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Ageing of bamboo culms. A review

W. Liese, G. Weiner

Summary Properties and utilization of bamboos are influenced by structural changes due to ageing. During the few months growth' of a culm only minor anatomical changes result in the meristematic tissue within one internode and along the culm length. Culms originating from a seedling or rhizome cutting show in subsequent years an age-related development until their full size is attained. The life cycle of an individual culm is of special interest. Investigations of culms up to the age of 12 years from *Phyllostachys viridiglaucescens* have shown definite anatomical changes during the maturation period, but also in later years. They appear as a cell wall thickening of the fibres. Tyloses and depositions in vessels and sieve tubes develop as age-related factors.

Introduction

The ageing of bamboo culms is a phenomenon of considerable interest. Since ageing influences certain properties and consequently the processing and utilization, numerous investigations have dealt with possible structural, chemical and physical-mechanical modifications. Age-related changes have to be considered under different aspects, first during the differentiation and growth of an individual culm, second along with the age of consecutive culms originating from a seedling bamboo, and third, and most important, during the life cycle of an individual culm from its immature stage towards maturation and death.

Since the term "ageing" is sometimes used for different phases, the various stages in the life cycle of a bamboo plant will be discussed in the following, with emphasis on the ageing of a fully elongated culm.

Growth phase

The elongation of a culm results from the expansion of its individual internodes, already present in the bud. In the beginning the whole internode consists of an intercalary meristem. Differentiation starts at its upper part by elongation of the different cell types

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W. Liese, G. Weiner
University of Hamburg, Institute of Wood Biology
Leuschnerstr. 91, D-21027 Hamburg, Germany

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and moves down to the base of the internode. The differentiation of one internode is completed in only a few days (Xiong et al. 1980). Longitudinally there is no difference in the composition and structure of the tissue within an internode, except for the length of the fibres. They undergo a most significant elongation during the differentiation from only a few μm to about 2–3 mm, an elongation of about 100 times. Along an internode, fibres near the upper and lower node are always much shorter than in the middle portion (Liese, Grosser 1972; Espiloy, Sasondoncillo 1978), thus resulting in an easier breakage especially in young shoots.

A bamboo culm grows to its full height of 3–30 m within a period of few months. In contrast to a palm or a dicot tree, where axial cell differentiation occurs by the apical meristem, in bamboo the meristematic tissue of the internodes moves with the growing parts telescopic-like upwards.

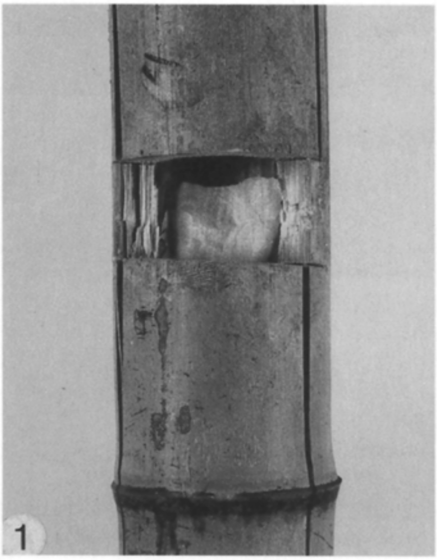
Along the culm length only minor anatomical changes exist. Obvious is the narrowing of the culm wall due to reduction of its inner portion containing more parenchyma and fewer vascular bundles. The size of the vascular bundles also decreases with their shape changing into oval or roundish. This influences also the appearance of the basic vascular bundle types II, III, IV present in the sympodial bamboos, which can become modified along the culm height (Grosser, Liese 1971). The upper part with more vascular bundles has a higher specific gravity and therefore bending and compression strengths increase with height, as influenced by the wall thickness of the species. Only the fibre length exhibits a slight decrease from the base to the top (Liese, Grosser 1972; Grosser, Liese 1974; Espiloy, Sasondoncillo 1978; Abd. Latif Mohmod et al. 1994).

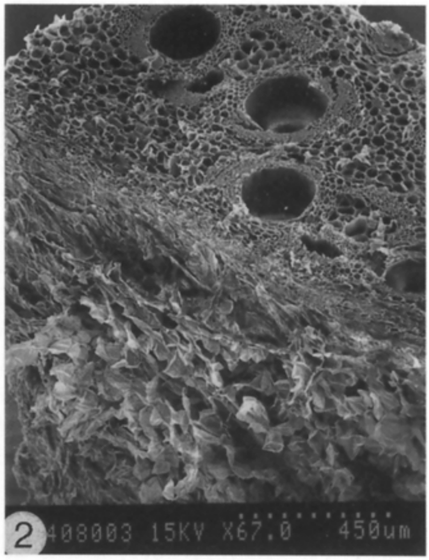
During the development of an internode a central pith cavity is formed (Mohiuddin, Alam 1992). The cells at the inner periphery often consist of layers of parenchyma and also of thickwalled cells, called 'sclereids'. This "terminal layer" (Grosser, Liese, 1971) can be composed of rectangular parenchyma with thicker cell walls than the adjacent ground parenchyma. A very thin membrane may be attached closely to the inner wall or loosely even in a one year old culm (Figs. 1 and 2). Whereas this occurs in some species (*Phyllostachys viridiglaucescens*, *P. aurea*) already in the first year, in *P. heterocycla* it appeared only after three years' growth and in others not at all (Nomura 1993). The varied nature of the lining cavity is indicated by the presence of sclereids, fibrous tissue or a sclerenchymatous zone. This offers a dignostic value, whereas differences in formation are of lesser significance as age-related modifications (Pattanah, Rao 1969; Sekar 1992; Hsieh, Wu 1994). Our TEM analyses with *P. aurea* have revealed a suberization of these inner, thin walled cells.

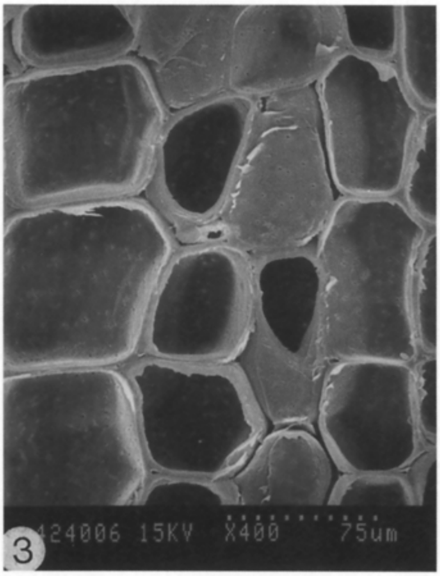
Ageing of seedling bamboos

Observations on the ageing of bamboo culms must distinguish between differences in the culms over consecutive years, for example in a plantation established by seedlings or rhizomes, and those within one single culm with the passing years. Precise information on age-related changes of seedling bamboos is important for determining yield, management and harvesting of a new plantation. It is generally known that over the years height and diameter of the annual culms increase. For culms of *Guadua angustifolia* an increase was registered even up to 10 years (2 y: d 1 cm, h 1–1.5 m, 4 y: d 7.5 cm, h 5–10 m, 7 y: d 8.5 cm, h 10–15 m, 10 y: d 9.5 cm, h 15–18 m, Londoño 1992).

Besides the dimensional changes, structural modifications are also evident. In seedling culms of *P. heterocycla* the average diameter of the vascular fibre sheath, metaxylem vessels and fibre length increased at about 6.7, 4.4 and 1.9 times,







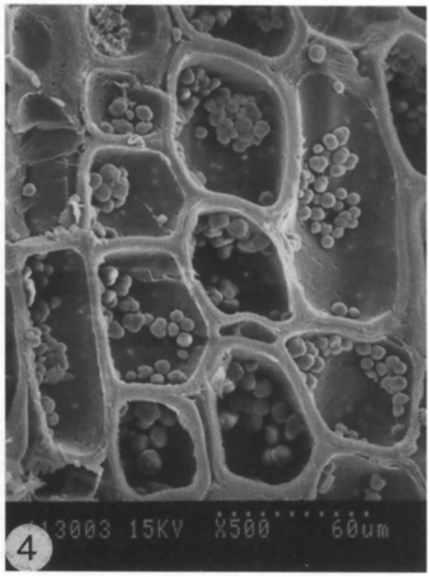


Fig. 1. Terminal layer of a 12 year old culm of *Phyllostachys viridiglaucescens*

Fig. 2. Inner culm wall with "terminal layer", *Phyllostachys viridiglaucescens*. Transverse section

Fig. 3. Ground parenchyma cells without starch of a 1 year old *Phyllostachys viridiglaucescens* culm. Longitudinal section

Fig. 4. Ground parenchyma cells full with starch of a 12 year old *Phyllostachys viridiglaucescens* culm. Longitudinal section

respectively, from the age of 1 to 5 years. The older culms developed a somewhat more stretched variation of the vascular bundle type (Nomura 1993).

Life cycle of an individual culm

General properties

Age-related changes within an individual culm are of special interest. Their significance is indicated by the terms "immature" and "mature". Definite modifications occur within a grown up culm during its life time. The influence of ageing on maturation, especially on strength properties is well proven. Many attempts have therefore been made to identify some characters, that may indicate a certain age class of a culm. During the younger stage, changes of external characteristics are obvious, related to the culm sheaths, bud break, branching pattern, number of leaf scars and the colour of the stem from fresh green to often yellow-grey. Banik (1993) could differentiate the ages from one to four years by such morphological characters for five major species of Bangladesh bamboos.

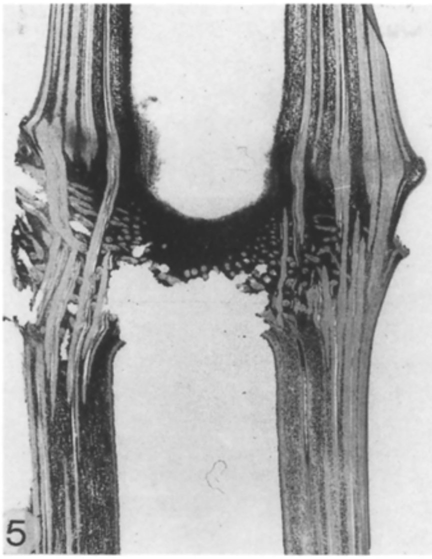
During the maturation phase of up to three years, the moisture content decreases distinctly (Abd. Latif Mohmod, Mohd. Zin Jusoh 1992; Espiloy 1994; Sattar et al. 1994), but also later, even up to 10 years (Liese, Grover 1961). More significant are the chemical and structural parameters that are reflected in the physical-mechanical properties. With regard to the chemical composition the percentage of holocellulose and α-cellulose tends to decrease in bamboo culms older than one year while the lignin content remains unchanged or increases slightly (Chen et al. 1987). In relation to strength properties, the ageing effect on lignification is of interest. Studies by Itoh (1990) on 2 to 14 years old culms of *P. heterocycla* have shown, that full lignification is completed within the first growing season, with no further effects by the increasing age of the culm. Chen et al. (1987) indicated in their studies on 1 to 7 year old *P. pubescens* a remarkable change in the ash composition, since copper, zinc, phosphorus, iron and potassium decrease, while calcium, magnesium and manganese increase.

Ageing involves the question of vitality, which is associated with the storage and mobilization of carbohydrates. Therefore, the presence of starch as an energy source has been investigated in 1-month to 12-years old culms of *P. viridiglaucescens* (Carr.) A.C. Riv. A young culm does not contain any starch during the growing phase, since all nutrients must be utilized immediately for metabolic processes (Fig. 3). However, in all the older culms starch was present, even in those of 12 years old (Fig. 4). The starch granules were located in the vertically elongated cells of the ground parenchyma, in the contact parenchyma cells and in the parenchyma cells of the diaphragma (Fig. 5). This also shows that the parenchyma cells are still alive in culms of such age.

No reports exist about residues that may result from cell metabolisms, although the sieve tubes, and parenchyma cells maintain their function for often more than 10–15 years. Since likewise no formation of toxic substances due to ageing is known, the natural resistance of bamboo against organisms is generally low. Nevertheless, certain differences between species are known from experience as well as field and laboratory tests, which are hard to be explained. The amount of starch present might have some influence.

In certain species, especially pachymorph ones from tropical regions, an amorphous silicious material is found inside the pith cavity of older culms (Fig. 6). It is called "tabashir", and is used for pharmaceutical purposes (Jones et al. 1966). Its origin and its formation as an age-related process are not known.

The activities of parenchyma and companion cells along the sieve tubes may lead to changes in the gas composition inside a culm over the years. The intercellular region between the short parenchyma cells could be a pathway (Fig. 7). Since the epidermis is



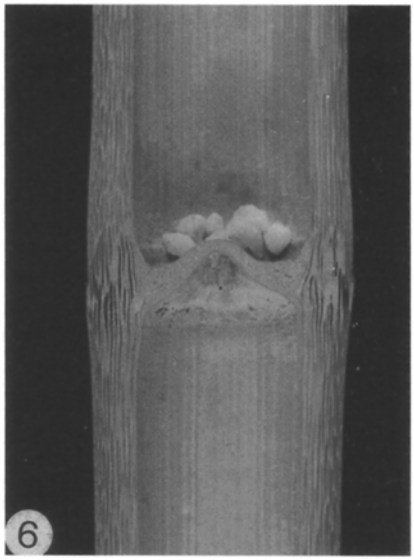


Fig. 5. Ground parenchyma cells with intensive accumulation of starch in the nodal region of *Phyllostachys quioli*. Longitudinal section, staining with Lugol's solution

Fig. 6. Tabashir granulae in a *Dendrocalamus spp.* culm

Fig. 7. Intercellular spaces (arrows) between ground parenchyma cells, *Dendrocalamus spp.* Longitudinal section

impermeable, the pith cavity, the lacuna, might be some kind of a buffer reservoir for the gas. However, for the inner terminal layer no stomata-like openings have been observed so far. An analysis of its gas composition in culms of increasing age could reveal interesting information.

With regard to the physical-mechanical properties, only few results can be mentioned from the many contributions (e.g. Zhou 1981; Espiloy 1987, 1994; Widjaja et al. 1987; Abd. Latif Mohmod et al. 1990; Sattar et al. 1994). Although a few contradictory observations have been reported, the general consensus is that a bamboo culm matures at about two to even three years and has then reached its maximum strength. Culms of

Bambusa bakooa and *Melocanna baccifera* from 1 to 5 years old also exhibited a decrease in static bending strength and compression strength (Sattar et al. 1994). In bloomed bamboo culms, however, a significant reduction of specific gravity and strength properties has been noted (Kitamura 1975), which could explain the breakage of culms after flowering.

Fibre characteristics

Changes in the physical-mechanical properties of bamboo tissue must be related to modifications of the cell structures. Particularly important in this respect are the fibres, which are arranged in fibre sheaths and the respective additional fibre bundles, depending on the genus. Therefore the cell structures of culms from different ages were analysed for possible structural modifications. Thanks to the kindness of M. Yves Crouzet, Prafrance, bamboo culms of *Phyllostachys viridiglaucescens* from growing shoots up to 12 years could be investigated. Samples from the basal 4 and the 20 internode were collected in May 1994 from freshly cut culms, immediately fixed in 4% formol, subsequently cut into smaller samples (5 mm wide × 10 mm length × wall thickness/complete cross section) and processed for scanning electron microscopy (Hitachi S520). To obtain a smooth surface, the fresh, although extremely hard samples were cut with a razor blade (angle 45°), air dried and sputter coated with gold. Transverse sections of 15 μm thickness were cut on a sliding-microtome, double-stained with acridin red/chrysoidin and astra blue and alternatively also with phloroglucinol. All sections were embedded in glycerol and examined by light microscopy (Olympus BH2).

An exact location and characterization of the specific fibres is required for comparison of the fibre structures of different culms. Each vascular bundle is surrounded by four fibre sheaths in a trifoil manner, embracing the phloem field, the two metaxylem vessels and the one protoxylem tracheid. Several fibre types are present in the fibre sheaths:

- Fibres in direct contact with the surrounding ground parenchyma show a distinct polylamellation with numerous, thin lamellae, more than the other fibres of the same sheath.
- Fibres in the centre are larger than the outer ones.
- The fibres in contact with the phloem field and the protoxylem tracheid are smallest.

Especially large cells within the fibre sheath near the protoxylem tracheid may represent groups of parenchyma cells (Fig. 8a and b), as also observed by Murphy and Alvin (1992). Besides these differences within one fibre sheath and the fibre sheaths around a vascular bundle, further modifications exist along the cross section of the culm wall. Fibres near the epidermis as well as near the pith cavity, are thinner and often possess one or more lamellae less than those in the middle part.

These general findings relate to samples from the base (4 internode) as well as from the top region (20 internode). However, in spite of this similarity, certain differences between base and top are distinct. In the base portion, the fibres are generally thicker than those at the top. This pattern becomes obvious both in a young culm and in older ones (Fig. 9). In the one-year old culm of *P. viridiglaucescens*, the fibre wall thickness differs between the base and top portion by about 1 μm, but in a 12-year old culm by 1.5–2.0 μm. Alvin and Murphy (1988) found for the same species a difference of 0.16 μm between the 6th and 20th internode in a young culm and of 0.3 μm in an older one. For *Gigantochloa scortechnii* a difference between base and top of 2 μm for 1 year and 3.2 μm for 2 years was observed (Abd. Latif Mohmod et al. 1994).

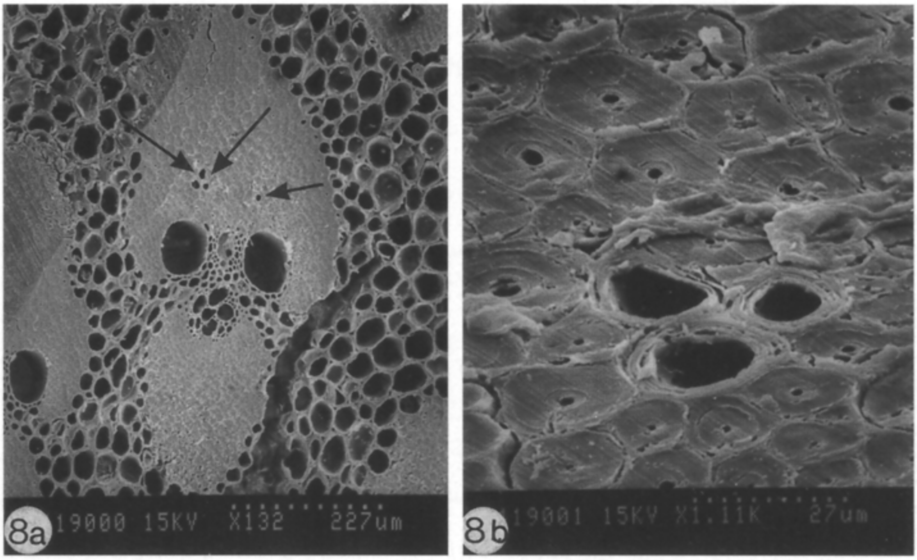


Fig. 8a, b. Parenchyma cells (arrows) inside a fibre sheath of a 8 year old *Phyllostachys viridiglaucescens* culm. b) Detail. Transverse section

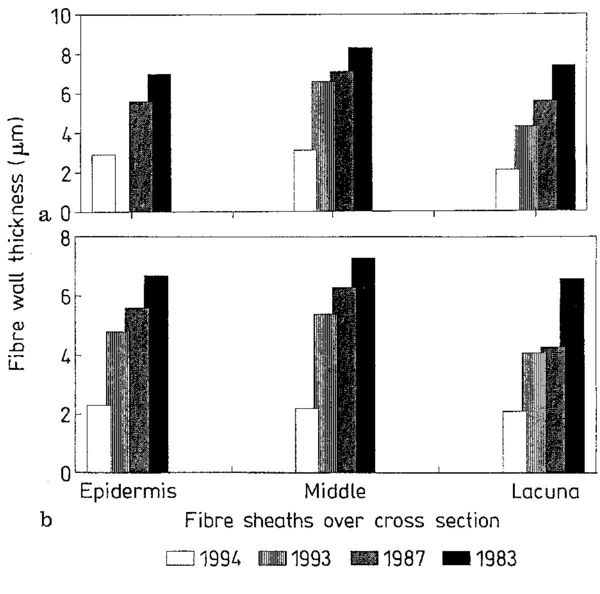


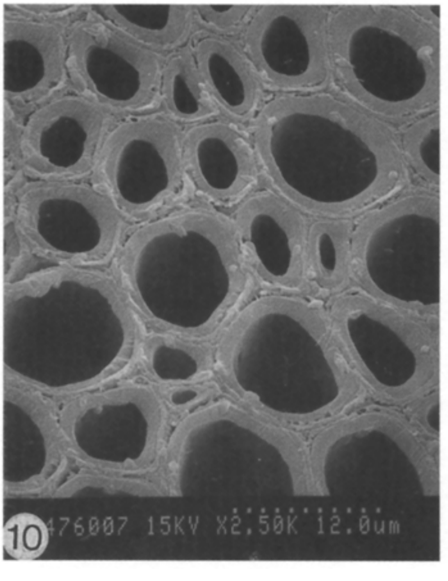
Fig. 9a, b. Fibre cell wall thickness over the cross section at the 4th (a) and 20th internode (b) from 3 month (1994), 1 year (1993), six years (1987) and eleven year (1983) old culms of *Phyllostachys viridiglaucescens*

The recognition of such a pattern of differences in the fibre structure within a culm wall is a prerequisite for any investigation of possible changes due to ageing. Results are only conclusive, when fibres are being compared at exactly the same position. Based on the findings mentioned above, detailed light microscopic measurements have been undertaken to elucidate any possible changes in the fibre wall architecture. Although spectacular results could not be expected from this time-consuming exercise, some findings merit the efforts.

In the first month of the growing period, all fibres of the culm are still unlignified. Within the 20th internode the fibres have a combined, very thin wall only 1.5–1.7 μm thick. In a fully elongated culm of the same year, the wall thickness at this internode was 2.3 μm and thinner than those at the lower 4th internode (2.6 μm). The fibre wall consists of three lignified lamellae (Fig. 10). After one year it contained four to five lamellae, and its thickness increased to over 5 μm at the top and around 6 μm at the base. Within the top portion of the two year old culm it was observed to be 5.5 μm, while about 6.8 μm at the 4th internode. Observations by Fujii (1985) on the cell walls of *Pleioblastus clino* showed a continued thickening late into the second year. Alvin and Murphy (1988) investigated three culms of *Sinobambusa tootsik* with an estimated age of less than one, one to two and more than two years, finding a similar significant increase in the average cell wall thickness.

Results for older culms are not available so far. The measurements of the culms between the third and ninth year showed no further deposition of lamellae. The wall thickness remains nearly similar. However, older culms of ages between 9 and 12 years, revealed an additional increase of wall thickness. The fibres contain 5–6 lamellae with a wall thickness of about 8 μm and 6 μm at the respective basal and top portions (Fig. 11). In Tables 1 and 2 the measurements of the fibre wall thickness at different ages and over the culm wall are summarized.

The formation of new lamellae was distinct in several samples by their still unlignified status, as seen after staining. An unlignified layer was earlier recognized in older culms of *Thyrsostachys oliveri* Gamble by Liese and Grosser (1971). A detailed analysis of



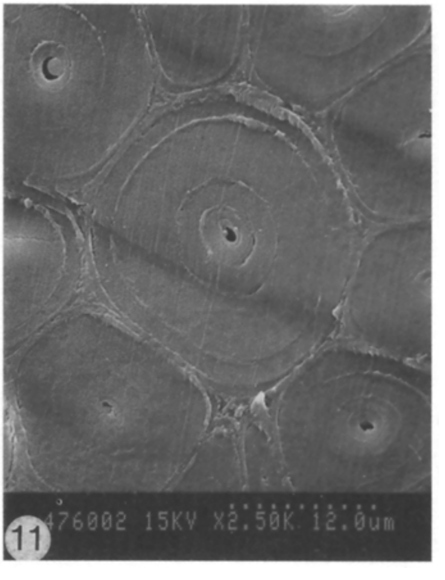


Fig. 10. Fibres of a 1 year old culm, *Phyllostachys viridiglaucescens*. Transverse section

Fig. 11. Fibre with 5 lamellae of a 12 year old culm, *Phyllostachys viridiglaucescens*. Transverse section

the culms however revealed their rather localized occurrence, so that this "gelatinous" layer is seen as an incomplete cell wall differentiation and not as a stage of further ageing.

These results indicate that within the material investigated development phases occurred in the fibres. The main one happened during the first two years that led to the development of fibres with lignified cell walls, still containing their cytoplasm. A further followed several years later by an additional formation of few lamellae by the cytoplasm. These are first observed as unlignified lamellae deposited onto the lignified wall. Later, they also become lignified.

The number of lamellae reported above were measured with the light-microscope and appear lesser than the polylamellate fibre structure observed from electron-microscopic measurements (Parameswaran, Liese 1976). This difference could be associated to the fact that the narrow lamellae became visible only after delignification and at high magnification. They may also be restricted to the outer vascular bundles with a distinct polylamellation.

The existence of living fibres and also parenchyma in older culms does not agree with observations on the widespread occurrence of a wart structure in these cells (Parameswaran, Liese 1977). Warts are considered as a final stage of cytoplasmatic activity before a cell dies. The material investigated in the earlier studies had not been characterized with respect to its age and location within the culm. It was air-dried, so that the wart structure might have developed during the death of the fibres and parenchyma. Studies on the formation of the wart structure in relation to ageing and dying of fibres and parenchyma in bamboo seem to be of interest.

Corresponding observations on developmental changes of fibre structures due to ageing were also made with the palms *Rhapis excelsa* Thunb. Henry and *Calamus axillaris* Becc. (Weiner et al. 1996). In contrast to bamboo, palms possess an apical meristem, so that in the 5-year old plants studied, the occurrence of age-related changes

Table 1. Mean fibre wall thickness of vascular bundles at the 4th internode from *Phyllostachys viridiglaucescens* [μm]

Culm age	Average value [μm]	Fibre sheaths in radial orientation over the culm wall										
		1 Epidermis	2	3	4	5	6	7	8 Near pith cavity	9	10	11
3m	2.6	2.9	3.0	2.8	2.9	2.9	2.5	2.3	2.3	2.3	2.3	2.1
1y	6.2	6.9	7.3	7.9	6.9	6.6	6.2	5.5	4.7	4.3		
2y	6.8	7.2	6.9	7.2	7.5	7.6	6.7	7.1	6.6	5.7	5.4	
3y	5.2	6.1	6.3	5.9	5.4	4.6	4.3	4.0				
4y	6.8	6.1	7.0	7.4	7.3	7.1	6.5	6.3				
5y	5.0	5.6	6.0	5.9	5.3	4.6	3.9	3.6				
6y	3.6	5.2	4.0	3.4	3.4	3.1	2.6	2.8	2.6	2.5		
7y	6.1	5.6	7.0	7.1	7.1	7.1	6.3	5.3	4.6	4.7		
8y	7.2	5.6	6.2	7.1	7.3	7.8	8.1	7.5	7.4	6.3	5.6	
9y	4.8	4.9	6.8	6.8	5.4	4.0	3.1	3.2	2.7			
10y	6.6	5.7	5.7	5.7	5.8	6.3	5.8	5.5	4.7			
11y	8.0	7.0	7.6	8.3	8.5	8.3	8.4	8.6	8.3	8.4	7.4	
12y	7.7	5.5	6.6	7.8	8.1	8.2	8.7	9.2	8.3	7.9	6.4	

m = month
y = year

Table 2. Mean fibre wall thickness of vascular bundles at the 20th internode from *Phyllostachys viridiglaucescens* [μm]

Culm age	Average value [μm]	Fibre sheaths in radial orientation over the culm wall										
		1 Epidermis	2	3	4	5	6	7	8 Near pith cavity	9	10	11
3m	2.3	2.3	2.6	2.4	2.1	2.2	2.3	2.2	2.1	2.1		
1y	5.2	4.8	6.4	6.2	5.4	5.2	4.6	4.1				
2y	5.5	4.7	5.8	5.8	5.7	5.9	5.6	4.9				
3y	5.2	5.5	5.5	5.1	5.3	5.1	4.6					
4y	6.7	6.3	6.6	7.1	6.9	7.5	5.6					
5y	4.6	5.2	5.3	4.8	4.5	4.2	3.5					
6y	3.6	3.8	3.7	3.7	3.3							
7y	5.8	6.6	6.7	6.6	5.6	4.8	4.3					
8y	7.2	6.5	7.2	7.7	7.0	7.4	7.3					
9y	5.8	5.1	5.9	5.9	6.1	6.0	5.5					
10y	6.6	5.3	6.4	7.3	7.4	6.8	6.2	6.6				
11y	7.2	6.7	7.1	7.7	7.6	7.3	7.3	6.6				
12y	6.0	4.9	6.0	6.5	6.4	6.2	6.0	5.8				

m = month
y = year

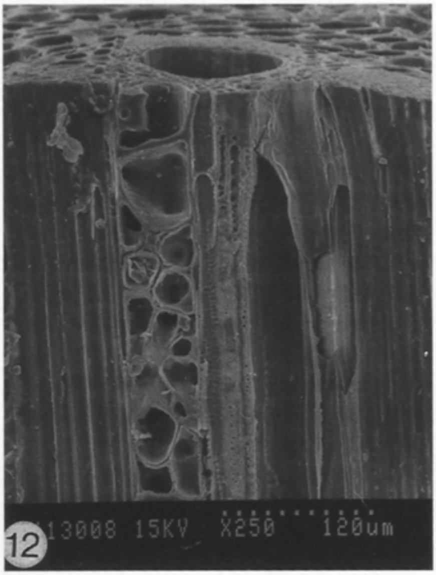
could be assessed along the stem. The results have shown within this period a similar formation of additional lamellae with an increase in fibre wall thickness. A chemical analysis of *R. excelsa* has indicated an additional lignification in the lower, older part of the stem.

Further symptoms of ageing

Senescence also leads to symptoms which are associated with the functional efficiency of the living culm. Most important, but also most endangered, is the conductivity for water, which is transported in the metaxylem vessels, and that of assimilates in the sieve tubes. It is remarkable that these crucial pathways are formed within a few days of differentiation and have to function in bamboo culms for many years and even much longer in palms. However, with increasing age certain symptoms can be observed in the conductive tissue. They are not related to a distinct age, but are more of a general nature.

Some effects should briefly be mentioned:

Tyloses in bamboo cause a blockage of the metaxylem vessels (Fig. 12). The balloon-like protuberances originate from the surrounding parenchyma cells. Tyloses develop within the protoxylem tracheid already at earlier stages and may there have lesser importance for the water transport. Older culms develop tyloses in the metaxylem vessels, which seals off the water conduction. Furthermore, slime substances may fill their lumina which also results in a blockage. In both cases, an air embolism must proceed, through which the vascular parenchyma cells are stimulated to form tyloses and slime. The sieve tubes of older culms can show a blockage by callose. The accumulation of such age-related changes finally leads to a breakdown of the transport system, thus resulting in the dying of the culm. These modifications due to senescence occur also as a consequence of mechanical wounding. An injured tissue has to develop defense reactions to protect its surrounding cells against the invasion of air and



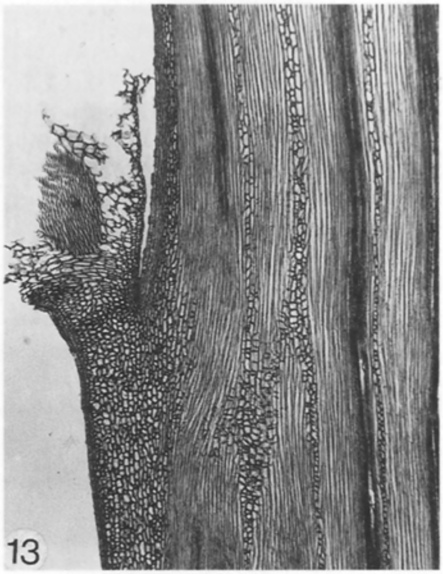


Fig. 12. Tyloses in a metaxylem vessel of a vascular bundle, *Phyllostachys viridiglaucescens*

Fig. 13. Cut off branch, *Thamnocalamus spp.* Longitudinal section

microorganisms. Damage of the culm could also be caused by insects, which penetrate the wall and use the pith cavity as their biotope (Kovac, Azarae 1995).

Following wounding, an additional thickening of parenchyma cell walls has been observed as a further reaction. Along the wounded tissue, the cell walls of the ground parenchyma exhibit the formation of new lamellae. Thus, the endangered tissue is also sealed off against the damaged area (Weiner, Liese 1996). A similar phenomenon occurs in branches, which are cut off or have died (Fig. 13). Above a node, a thickening of parenchyma walls takes place. Thus a zone is formed that separates the living tissue from the dying one. Since branches also die due to ageing, this parenchymatic response can also be seen as an age-related reaction.

A treatise on the ageing of bamboo culms may include considerations at the long-time behaviour of culms in use. It should be added therefore that bamboo used for buildings or as material like for music instruments or sculptures, has not indicated any change of properties. Building-constructions in Manizales, Colombia, the bamboo organ in Las Pinas, Philippines and the art objects in Chinese museums are impressive examples since over 100 years.

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