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Anatomical changes during culm maturation in *Bambusa bambos* (L.) Voss and *Dendrocalamus strictus* Nees

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Abstract—The anatomical changes occurring during the maturation of culms were investigated in two common species of Indian bamboos, namely *Bambusa bambos* (L.) Voss and *Dendrocalamus strictus* Nees by a comparative study of culm internodal material of different ages between 2 and 60 months. The culm wall consisted of ground parenchyma tissue enclosing a large number of fibro-vascular bundles, which varied in size, structure and abundance in different parts of the culm, both in the axial and radial direction. The main change that occurred during culm maturation was the thickening of cell walls and lignification. Cell-wall thickening and lignification progressed from the outer to the inner parts of the culm wall, and from the culm base towards the top. Within a fibro-vascular bundle, these changes first occurred in fibres contiguous to the vascular tissues and then progressed to outer parts of the bundle. In the peripheral fibrous strands of the bundles, the outermost fibres matured first followed by the inner ones. Cell-wall thickening of fibres was accomplished by addition of lamellae leading to a polylamellate cell-wall structure. In ground parenchyma, although the wall thickening was evident, lamellation was not distinct. These changes in cell-wall structure led to increase in basic density of the culm material. The increase in density was dramatic during the first two years in both *B. bambos* and *D. strictus*. It became more gradual during the third year and stabilized thereafter. The moisture content percentage, which showed an inverse relationship with density, declined rapidly during the first two years and reached a stable value in later years. The study suggested that the maturation process of newly emerged culms was rapid during the first two years, and stabilized after the third year in both species.

Key words: Bamboo maturation; anatomical changes; fibre wall thickening; vascular bundles.

INTRODUCTION

The fibro-vascular tissue of bamboos undergoes continuous maturation changes with increasing culm age, and harvesting the culms at appropriate stages of their maturity to suit the particular end-use has great importance in its utilization. Thus, studies on bamboo maturation are vital, not only for a deeper understanding of

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the raw material properties for utilization, but also for developing appropriate harvesting practices for optimum use of this important non-wood forest resource.

Investigations on structural changes taking place during growth of bamboo culms have shown that the longitudinal growth of culm internodes is due to elongation of cells, mainly fibres, and is completed in a few days after the emergence of new culms. During the maturation phase that follows, there is a thickening and lignification of cell walls, which proceeds at different rates across the radius of the culm wall [1–5]. Studies on the ultrastructure of fibre walls have shown that the thickening of cell walls is due to deposition of additional lamellae. The process of fibre maturation is believed to prolong over many growing seasons [6]. However, in some species it has been observed that lignification of culm tissues is completed within one growing season [7]. Cell-wall thickening of fibres and parenchyma is found to continue even after maturation phase and is believed to be due to ageing [1, 6].

MATERIALS AND METHODS

Culm internodal samples of *Bambusa bambos* and *Dendrocalamus strictus* were collected mostly from homesteads and also from forest areas in the Thrissur and Palakkad districts of Central Kerala during the period from October to March. Culms were selected so as to represent approximate age classes such as 2, 6, 12, 18, 24, 36, 48 and 60 months. *B. bambos* was collected from 11 different sites and *D. strictus*, from 9 sites. Culm age was recorded as known to the owners of the respective holdings and also by counting the number of months lapsed after normal culm production in the period July–August. In total, 21 culms of *B. bambos* and 30 culms of *D. strictus* were used in this study. After felling the selected culms, 1-m-long cuttings with 4–6 intact internodes were collected from the base (fifth to seventh internode from ground level), mid-height and top portions of each culm. Additionally, for moisture content determination, samples of 5 cm length were collected from each of the three representative portions of the culm and were enclosed in polythene bags to prevent moisture loss during transit. The culm outside and inside diameter and culm-wall thickness were recorded. After reaching the laboratory, samples of suitable size were prepared from mid part of the internodes for anatomical study and determination of basic density. The samples meant for microtomy were fixed in FAA (formalin-acetic acid-alcohol) and later transferred to 50% ethyl alcohol. Basic density and moisture content percentage of the samples were determined gravimetrically following the conventional method of oven-drying the material. The presence or absence of starch in culm tissues was disregarded during determination of basic density. For anatomical study, 1-cm^3 blocks of culm internode were prepared by trimming off the outer portions. Transverse and longitudinal sections of 20 μm thickness of the blocks were cut directly using a Reichert sliding microtome. The sections were stained in tannic acid–ferric

chloride and Safranin [8], dehydrated and mounted in DPX (a commercial name for a suitable mounting medium).

The abundance of vascular bundles was estimated by counting the bundles per cm^2 and tissue proportions across the culm wall were estimated by tracing the cross-sectional views on tracing film and measuring the area occupied by each tissue. Fibre dimensions, such as length and double wall thickness, were measured from macerated material. Maceration was done using a 1 : 1 mixture of hydrogen peroxide and glacial acetic acid. The fibre length was measured from three samples each for an age group. Per sample 40 fibres were measured and the measurements of an age group were pooled together for calculating the mean. The diameter was measured at the mid part of the normal fibres where the diameter was maximal and the lumen diameter at the same point was subtracted from this width to get the double wall thickness. The latter was halved to obtain the cell-wall thickness.

RESULTS AND DISCUSSION

Structural variation within and between culm internodes

A cross-sectional view of the culm internode of *B. bambos* and *D. strictus* exhibited the structural features of a monocot shoot. The peripheral portion of the culm wall consisted of a single layer of epidermis and a narrow homogeneous cortical region of thin-walled parenchymatous cells while the major part of the culm wall consisted of a broad zone of ground tissue enclosing numerous fibro-vascular bundles. On the inner side facing the culm cavity, a pith ring was found which was 8–12 cells thick in *B. bambos* and 6–8 cells thick in *D. strictus*.

The size, structure and distribution of the fibro-vascular bundles across the culm wall showed a gradation from the periphery inwards. The outer, denser, part of the culm wall was compactly arranged into smaller bundles with massive fibrous sheaths and a lower proportion of vascular tissue. Towards the inner side, there was a decrease in the proportion of fibrous tissue and an increase in the proportion of vascular tissues within the bundles. These changes were accompanied by a decrease in compactness or frequency of bundles per unit cross-sectional area. The bundle size that increased from outer to inner parts of the culm wall had a little reduction towards the inner boundary. The average values of tissue proportions obtained for different portions of culm wall in *B. bambos* and *D. strictus* are given in Table 1.

From Table 1 it is evident that the proportion of fibrous tissue that imparts rigidity and hardness to the culm material decreased from the culm periphery towards the inner regions with a concomitant increase in softer ground tissue. This variation resulting from change in size, form and proportion of vascular bundles has been the main reason for the wide difference in physical and mechanical properties across the culm wall in most bamboos. Variation of morphology of vascular bundles across the culm wall and along the culm height has been intensively investigated in a number of bamboos as a means for characterization of bamboo taxa [9–14].

Table 1.
Tissue proportion in different parts of culm wall in *B. bambos* and *D. strictus*

	Bambusa bambos			*Dendrocalamus strictus*		
	Outer part	Mid part	Inner part	Outer part	Mid part	Inner part
Fibrous tissue (%)	45.0	36.0	27.0	40.0	33.0	28.0
	(9.6)	(5.6)	(5.8)	(8.7)	(10.3)	(6.4)
Vascular tissue (%)	5.0	6.0	9.0	7.0	7.0	8.0
	(1.1)	(1.7)	(2.4)	(1.8)	(2.1)	(1.5)
Ground tissue (%)	50.0	57.0	65.0	53.0	60.0	64.0
	(8.0)	(6.2)	(7.5)	(9.1)	(8.5)	(7.5)
No. of bundles per cm^2	283	111	116	379	201	148
	(67)	(37)	(28)	(75)	(62)	(38)

Values in parentheses are SD of the mean.

Table 2.
Variation in tissue proportion at different height levels of the culm in *B. bambos* and *D. strictus*

	Bambusa bambos			*Dendrocalamus strictus*		
	Culm base	Mid-height	Culm top	Culm base	Mid-height	Culm top
Fibrous tissue (%)	34.0	39.0	35.0	29.0	33.0	39.0
	(9.7)	(9.8)	(7.8)	(5.8)	(5.4)	(8.7)
Vascular tissue (%)	5.0	7.0	8.0	5.0	7.0	9.0
	(1.9)	(1.6)	(1.9)	(1.5)	(1.3)	(1.7)
Ground tissue (%)	61.0	54.0	57.0	66.0	60.0	51.0
	(10.4)	(9.0)	(7.8)	(5.9)	(5.5)	(8.0)
No. of bundles per cm^2	160	167	184	206	225	298
	(59)	(65)	(53)	(42)	(61)	(58)

Values in parentheses are SD of the mean.

Appreciable variation in bundle distribution and tissue composition was also found between different height levels of culms in both *B. bambos* and *D. strictus*. Notable among them was the increase in the number of bundles per unit cross-sectional area and proportion of vascular tissue (Table 2) from culm base to top which resulted from more compact arrangement and reduction of average size of bundles. This variation along the culm height is often found to influence physical, mechanical and machining properties of culm tissue [15–18]. From several earlier studies it has also been found that the form, size and pattern of bundles are distinctly variable along the culm length and these changes are found to coincide with change in culm wall thickness that occurs from the culm base to the top [6].

With regard to the fibre-wall thickness and lignification, indices of fibre maturation, a similar gradation was evident from periphery towards interior parts of the wall at each height level at any particular culm age. Figures 1 and 2 reveal such differences in both morphology and maturity status of fibres in *D. strictus*. At the outer part of the culm wall, the fibres in the bundle sheath were more thick-walled and

lignified, whereas in the inner parts thickening of cell walls and lignification were limited to fibres in the immediate vicinity of vascular tissues (Fig. 2). In *B. bambusa* also the peripheral fibrous sheaths away from the vascular tissues were largely unlignified in the inner bundles (Fig. 3) as compared to the outer bundles at the same age (Fig. 4). Such a difference is partly responsible for imparting higher density and hardness to the outer shell of the culm wall as compared to the inner part at any stage of maturation. Further, it is also indicative of the sequential progress of cell-wall maturation from the peripheral part of the culm wall towards the inner side as observed in several other bamboo species [1–5, 19].

Besides the variation evident across the culm wall, a remarkable difference was observed in fibre-wall thickening and lignification between different height levels in both *B. bambos* and *D. strictus.* Comparison of Figs 1 and 4 reveals the difference in cell-wall thickening and lignification of bundle fibres in the outer part of the culm wall at basal (Fig. 1) and top (Fig. 4) portions of a two-month-old culm of *D. strictus*. While the fibrous sheaths of the bundles at the culm base at this stage consisted of thick-walled and lignified cells, those at the culm top comprised of relatively thin-walled and unlignified fibres. This observation supports the earlier findings [1, 3, 6, 7] that cell-wall thickening and lignification of fibrous tissues in the bamboo culm starts from the base and progresses upwards. Within an internode, however, these processes progress downwards [6, 7]. However, there are a few studies where no significant correlation has been found between age and cell wall thickness of fibres [16].

Structural changes during culm maturation

Mean fibre length between different age groups of *B. bambos* varied between 2900 μm and 3200 μm and in *D. strictus* between 2910 μm and 3090 μm, and there was no definite trend of increase in fibre length in relation to increase in age of the culms from second month onwards. This suggests that whatever fibre elongation occurring during culm development is completed before the culms are 2 months old and there is no continued elongation of fibres thereafter. The elongation of fibres in bamboos is said to complete within a few days early during the differentiation of culm internodes [20].

The most noticeable change in culm structure with increasing culm age was the thickening of cell walls of bundle sheath fibres and ground parenchyma tissues and their lignification. The fibres of the outer bundles of the culm wall were the first to undergo these changes. Subsequently, wall thickening and lignification of fibres progressed inwards in the radial direction and upwards in axial direction. Within a bundle, all the fibres did not mature simultaneously; in the outer part of the culm wall where the vascular and fibrous tissues were fused into a composite structure, fibres lying adjacent to vascular tissues matured first and those away from the vascular tissues matured later (Fig. 5). In inner bundles, fibres flanking the protoxylem and metaxylem vessels and phloem underwent cell-wall thickening and lignification first (Fig. 6). Thickening and lignification of fibre walls subsequently

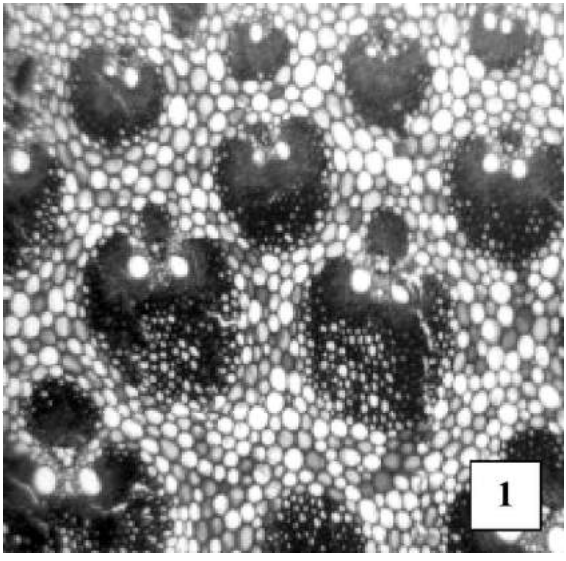

Figure 1. Cross-sections of 2-month-old culms of *D. strictus* and *B. bambos* showing vascular bundles with their fibrous sheaths. *D. strictus* culm base, outer part; note thick walled, mostly lignified fibres.

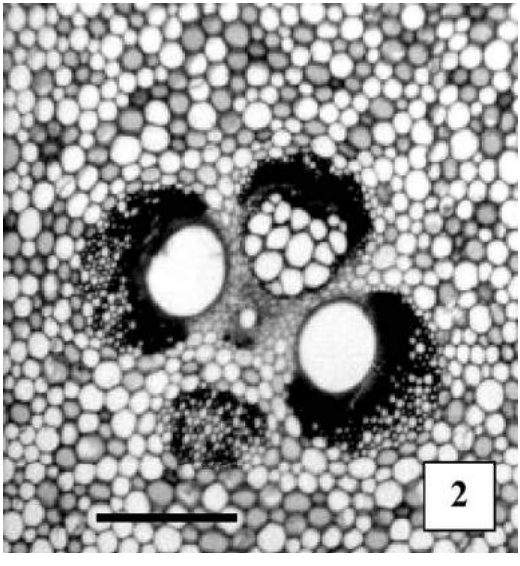

Figure 2. Cross-sections of 2-month-old culms of *D. strictus* and *B. bambos* showing vascular bundles with their fibrous sheaths. *D. strictus* culm base inner part with only a few lignified fibres.

progressed to the outer parts of the bundle. In peripheral fibrous sheaths of inner bundles, the fibres matured in a different sequence; mostly those situated at the outer boundary of these sheaths were the first to undergo cell-wall thickening and lignification (Fig. 6, arrows) while fibres in the core part of the sheath matured at random (Fig. 6).

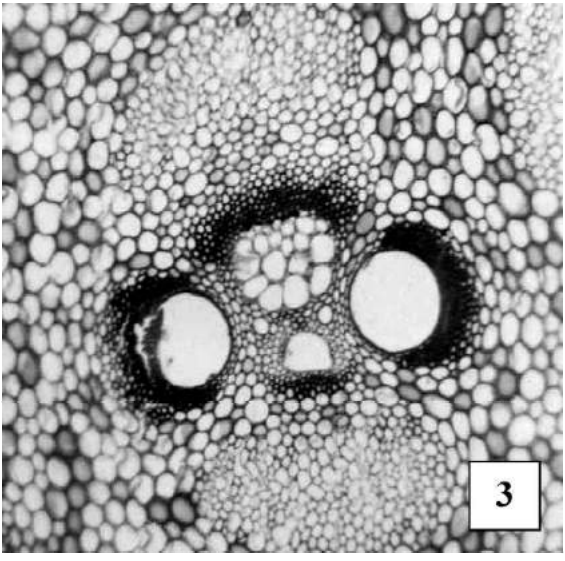

Figure 3. Cross-sections of 2-month-old culms of *D. strictus* and *B. bambos* showing vascular bundles with their fibrous sheaths. *B. bambos* culm base inner part with only a few lignified fibres.

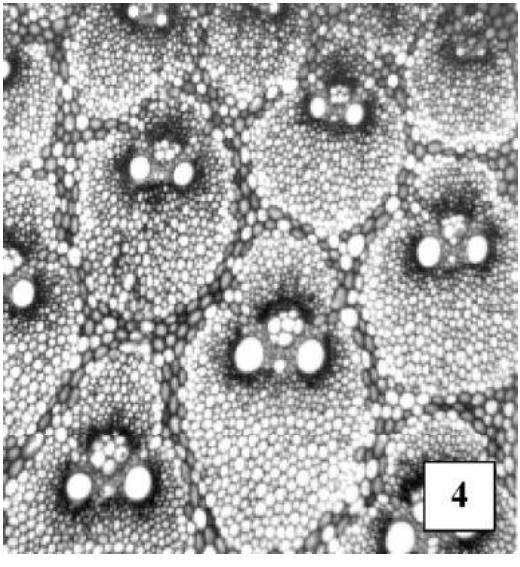

Figure 4. Cross-sections of 2-month-old culms of *D. strictus* and *B. bambos* showing vascular bundles with their fibrous sheaths. Culm top, outer part with mostly thin walled unlignified fibres. The scale bar in Fig. 2 indicates 325 μm for Figs 1, 2 and 3, and 360 μm for Fig. 4.

The sequence of changes in cell-wall structure during maturation of fibrous and ground tissues has been studied in great detail [1–5, 19]. Based on these studies it is found that the maturation process proceeds quite differently across the culm wall, being influenced by the position of vascular bundles and the position of fibres

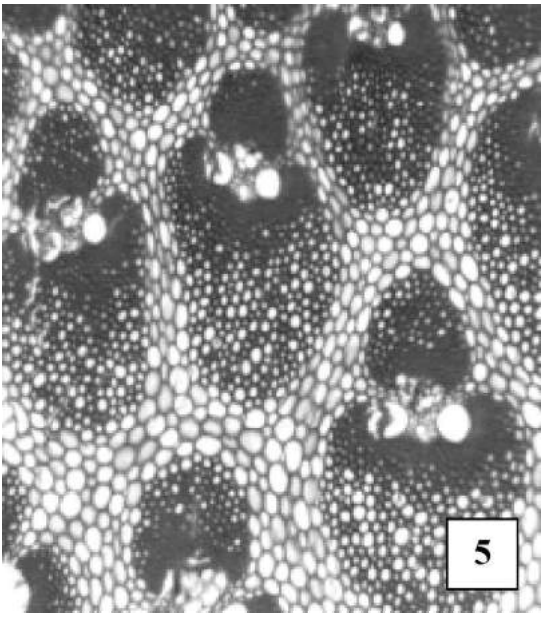

Figure 5. Cell-wall thickening and lignification in fibres in outer bundles in *B. bambos.*

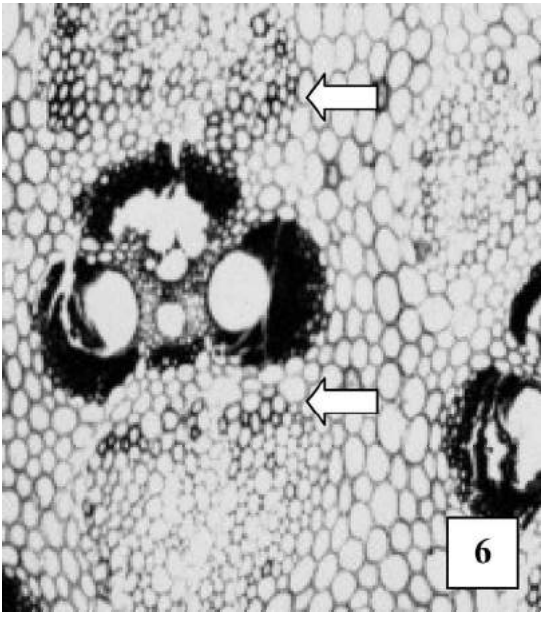

Figure 6. Initiation of wall thickening in fibres of peripheral fibrous sheaths in *B. bambos*; note a few fibres (at arrows) that have begun cell wall thickening.

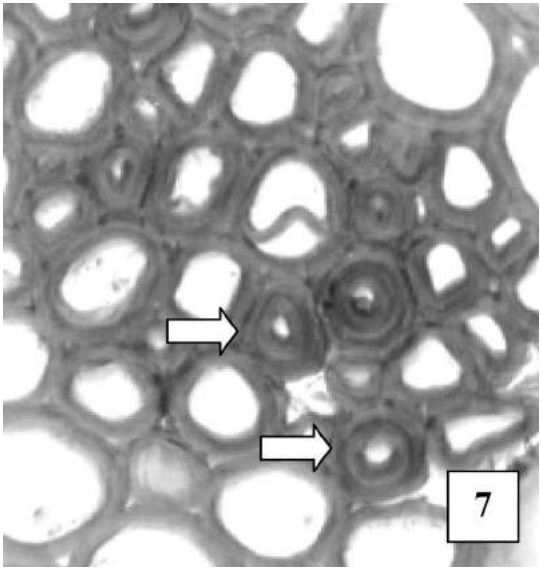

Figure 7. Fibres with polylamellate cell wall structure and thick-walled parenchyma cells in outer part of the 1-year-old culm wall in *D. strictus* (at arrows).

within the bundle. Wall thickening of bundle sheath fibres within a bundle is found to start from inner vascular side and proceed outwards.

Thickening of fibre walls was accomplished by the deposition of additional cell-wall lamellae, as evident from the structure of fibre walls; some of the fibres within the outer bundles showed polylamellate wall structure even in one-year-old material (Fig. 7, arrows). Even the ground parenchyma cells showed thick cell walls but lamellated structure of walls was not discernible (Fig. 7). In five-year-old culms highly thickened walls showing a distinct polylamellate structure and a narrow lumen (Fig. 8) were common in a large proportion of fibres in outer bundles. The thickened cell walls of the ground parenchyma were also lignified at this stage. However, even at the age of five years, the fibre walls of inner vascular bundles were not fully thick-walled and lignified. This indicates a lag in maturation of at least some fibres in the inner bundles. It has been found in several earlier studies [3, 4, 21] that fibre maturation is a process prolonged over many growing seasons and the number of lamellae in the cell walls continues to increase with culm age during, and even after culm maturation.

The thickening of fibre walls during culm maturation and ageing has been demonstrated by Liese and Weiner [3, 19] in *Phyllostachys viridioglaucescens* through measurement of fibre-wall thickness in culms of different age groups. Since the dimensions of fibres across the culm wall are highly variable at any stage, depending on their position, careful characterization of fibre types was found important for measurement of their wall thickness. Generally, the contiguous parenchyma of fibres shows polylamellate thick walls; those in contact with vascular

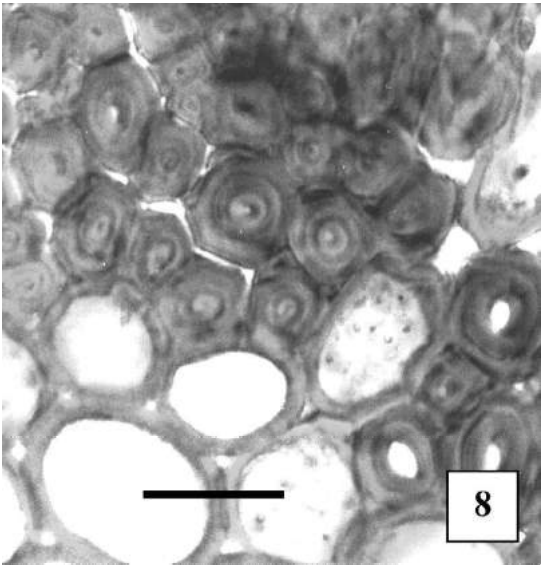

Figure 8. Thick-walled fibres with polylamellate cell-wall structure common in a 5-year-old culm. The scale bar in Fig. 8 indicates 400 μm for Fig. 5, 360 μm for Fig. 6 and 65 μm for Figs 7 and 8.

Table 3.
Changes in average double wall thickness (μm) of different types of fibres and ground parenchyma cells in culms of different age groups in *B. bambos* and *D. strictus*

Cell type	*Bambusa bambos*			*Dendrocalamus strictus*		
	2 months	1 year	5 years	2 months	1 year	5 years
Thick-walled fibres	8.4	9.1	9.3	8.0	7.4	7.8
	(0.7)	(0.6)	(0.6)	(0.6)	(0.6)	(0.5)
Medium thin-walled fibres	7.7	8.1	9.1	6.9	7.9	8.0
	(0.5)	(0.6)	(0.6)	(0.5)	(0.7)	(0.5)
Thin-walled fibres	5.6	6.0	6. 9	3.8	5.1	7.4
	(0.3)	(0.8)	(0.6)	(0.6)	(0.5)	(0.7)
Ground parenchyma cells	4.1	4.9	6.3	3.3	4.3	7.8
	(0.6)	(0.8)	(0.4)	(0.8)	(0.7)	(0.3)

Values in parentheses are SD of the mean.

tissue are narrow while those lying in the centre are larger [3]. In the present study, the extent of cell-wall thickening of three categories of fibres and ground parenchyma cells at the culm base in three selected age groups of *B. bambos* and *D. strictus* was compared (Table 3) only to further confirm the microscopic observation on cell wall thickening in relation to age, and to see if the different categories of fibres behaved differently with regard to cell-wall thickening.

From Table 3 it is evident that, in general, there was an increase in cell-wall thickness of culm tissues as age increased. While the increase in wall thickness of thick-walled fibres was either inconsistent or less pronounced, that of other

categories of fibres and ground parenchyma cells showed a consistent increase with age. This suggests that cell-wall thickening proceeds at different rates and at different age stages in various categories of fibres and parenchyma cells; thick-walled fibres are probably the first to undergo this process, as supported by microscopic observations. In ground parenchyma cells, wall thickening steadily increased between age groups analysed.

Age-related changes in physical properties

It is generally accepted that the changes in cell-wall thickening and lignification of tissues accompanying increase in age of the culms have got direct influence on physical and mechanical properties of the culm material. It is found that the density increases and the moisture content decreases with increase in culm age [3, 6, 22]. In order to verify these observations in *B. bambos* and *D. strictus*, the average density and moisture content percentage values of different age groups were compared. The results are shown in Fig. 9.

It is clear from Fig. 9 that the basic density was less than 300 kg/m^3 in 2-month-old culm material in both *B. bambos* and *D. strictus*, which increased sharply to nearly 600 kg/m^3 during the initial two years. The subsequent increase in density was comparatively less pronounced in both the species. The moisture content percentage which, in contrast to density, decreased with age, showed a sharp decline from a high value during the initial two years of culm age and subsequently maintained more or less a stable value. The seasonal variation in the moisture content reported in bamboo tissues [23, 24] was not analysed in the present study. In general, the density and M.C. (moisture content) curves in both the species indicate an initial phase of abrupt change up to the first 2 years and a gradual change up to three years which can perhaps be attributed to the maturation process of culm tissues. Microscopic examination of cell walls of fibres and ground parenchyma also support this observation, since considerable cell-wall thickening and lignification occurred during the first year of the culm development. Decrease in moisture content with age which has also been observed in other instances has been thought to be result of thickening of fibre walls [16, 23, 25]. Studies have shown that the developmental processes of culm maturation of bamboos are completed within 2 to 3 years and the cell-wall thickening and lignification of tissues that subsequently occur in a second phase are related to the ageing process [3, 6, 22].

CONCLUSIONS

From the anatomical observations and related data gathered in the present study it is concluded that culm maturation in *B. bambos* and *D. strictus* involves developmental changes, such as cell-wall thickening and lignification of culm tissues; these changes do not occur simultaneously throughout the culm but follow a definite sequence across the culm wall and along the culm axis. In both *B. bambos*

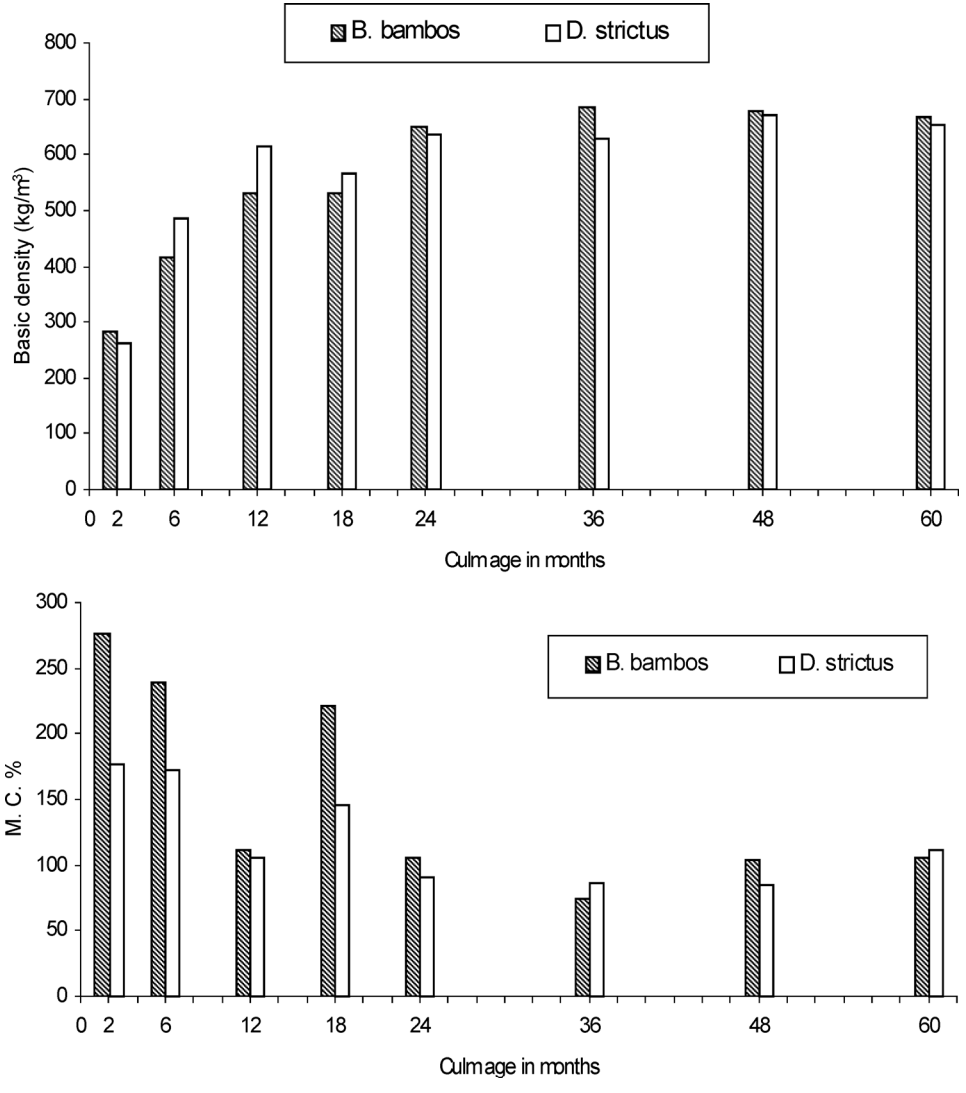

Figure 9. Changes in basic density and M. C. in relation to age in *B. bambos* and *D. strictus.*

and *D. strictus* maturation process was rapid for the first two years before it slowed down during the third year and stabilized after the third year. This suggests that for harvesting mature bamboo, the culms should have completed at least two years development so as to take advantage of the rapid phase of cell wall thickening and lignification.

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