tracheids are mainly characterized by thickening of their secondary walls and also by an increasing lignin content. Modification of cell walls, as a response to mechanical stress, are a part of tree survival strategies.

Key words: Tree xylem, wounding, wind exposure, cell wall modification, light and electron microscopy, UV-microspectrophotometry.

INTRODUCTION

Mechanical stress on tree stems, such as xylem wounding and pronounced sporadic bending from extreme wind exposure, variously affect certain wood portions and are responsible for the initiation of responses. In case of xylem wounding, passive resistance of structures existing at the time of wounding, e.g. cell walls, pits and rays, can be identified, which mainly restrict the rapid spread of air embolism and desiccation. Active responses are initiated in living cells around the wound, i.e., in xylem parenchyma cells. These cells to a large extent contribute, with their modified metabolic activities, to the compartmentalization of xylem tissue surrounding the wound, which finally leads to a restriction of deleterious effects, including invasion of micro-organisms (e.g. Shigo & Marx 1977; Shortle 1979; Dujesiefken & Liese 2006). Cell walls in such tissues often display structural modifications, such as encrustation or deposition of additional layers (Schmitt & Liese 1991, 1993; Melcher et al. 2003; Frankenstein & Schmitt 2006). Also hardwood pit membranes between parenchyma cells and neighbouring vessels or fibres frequently show distinct structural and chemical modifications (Schmitt & Liese 1992). Beside these reactions in differentiated xylem tissue, differentiating xylem cells at or close to the wound surface undergo altered cell development, which also becomes obvious mainly at the cell wall level (Frankenstein & Schmitt 2006). Furthermore, cambial and phloem parenchyma cells respond to mechanical injuries for restoring the cambial zone and building up callus tissue for successive closure of the wound surface in subsequent years (Grünwald et al. 2002; Frankenstein et al. 2005).

Bending of a tree stem by wind is another type of mechanical stress, which can mostly be compensated by the natural elasticity of tree's woody tissues. However, extreme wind exposure may either cause stem fracture or destabilize xylem tissue by structural damages that are observable already at the macroscopic level. At the microscopic level, slip plane formation in cell walls represents one of the most prominent fine structural characteristics of such structural damages (Koch et al. 1996, 2000). This type of injury is known to stimulate the cambial area to form response tissue, the so-called "Wulstholz".

The present paper summarizes observations made on above described xylem responses due to mechanical stress, resulting in modifications at the cell wall level, as obtained during the work on various research projects at the Federal Research Centre for Forestry and Forest Products and the University of Hamburg. Special emphasis is given to modifications at the fine structural level, as determined by conventional light and electron microscopy, as well as to topochemical analyses at the cell wall level carried out using UV-microspectrophotometry.

MATERIAL AND METHODS

For the investigations of xylem modifications due to wounding, branches (Fig. 1) and stems (Fig. 2) were wounded during the vegetation period. Analyses of cellular wound responses were carried out on various hardwood species, i.e., *Tilia americana* L., *Betula pendula* Roth., *Quercus robur* L., *Populus deltoides* L., *Populus tremula* L. *x P. tremuloides* Michx., *Fagus sylvatica* L., *Robinia pseudoacacia* L., and *Fraxinus excelsior* L.

Fig 1: Branches of *Tilia americana* with two types of wounding. Left: Wounding type for the determination of responses in axial direction. Right: Wounding type for the determination of responses in radial direction.

At the time of wounding, the experimental trees were 15-25 years old with the duration of wound responses from a few days up to 95 weeks. Responses of xylem parenchyma cells were analysed with branches (type of wounding see Fig. 1). Samples of wounded stem portions were collected from the lateral edge of wounds (type of wounding see Fig. 2).

To examine xylem modifications due to extreme wind exposure, 80 to 90 year-old spruce trees (*Picea abies* L. Karst.) from mountainous regions in Germany (altitude around 750 m a.s.l.) were selected. Experimental trees with pronounced "Wulstholz" came from sites in the state "Niedersachsen" in the northern part of Germany close to Göttingen ("Harz" region) and from the state "Sachsen" ("Erzgebirge" region) close to the Czech border. Climatological conditions at both sites were similar. Wind-stress situation for trees from the "Erzgebirge" region, however, was extreme due to the exposure to severe wind of the remaining trees after the decline and felling of numerous trees as a consequence of long-term SO_2 impact.

Fig. 2: Wounds on a poplar stem with dimensions of about 5x10 cm^2. After removal of the bark, remnants of the cambium and differentiating xylem tissue was also removed with a razor blade to avoid formation of surface callus tissue.

For light microscopy of "Wulstholz" tissue, 15µm sections were directly prepared with a sliding microtome with subsequent safranin and astrablue staining.

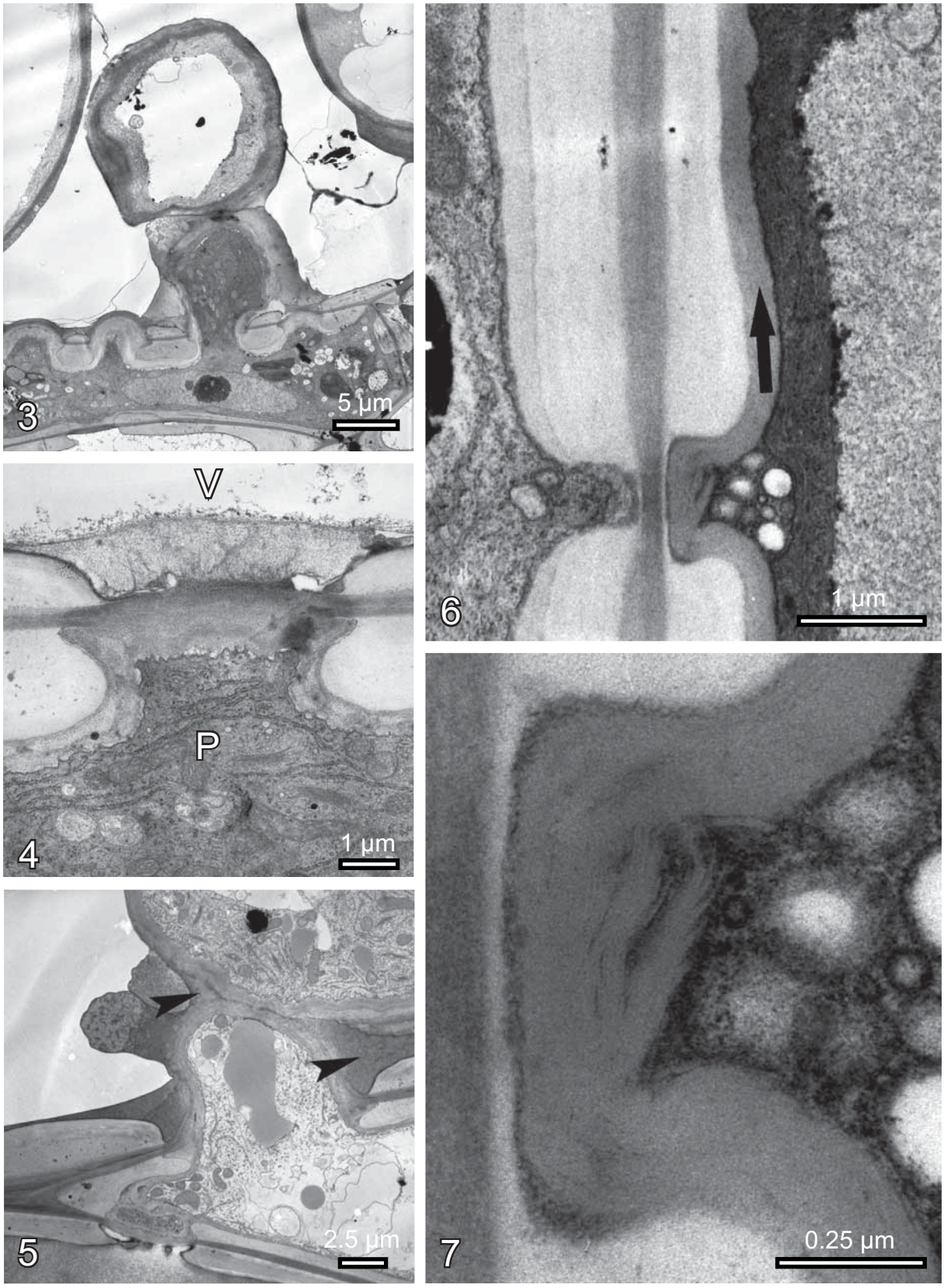
For transmission electron microscopy, branch samples of control and wound response tissue close to a wound were collected after responses of a few days up to several weeks. After dissecting, the samples were immediately fixed for one to two days in a cacodylate buffered paraformaldehyde-glutaraldehyde solution (Karnovsky 1965), osmicated for 12 hours in a 2% aqueous OsO_4 solution, dehydrated in a graded series of acetone and finally embedded in Spurr's epoxy resin. Sections were stained with uranyl acetate and lead citrate and examined with a Philips CM 12 TEM at an accelerating voltage of 80 or 100 kV. Samples of stem wounds were taken after response periods of 1-95 weeks; they were then processed as described above, except for osmication which was omitted. For section-staining, potassium permanganate was used according to Donaldson (1990) to reveal lignin distribution on a subcellular level (see also Schmitt & Melcher 2004). Sections were examined with the TEM at a lower accelerating voltage of 40 or 60 kV to enhance the contrast.

Topochemical studies for the determination of lignin distribution within cell walls were carried out with a ZEISS UMSP 80 UV-microspectrophotometer using 1µm thick sections of Spurr-embedded, unosmicated material. An integrated scanning system enabled analyses at a constant wavelength of 280nm for recording absorbance profiles (local resolution 0.25µm). Point analyses at a wavelength range of 240-700 nm (spot size 1 μm^2) were occasionally used to further indicate the quantitative lignin distribution in various cell wall portions.

RESULTS AND DISCUSSION

Wound-associated responses in differentiated xylem

In softwoods, initial wound responses are the deposition of resins on the wound surface and the blockage of bordered pits by aspiration (lateral displacement) of their centrally thickened membranes (review: Liese & Dujesiefken 1996; Dujesiefken & Liese 2006). Both types of wound responses rapidly restrict water loss and air embolism. Parenchyma cells may also be involved by producing tylosis-like structures protruding from parenchyma cells through pits into adjacent tracheids as observed in pine (Peters 1974, Oven et al. 2000). In hardwoods, xylem parenchyma cells are mainly responsible for active wound responses. Some hardwoods, such as oak, black locust and beech develop tyloses in their vessels (Fig. 3), which are outgrowths of ray or axial parenchyma cells through pits into adjacent vessels (e.g. Schmitt & Liese 1994).



Figs. 3-7: TEM micrographs of cellular wound responses. Fig. 3: Wound-associated tylosis formation in oak. Fig. 4: Early stage of wound-associated secretion of fibrillar/granular material from a parenchyma cell (P) into a vessel (V). Fig. 5: Wound-associated tylosis formation in a vessel and deposition of fibrillar/granular substances between tyloses (arrowheads). Fig. 6: Wall between parenchyma cells with suberin-like structure deposited on the secondary wall (arrows). Fig. 7: Detail of Fig. 6 showing the lamellar composition of the additional wall layer structurally resembling suberin.

Pit membranes between a parenchyma cell and a vessel become modified and represent initial cell walls of an enlarging tylosis extending into the vessel lumen.

Common to all hardwoods and intensively studied during the past decades (e.g. Hillis 1987; Blanchette & Biggs 1992; Schmitt & Liese 1990, 1993; Liese & Dujesiefken 1996; Pearce 2000) are reactions of parenchyma cells close to a wound. Parenchyma cells at or near the wound surface degenerate soon after wounding, whereas parenchyma cells behind are involved in the formation of a reaction zone for protection of the inner xylem. Such reaction tissue mostly appears as a discoloured zone around the wound. Parenchyma cells within this zone synthesize aromatic constituents, first accumulating as fibrillar or granular material mainly along the membranes of half-bordered pits of adjacent vessels and fibres. Simultaneously with a distinctly visible pit membrane modification, probably by dissolution of encrusting material, fibrillar/granular substances are later on secreted into the lumina of the neighbouring vessels and fibres (Fig. 4), which may completely block the conduction of water. Such a mechanism is solely responsible for blockage of vessels and often also of fibres in non-tylosis-forming species, such as birch, lime, poplar or maple and may also additionally occur in tylosis-forming species to fill spaces between individual tyloses within vessels, as regularly observed in oak (Fig. 5). A detailed chemical analysis of wound-associated deposits of lime trees revealed the presence of 5-hydroxy-calamenene, a sesquiterpene, which is well known for its antimicrobial activity (Melcher et al. 2003). Pearce (1996) listed the chemical classes of substances identified after wounding or fungal infection in the sapwood of several softwood and hardwood species, such as phenols, stilbenes, lignans, phenyl-propanoids, flavonoids and terpenoids. There is evidence that some of these substances are able to penetrate cell wall regions adjacent to lumen. All these reactions with deposition of phenolic compounds and tyloses formation are very intense within a narrow boundary layer limiting the reaction zone against the unaffected inner xylem. Living cells of the reaction zone and the boundary layer degenerate with increasing duration of the wound response. Along the transition between such degenerated xylem close to the wound surface and the boundary layer, parenchyma cells regularly develop an additional, innermost wall layer consisting of suberin or suberin-like substances (Figs. 6 and 7) (see also Biggs 1987; Schmitt & Liese 1993). With the synthesis and deposition of these aromatic compounds, including impregnation of lumen-adjacent wall regions and the formation of a probably suberized innermost wall layer, resistance against invasion of micro-organisms increases enormously.

Wound-associated responses in undifferentiated xylem

A second type of active response in hardwood xylem present at the time of wounding was recently described for differentiating fibres of poplar trees (Frankenstein & Schmitt 2006). Those fibres close to a wound and along a transition zone between the xylem fully differentiated at the time of wounding and xylem tissue laid down after wounding display thickened walls, visible at the light microscope level (Fig. 8). With increasing distance from the wound, this zone gradually disappears with again normally developed xylem at a distance of a few millimetres.

Electron microscopy revealed that cell walls of fibres in unaffected xylem have the typical three-layered fine structure. Accordingly, the fibre wall consists of a dark-stained compound middle lamella, a less stained outer secondary wall layer, i.e., the S1-layer, and a thicker and similarly grey stained inner secondary wall layer, i.e., the S2-layer. In comparison, the thickened fibre wall close to a wound develops either an additional secondary wall layer or a distinctly thickened S2-layer. Rarely, a multilayered wall structure was found resembling the wall of sclereids. Vessels and parenchyma cells within this zone did not develop structurally altered cell walls.

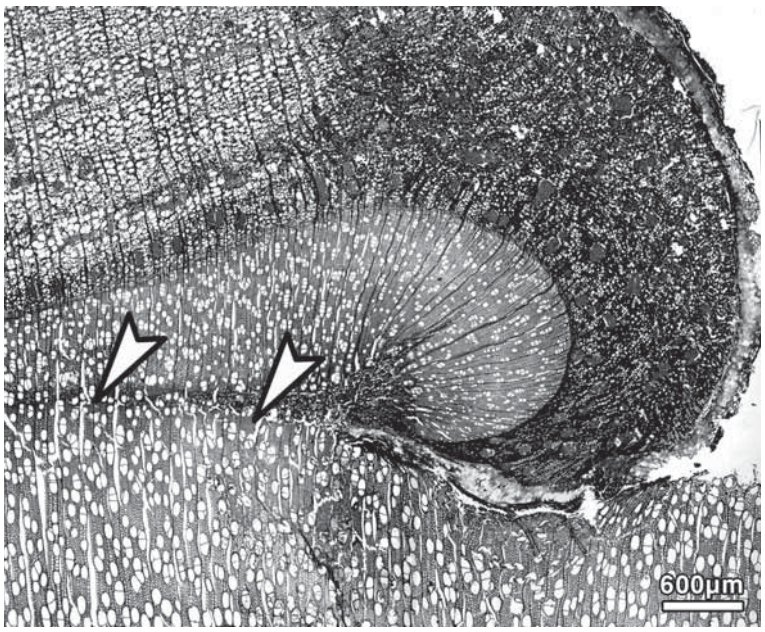


Fig. 8: Light micrograph indicating the position of modified xylem (arrowheads) along the transition zone between unmodified xylem laid down prior to wounding and callus tissue laid down after wounding. Duration of response period was six weeks.

UV-microspectrophotometry was used to semi-quantitatively determine the lignin distribution in cell walls of this tissue region. As variously analysed by several authors (Grünwald et al. 2002; Frankenstein & Schmitt 2006), the lignin concentration in the walls of control fibres of poplar is highest in cell corner regions with maximum absorbencies of mainly 0.35 and in intercorner middle lamella portions with values of about 0.2, whereas the thin secondary wall normally has an absorbance of around 0.1, sometimes of up to 0.16. The lignin distribution in the middle lamella as well as in the secondary wall was shown to be rather homogeneous. However, the modified fibres with thickened walls, as analysed with the scanning technique at a constant wavelength of 280nm, generally showed distinctly higher absorbencies with values of over 0.8 for cell corners, between 0.6–0.8 for intercorner middle lamella regions and between 0.2 and 0.4 for the secondary wall (Fig. 9a). When examining the distribution of lignin in the cell walls, it also became apparent that the lignin distribution was now inhomogeneous with fibres sometimes displaying a layered structure with lowest lignin concentrations preferably in inner secondary wall regions close to the cell lumen (Fig. 9b). Point analyses with a varying

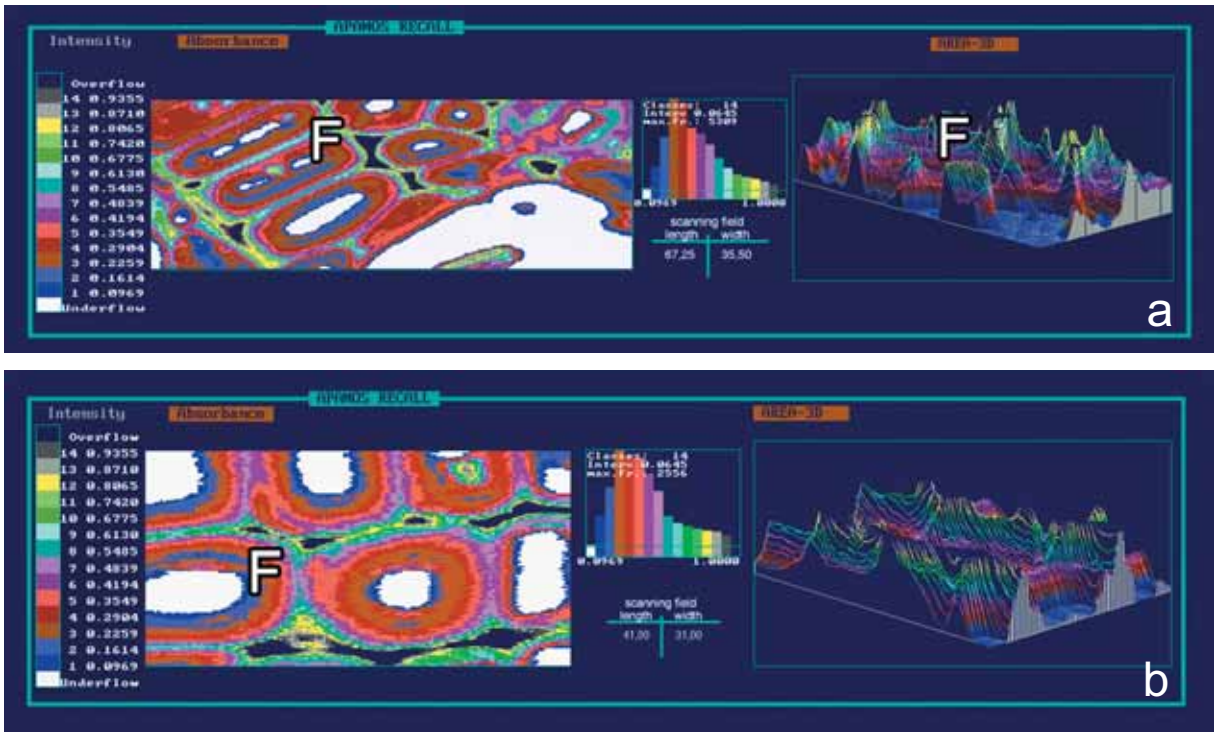


Fig. 9: UV-scanning profiles at 280 nm. **a.** Modified fibres (F) with distinctly increased absorbencies in cell corner and middle lamella regions. **b.** Modified fibres with increased lignin contents and inhomogeneous lignin distribution mainly in the secondary wall.

wavelength in the range of 240-400nm revealed that the absorbance maximum remains at around 274nm, indicating a more or less unchanged guaiacyl/syringyl ratio (Fergus & Goring 1970 a, b; Fukazawa 1992; Koch & Kleist 2001; Takabe 2002). Although the vessel walls appear structurally unmodified, they contain more lignin in their wall layers as revealed by UV-microspectrophotometry. This was also true for neighbouring parenchyma cells, which additionally contain phenolic deposits with a high UV-absorbance capacity. Such structural and topochemical modifications were restricted to a narrow zone of xylem tissue laid down prior to wounding. According to their position, these cells were probably differentiating at the time of wounding and became stimulated to especially develop modified walls, which confer increased resistance against invading microorganisms.

Response due to severe stem bending

Bending of trees by strong winds normally becomes compensated by the elastic properties of their stem tissues. However, when bending exceeds a certain limit, stem fractures may occur (Bäucker et al. 1996; Dünisch et al. 1996) or less severely slip planes in locally overstressed xylem portions may develop (Koch et al. 1996, 2000). As a consequence of such a dynamic stress with numerous slip planes as well as fibre fractures on the compression side, large xylem segments become affected without leading to stem fractures (Fig. 10). Such a mechanical stress also affects outer stem regions, i.e., bark and cambium. During the vegetation period, cambium then starts to form modified xylem, which is called "Wulstholz". "Wulstholz" develops as a tissue for mechanical restabilization of a stem (Trendelenburg 1940). This phenomenon is well known for spruce trees and is initiated on the compression side of a mechanically stressed stem. Morphologically, it is characterized by the deposition of distinctly broadened tree rings finally leading to stem bulges (Figs. 10 and 11). On the cellular level, the tracheids display distinctly thickened walls also in earlywood regions (Fig. 11), frequently wall thicknesses being doubled. Tracheid lengths of normal spruce wood regularly ranges between three and four micrometers, whereas in "Wulstholz" this value is reduced to an average of 2.5 µm (Koch et al. 2000).

Fig. 10: Tangential view of „Wulstholz" formation in a spruce tree. Note the compression damage in the regular wood tissue and discolouration by fungal infection.

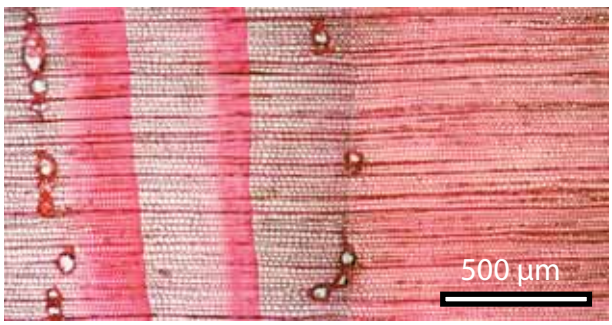


Fig. 11: Transverse section along the transition between regularly formed xylem (two narrow rings on the left) and "Wulstholz" (broad ring on the right). Most of the earlywood tracheids in the "Wulstholz" ring display thickened cell walls. Light micrograph after safranin/astrablue staining.

For thick-walled latewood tracheids of control xylem, UV-microspectrophotometric measurements revealed an absorbance of up to 0.7 for cell corner regions and just below 0.5 for intercorner middle lamella regions (Fig. 12a). Fig. 12b demonstrates that UV-absorbance in the secondary wall of normal latewood tracheids does not exceed an

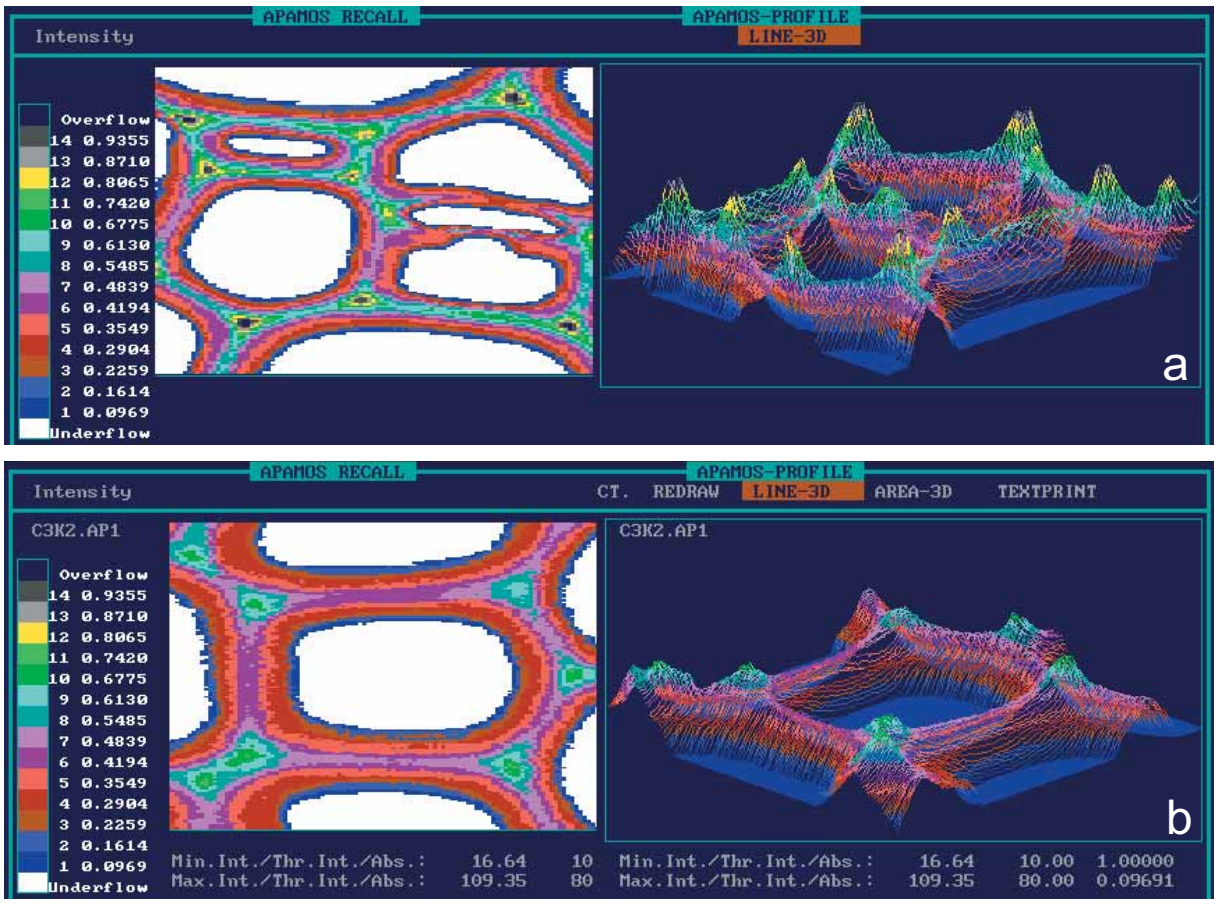


Fig. 12: 2- and 3-dimensional UV scanning profiles. **a.** Distinctly increased lignin contents in wall layers of a „Wulstholz“ tracheid. **b.** Absorbances of regularly formed latewood tracheids.

absorbance value of 0.4. However, the “Wulstholz” tracheids in all wall layers contain increased amounts of lignin as indicated by absorbance values of 0.8 and sometimes above this value for cell corners, of around 0.6 and occasionally slightly above for intercorner middle lamella, and of 0.4 and sometimes close to 0.5 for the secondary wall.

In addition to these topochemical wall modifications, “Wulstholz” is also characterized by an altered chemical composition. It was found that this tissue generally contains more lignin than normal wood, but less hemicelluloses (Koch et al. 2000). Despite distinctly reduced compression strength and modulus of elasticity, the anatomical and chemical/topochemical modifications of “Wulstholz” together with an extremely flat microfibril angle of 60° versus the longitudinal cell axis (Trendelenburg 1940) are responsible for an increased deformation capacity without causing buckling of individual tracheids or slip plane formation as revealed by mechanical tests (Koch et al. 2000). “Wulstholz”tissue therefore is ideally adapted to resist extreme stem bendings caused by severe wind forces as described above.

CONCLUSIONS

Mechanical stress on xylem tissue of trees causes various cellular responses, which may result in wall modifications. Differentiated xylem cells around a mechanical injury of outer xylem regions frequently display modifications of their pits between living parenchyma cells and neighbouring fibres and vessels, whereas living parenchyma cells sometimes are characterized by the deposition of a suberin-like innermost wall layer. Pit membrane modifications are always

related to the deposition of wound-associated substances, which are synthesized in parenchyma cells and then secreted through the pits into neighbouring fibres and vessels. All these responses are part of compartmentalization processes around a wound, which confer increased resistance of woody tissue to invading air and desiccation as well as invading micro-organisms. The walls of xylem cells, which are either differentiating at the time of imposition of mechanical stress or which are newly formed after stress imposition, develop modified structures or chemical compositions. A variously observed phenomenon was the formation of thickened walls with mostly increased lignin contents. Such modifications may occur simultaneously within an individual cell wall as found in differentiating xylem cells of poplar affected by wounding. They contribute to the compartmentalization around a wound, and probably increase resistance against micro-organisms. “Wulstholz” tissue in spruce trees is especially formed to restabilize a stem, which was affected structurally on the compression side by extreme bending. Additionally, these tissue regions show thickened cell walls with increased lignin content. In general, cell wall modifications in woody tissues as the consequence of mechanical stress situations are part of the strategies that enhance the survival potential for trees.

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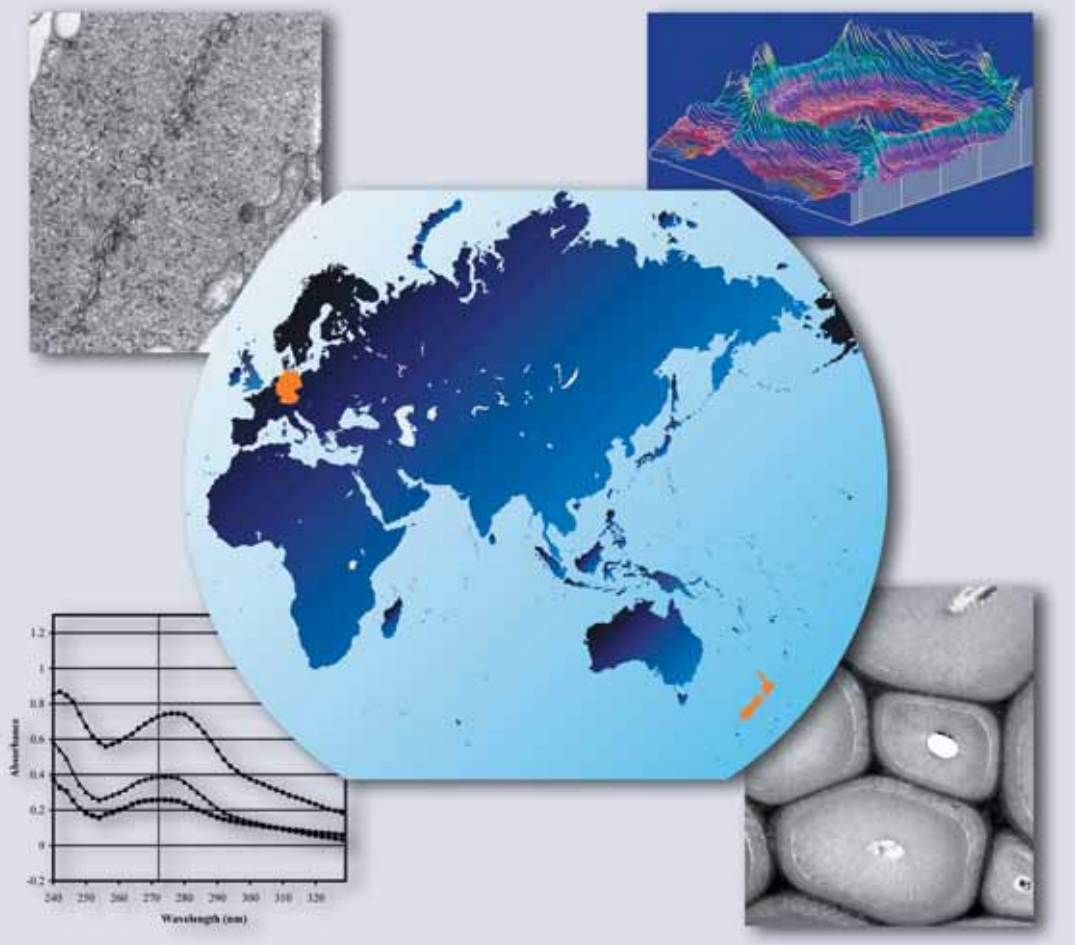

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