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VARIATION IN PHENOLOGY, GROWTH, AND WOOD ANATOMY OF *TOONA SINENSIS* AND *TOONA CILIATA* IN RELATION TO DIFFERENT ENVIRONMENTAL CONDITIONS

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Tree-ring proxy data from subtropical to tropical Australasia are valuable though rare sources for climate reconstructions. *Toona sinensis* (A. Juss.) M. Roem. and *Toona ciliata* M. Roem. occurring naturally in this region are among the most promising tree species for future tree-ring research. However, little is known about their phenological behaviors and the influence of environmental conditions on their intraseasonal growth and wood anatomical properties. Growth experiments were conducted on young trees of both species to investigate their responses to different treatments. The results show that phenology and growth were adjusted according to the severity of the treatments. Restricted growth conditions often caused longer leafless periods, shorter flushes of leaves, and decreased height and diameter growth increments, and they resulted in more but smaller vessels. Under optimum conditions, *T. ciliata* did not become leafless, had multiple leaf flushes, sustained growth throughout the experiment, and did not form a tree-ring boundary. All other specimens of both species entering leafless or at least semileafless periods formed one tree-ring boundary during the experiment. The growth reaction was more distinct in the latewood than in the earlywood, in extreme cases suppressing the latewood totally. Although the experiment was conducted on young trees and hence should not simply be generalized and applied to adult specimens, the results indicate that both species are well suited for reliable future dendroclimatological investigations. Such studies need to pay attention to possible missing rings in the young parts of tree-ring series.

Keywords: growth experiment, tree-ring boundary, deciduousness, dormancy, vessel characteristics.

Introduction

Toona sinensis (A. Juss.) M. Roem. and *Toona ciliata* M. Roem. appear exclusively in Australasia. *Toona ciliata* extends naturally from eastern Pakistan and India through southeast Asia and southern China and through Hainan Island to the Philippines and eastern Australia. Natural populations of *T. sinensis* occur in southeast Asia from India and Nepal eastward through China, Burma, and Thailand to Malaysia and Indonesia. The species are similar in their habitat demands; that is, both are present in tropical to subtropical highland forests. In Asia, both species grow in the same forest types, but they occupy different niches, with *T. ciliata* preferring the wetter locations with richer soils. Both species grow best under a uniform summer rainfall regime but at most locations have to adjust to a dry season during the winter months. In comparison to *T. ciliata*, *T. sinensis* can flourish on a wider range of soil types and is slightly more frost and drought hardy (Floyd 1979; Edmonds 1995; Edmonds and Staniforth 1998; Boland et al. 2002).

Both species are susceptible to attacks by shoot borers (*Hypsipyla robusta* and *Batocera horsfieldi*), which bore into the new shoots and excavate a hollow, causing the growing tip above to die. The attack on young trees can destroy the form, result in partial defoliation, suppress growth, and even kill them. It is probable that at least several generations of the insect would occur each year, but long-term fluctuations of its populations have not been reported. In contrast to insect infestations of other tree species, for example, in Europe, the effects of the *Toona* shoot borers on stem growth and wood anatomy are not known (Mo et al. 1997*a*, 1997*b*).

The causal connections between environmental conditions, phenological behavior, cambial periodicity, and tree growth are relatively well known for tree species from temperate regions of the Northern Hemisphere. However, for tropical tree species from the Southern Hemisphere, comparable data are rather scarce. In Indonesia, first studies examined the phenology and physiology of local and exotic tree species (Volkens 1903; Simon 1914; Coster 1923, 1927, 1928). Coster (1928) concluded that the tendency of rhythmic growth is genetically fixed but the periodicity can be altered by changing the growing conditions. These early results were confirmed by Fahn and Werker (1990) and Koriba (1958), working on *Eucalyptus camaldulensis* Dehnh. and *Acacia dealbata* A. Cunn., respectively. In contrast, Daubenmire (1972) observed no differences in the phenology of phreatophytes growing at different locations with diverse site conditions.

Several studies report that the phenological behavior and growth periodicity of tropical trees are influenced by different environmental factors, including day length (Njoku 1963,

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1964; Daubenmire 1972; Frankie et al. 1974; Breitsprecher and Bethel 1990; Rivera and Borchert 2001), internal water status, soil moisture, and relative humidity (Reich and Borchert 1984; Wright and Cornejo 1990; Williams et al. 1997; Myers et al. 1998; Schöngart et al. 2002), thermoperiodic mechanisms (Alvim 1964), and temperature (Paliwal and Prasad 1970; Paliwal et al. 1975; Ghouse and Hashmi 1979; Iqbal and Ghouse 1982; Ajmal and Iqbal 1987).

Annual tree-ring formation relies on a shift of the cambium into dormancy once a year (Strasburger et al. 2002). In the tropics, saplings of many tree species remain evergreen and show continuous growth for several years. With increasing size, the trees start to shed their leaves during the dry season and become dormant for increasingly longer periods (Coster 1928; Chowdhury 1961; Fahn et al. 1981; Tomlinson and Longman 1981; Priya and Bhat 1999). While deciduousness is an obvious sign of dormancy, ring formation might also be related to bud flushing, as has been shown for more than a dozen tree species in India (Iqbal 1981) and Africa (Amobi 1972) that usually produce several growth rings per year, often in phase with multiple bud flushes. Furthermore, Amobi (1973, 1974) found that the initiation of the cambial activity was correlated with bud break and leaf formation. While in seedlings the number of tree rings did not tally with the total number of bud flushes, the numbers corresponded well in the wood formed by older cambium. Alternatively, Tomlinson and Craighead (1972) described that *Swietenia macrophylla* King underwent several periods of leaf flushing each year but tended to produce strictly annual rings. In a similar study in India, Chowdhury (1958) counted up to four flushes of extension growth but only one period of radial growth and suggested that extension and radial growth can be separate processes even within the same tree.

There is clear evidence in the literature proposing that wood anatomy is a good indicator of different environmental conditions. For example, in an extensive study, Carlquist (1966) examined 328 different Compositae species and discovered general trends in wood anatomical properties, for instance, that the vessel numbers increased and their diameters decreased in a transition from mesic to arid environments. Similar results were reported by Baas (1973), Barajas-Morales (1985), Wilkins and Papassotiriou (1989), Wheeler and Baas (1993), Lindorf (1994), and Woodcock and Ignas (1994). Additional variances because of different environmental conditions within wide latitudinal ranges were found in the distinctiveness of the growth rings and parenchyma bands delimiting individual rings (Dadswell and Ingle 1954) and in the porosity of the tree-ring structures changing from ring-porous to diffuse-porous (Liphschitz and Waisel 1970; Priya and Bhat 1999).

Both *T. ciliata* and *T. sinensis* also exhibit large latitudinal distributions, and thus it can be expected that their wood anatomies also vary because of shifts in the environmental conditions of the respective climate zones they grow in. Several examples of false rings and difficult ring-boundary zones, for instance, zones of very narrow tree rings in *T. ciliata*, have been presented by Heinrich and Banks (2006) (fig. 1). Since tree-ring analysis of the two species is planned, it seems necessary to first conduct growth experiments to examine the influence of the environment on the wood anatomy and the periodicity of the two *Toona* species. Our study tries to cover all aspects of the relationship between phenology, cambial activity, tree-ring structure, and wood anatomy, accounting for the fact that the ecology of the two species is poorly understood.

Material and Methods

A growth experiment with six groups was set up on December 5, 2001, in Canberra to examine the growth responses of trees to different stress factors imposed by the treatment (table 1). Each group X_1–X_6 consisted of six 2-yr-old individuals with heights and diameters of ca. 1.3 m and 1.5 cm, respectively. Each group contained four specimens of *Toona sinensis* (plants 1–24) but only two of *Toona ciliata* (plants 25–36) because of the limited availability of suitable *T. ciliata* seedlings. All groups were kept in glass houses with an automatically regulated optimum temperature of ca. 25°C. Only group X_4 was positioned outside under thin shade cloth to expose the plants to seasonal temperature variations and to filter detrimental effects of direct sunlight. The plants in the optimum water groups were watered at least every day, in summer two to three times a day. In comparison, in the minimum water group, to imitate a much drier environment, the trees were only watered once every 2–7 d, depending on the season. Groups X_1–X_4 received an optimum supply of nutrients by application of slow-release fertilizer tablets Scout Osmocote (nitrogen 18%, phosphorus 4.8%, and potassium 9.1%), while groups X_5 and X_6 did not obtain any nutrition, in order to simulate poor soil growth conditions. Most of the time, group X_3 was treated exactly like optimum group X_1, but in the middle of the growing period, the plants were not watered for 11 d. Optimum watering was resumed after the trees started to shed leaves and leaves showed

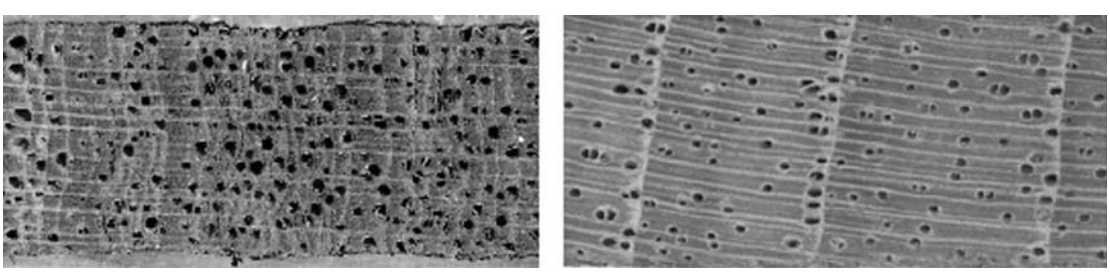

Fig. 1 Examples of narrow (left) and wide (right) rings in *Toona ciliata*.

Table 1

Treatment Groups in Growth Experiment

Treatment	Fertilizer	No fertilizer
Optimum water and optimum temperature	X_1 (trees 1–4, 25–26)	X_5 (trees 17–20, 33–34)
Minimum water and optimum temperature	X_2 (trees 5–8, 27–28)	X_6 (trees 21–24, 35–36)
No water for 11 d and optimum temperature	X_3 (trees 9–12, 29–30)	
Optimum water and minimum temperature	X_4 (trees 13–16, 31–32)	

distinct signs of wilting, indicating that the treatment had imitated well conditions experienced during natural droughts or shoot borer attacks.

The Pinning Method

The pinning method was first employed and described by Mariaux (1967) and Wolter (1968). They found that an injury of the cambium, applied by a nail, needle, or scalpel, resulted in the formation of aberrant parenchyma-like cells that were permanently retained, recognizable, and datable within the growth zone. Kuroda and Shimaji (1984) demonstrated for the first time that the pinning method also works for hardwoods on an intraseasonal timescale. They found that hardwood species started to form wound tissue even faster than softwood species. Because of a less delayed response time, dating of injury events would be more accurate in hardwood species. The findings were supported by the application of the method to tree-ring analysis (Kuroda and Shimaji 1985; Kuroda 1986; Shiokura 1989; Nobuchi et al. 1995; Sass et al. 1995; Fujii et al. 1999; Bauch and Dünisch 2000).

For this study, small pins were inserted into the stem from the four cardinal points in order to induce minute wound tissue discernible as a useful marker during the subsequent wood anatomical analysis. In the course of the experiment, the plants were pinned quarterly, on February 5, May 7, August 3, and November 12, 2001, and pinning areas were marked with different colors for later identification. The quarterly pinning areas were located adjacent to each other along the stems, preventing interference between the pinning zones. Initial measurements of plant heights and diameters were taken and were repeated every quarter parallel to the application of the pinning. The phenology and general condition of the plants were recorded weekly. On January 29, 2002, the experiment was terminated by crosscutting the stems close to the different pinning areas.

Preparation of Samples for Microscopy and Digital Imagery

For further microscopic analysis, thin transverse sections of the consecutive pinning areas were cut. A Zeiss Axioskop equipped with a digital camera was utilized to conduct light microscopy. First, the samples were examined for possible tree-ring boundaries and false rings formed during the experiment. Tree-ring boundaries were delimited by a light-colored line of parenchyma cells and a zone of large earlywood vessels, visible to the naked eye. These observations were then combined with weekly phenology data, that is, occurrences of semileafless (ranging from only a few leaves to almost all leaves shed) and leafless (all leaves lost) periods and leaf flushes collected during the experiment. Second, the images of the pinning areas were imported to the digital imagery software ImageJ (supplied by the National Institutes of Health). The distance from each wound tissue to the cambium was measured at four randomly chosen radii. Along these radii, outside the wound tissue zones, the numbers and diameters of all individual vessels that were cut or touched by the radii were measured manually, and results were averaged for each quarterly pinning zone per tree (fig. 2). This method is similar to the line intersect method often used in forest ecology studies (Van Wagner 1968). In wood anatomy studies, vessel area measurements are usually related to a standard area to standardize the data obtained from trees of different ages and sizes or from different parts of a tree for better comparability. In this study, the application of the less time-consuming line intersect method was justified because the material analyzed was formed at the same time of the year, ensured by the quarterly pinning procedure, and because the seedlings were all of exactly the same age and size at the beginning of the experiment.

The vessel diameters were classified into large and small size classes. The limits for *T. ciliata* were set at 160–80 and 40–20 μm, and for *T. sinensis*, at 160–60 and 30–10 μm. The remaining vessels were excluded from further analysis. The gaps between the size classes were set deliberately to concentrate on only the largest and smallest vessels and to accentuate the differences between the two size classes. Vessel diameter measurements were converted into values of area, accepting a systematic error due to the assumption that all vessels exhibit a circle shape in cross section. Sums of vessel diameter measurements along individual radii between the pinning wound tissues and the cambium were divided by the length of the corresponding radii in order to relate the sums of vessel areas to the growth increments. The results are presented as box plots of vessel areas and of vessel areas in relation to growth increments of *T. ciliata* and *T. sinensis* for the different treatment groups separately.

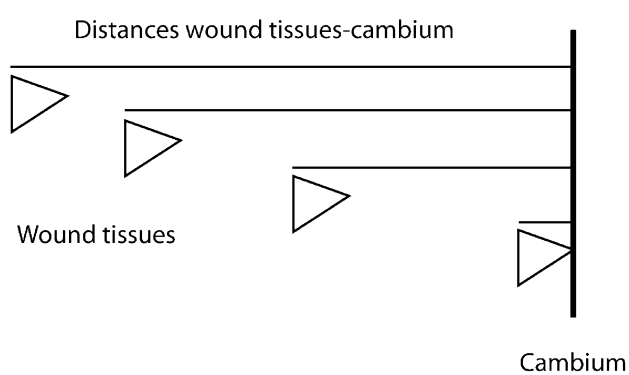

Fig. 2 Diagram of measurements along individual radii between pinning marks and cambium.

The influence of the different treatments on the vessel areas unrelated and related to the distance between pinning wound tissue and cambium was investigated quantitatively using the software package S-PLUS. The analysis started with an assessment of the normality of the data using histograms. The distribution of the data was skewed and had to be log-transformed in order to conform to a normal distribution before further analysis could be applied. The S-PLUS diagnostic plots (i.e., residual plots) and Cook's distance were used to ensure constant variance and absence of outliers, respectively. ANOVA was conducted for *T. ciliata* and *T. sinensis* separately to check the variances of the data between and within groups X_1–X_6. Furthermore, a linear model was computed to determine which group means differ from the optimum group X_1, and significant values are printed in boldface in tables 2 and 3.

Results

Phenology and Ring Formation Data

Phenological observations and tree-ring formation data are combined in figure 3. The bars indicate periods of semileaflessness (*a*), full leaflessness (*b*), leaf flushes (*c*), and ring-boundary formation (*d*). The figure is subdivided into groups according to treatments X_1–X_6. It shows that most trees of *Toona sinensis* became semileafless and then fully leafless, except for trees 1, 3, 4, 9, and 12, which became only semileafless. The deciduous phase in *T. sinensis* was always followed by a leaf flush and ring-boundary formation. In comparison to groups X_1 and X_4, the periods of leaf flushes were shorter in X_2 and X_3 and much shorter in X_5 and X_6. Most trees of *T. sinensis* formed ring boundaries after the third pinning in early August, except for tree 1, which did not form a ring at all, and tree 21, which formed a ring at the end of the experiment.

Table 2

Linear Model of Small- and Large-Vessel Area Data for *Toona sinensis* and *Toona ciliata*

	T. sinensis			*T. ciliata*		
Treatment group	Value (log)	SE	*t*	Value (log)	SE	*t*
Small-vessel data:						
X_2	−1.57	0.17	**−9.34**	−0.21	0.22	−0.94
X_3	0.06	0.13	0.49	−0.44	0.22	**−2.01**
X_4	0.10	0.12	0.84	−0.66	0.24	**−2.77**
X_5	−1.02	0.21	**−4.86**	−0.70	0.21	**−3.33**
X_6	−1.24	0.16	**−7.72**	−0.97	0.22	**−4.42**
F	41.36			5.116		
P	0			0.0003		
Large-vessel data:						
X_2	−0.37	0.12	**−3.20**	−0.55	0.22	**−2.44**
X_3	0.13	0.12	1.11	0.39	0.20	1.95
X_4	0.70	0.11	**6.17**	0.01	0.24	0.05
X_5	−0.07	0.13	−0.53	−0.73	0.24	**−3.01**
X_6	−0.65	0.20	**−3.31**	−0.68	0.30	**−2.22**
F	24.65			7.063		
P	0			0.00001		

Note. Boldface indicates significant results.

Table 3

Linear Model of Small- and Large-Vessel Area Data in Relation to Each Distance between Pinning Wound Tissue and Cambium for *Toona sinensis* and *Toona ciliata*

	T. sinensis			*T. ciliata*		
Treatment group	Value (log)	SE	*t*	Value (log)	SE	*t*
Small-vessel data:						
X_2	0.45	0.18	**2.53**	0.72	0.29	**2.45**
X_3	0.03	0.13	0.23	−0.55	0.29	−1.91
X_4	0.20	0.13	1.52	0.40	0.31	1.28
X_5	1.13	0.22	**5.14**	1.13	0.28	**4.10**
X_6	1.98	0.17	**11.72**	1.96	0.29	**6.76**
F	37.69			18.55		
P	0			0		
Large-vessel data:						
X_2	1.43	0.14	**10.55**	0.38	0.27	1.42
X_3	0.05	0.14	0.36	0.36	0.24	1.53
X_4	0.63	0.13	**4.85**	0.69	0.28	**2.42**
X_5	2.15	0.15	**14.41**	0.53	0.29	1.80
X_6	1.68	0.23	**7.39**	1.59	0.36	**4.36**
F	68.54			4.196		
P	0			0.001717		

Note. Boldface indicates significant results.

Only trees 28 and 31 of the *Toona ciliata* specimens became fully leafless, while trees 27, 32, 33, 34, 35, and 36 stayed semileafless, although all of them formed a ring boundary. In contrast, trees 25, 26, 29, and 30 had multiple leaf flushes for an extended period of time, but they neither entered leafless periods nor formed a ring. Periods of leaf flushes were shorter in group X_4 compared to X_1 and X_3 and even shorter in X_5 and X_6. Most trees formed ring boundaries after the third pinning in early August, except for trees 28 and 34, which had already formed a ring after the second pinning in early May.

Diameter and Height Growth Data

Figure 4 displays height (*left*) and diameter (*right*) growth data of *T. sinensis* (*gray bars*) and *T. ciliata* (*black bars*), showing distinct differences between the treatment groups. *Toona ciliata* generally exhibits larger height and diameter growth in all treatment groups, except for smaller height values in group X_4. The largest and smallest values of height and diameter growth in *T. sinensis* are found in groups X_4 and X_2 or X_3 and X_6, respectively, while the corresponding groups for *T. ciliata* are X_3 and X_4 or X_3 and X_6, respectively. Both height and diameter growth of *T. sinensis* are divided in two: good growth in groups X_1, X_3, and X_4 and slow growth in X_2, X_5, and X_6. In contrast, large height increments of *T. ciliata* occur in X_1–X_3 and slow growth in X_4–X_6. Diameter growth of *T. ciliata* was most limited in groups X_5 and X_6, less limited in groups X_2 and X_4, and least limited in groups X_1 and X_3.

To illustrate the growth activities of both species in time, growth percentages summed to 100 for the individual treatment groups derived from the quarterly diameter measurements over bark are presented (fig. 5). Between February and August, the percentage increases of all *T. sinensis* are low

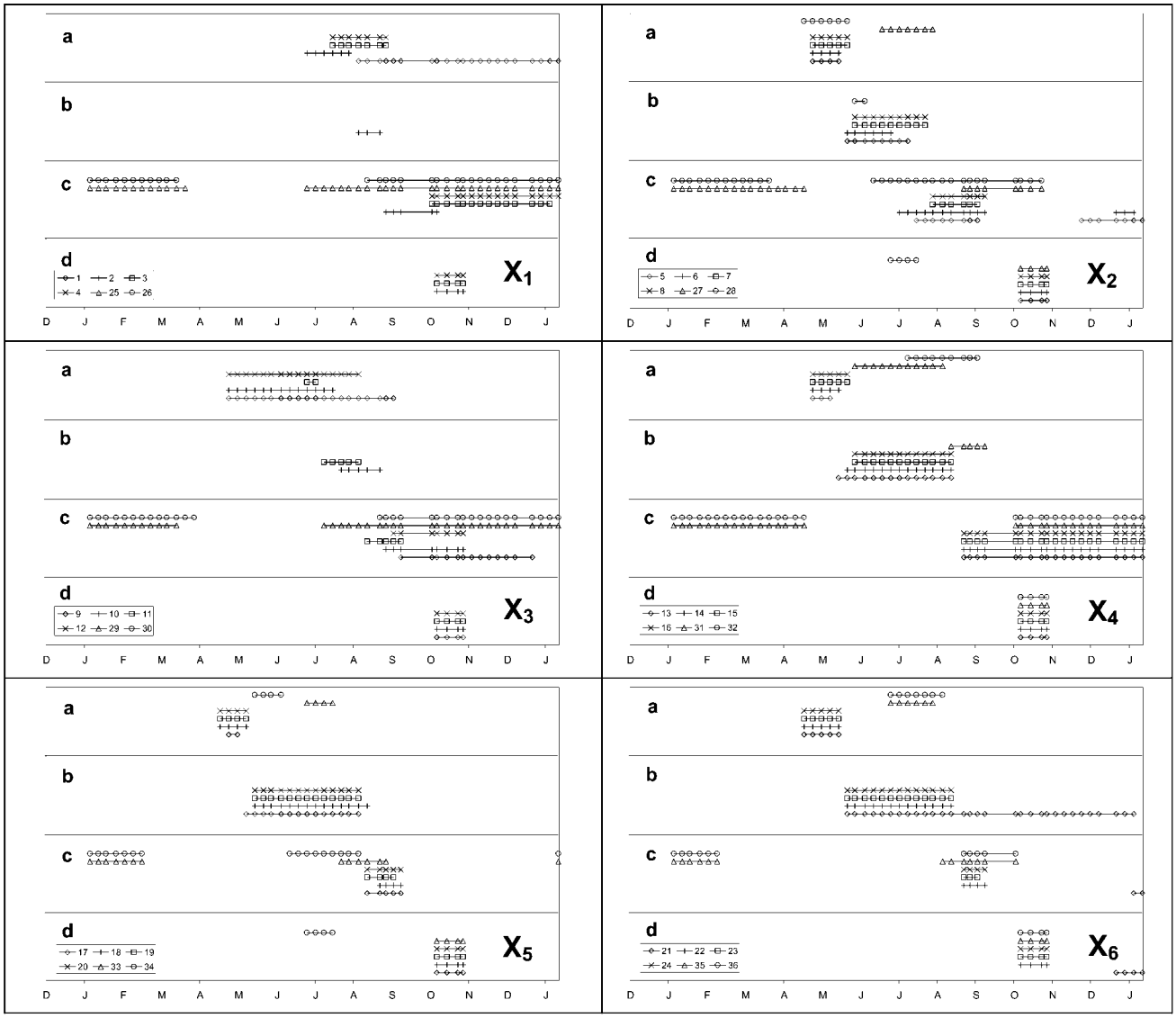

Fig. 3 Monthly periods of semileaflessness (*a*), leaflessness (*b*), leaf flushes (*c*), and tree-ring formations (*d*) of *Toona sinensis* (trees 1–24) and *Toona ciliata* (trees 25–36) in treatment groups X_1–X_6.

compared to the other periods, indicating dormancy during this time. Diameter growth of *T. ciliata* in groups X_1 and X_3 did not slow, and thus the trees probably did not enter a dormant period. However, trees in group X_6 stopped growing completely between May and August, while the specimens of the remaining groups X_2, X_4, and X_5 exhibit distinct growth reduction only between May and August.

Vessel Characteristics

The vessel counts in the different treatment groups also vary significantly (fig. 6). Large vessels of *T. sinensis* are most common in groups X_1–X_4, while small vessels are most abundant in groups X_1, X_3, and X_4 but less plentiful in the other groups. In *T. ciliata,* the most large vessels are found in groups X_1 and X_3 and the fewest in group X_6. The differences of the vessel counts in the small-size class are not as distinct as in the large-size class, with the largest and smallest values displayed in groups X_5 and X_4, respectively.

Box plots present the distribution of the vessel areas per treatment group (fig. 7). The data of *T. sinensis* for the small-vessel area in groups X_1, X_3, and X_4 are significantly larger than those in the other groups. In the large-vessel box plot, the vessel area is significantly larger in group X_4 than in the other groups. The groups X_1, X_3, and X_5 display approximately average values, while groups X_2 and X_6 show the smallest values.

The box plots for the small-vessel area of *T. ciliata* show decreasing values from groups X_1 through X_6. The values in group X_1 are significantly larger than those in groups X_4–X_6, with group X_6 exhibiting the smallest values. The box plot

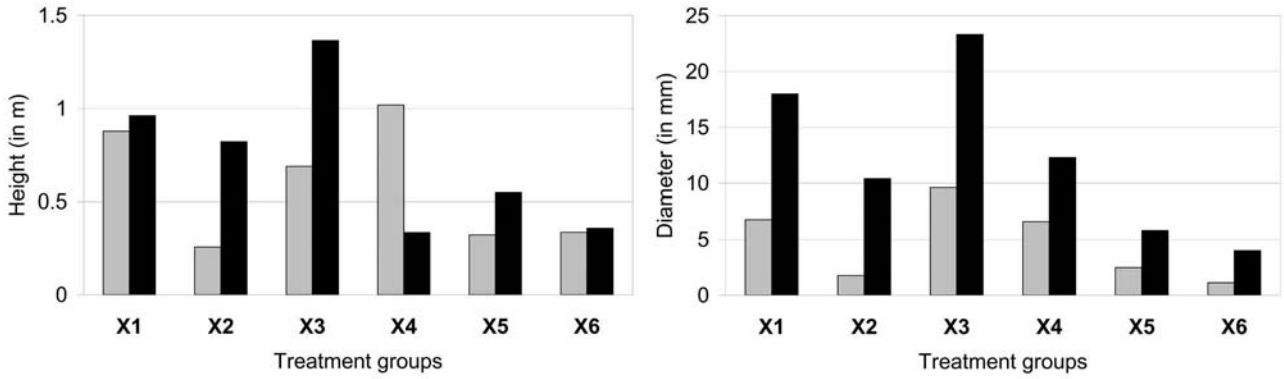

Fig. 4 Total height (left) and diameter (right) growth increments per treatment group of *Toona sinensis* (gray bars) and *Toona ciliata* (black bars).

for large vessels shows large values in groups X_1 and X_3 and smaller values in groups X_2, X_5, and X_6.

The box plot for the small-vessel area of *T. sinensis* illustrates that groups X_2, X_5, and X_6 have the largest ratios of vessel area to diameter increment, a pattern that is repeated even more significantly in the large-vessel class (fig. 8). Similar results are evident in the box plots for *T. ciliata*. The small-vessel area classes show larger values in the minimum treatment groups X_2, X_5, and especially X_6. Group X_6 has significantly larger values than the other groups in the large-vessel area class.

The results of the ANOVA indicate that the vessel area measurements in both vessel size classes and species differ significantly between the treatment groups. The linear model computations confirm the graphical results from the box plots. For *T. sinensis*, significant differences from group X_1 in the small- and large-vessel areas are shown for X_2, X_5, and X_6 and for X_2, X_4, and X_6, respectively. The optimum group X_1 displays significant differences from groups X_3–X_6 in the small-vessel class and from X_2, X_5, and X_6 in the large-vessel class in *T. ciliata* (table 2). The values for *T. sinensis* exhibit significant differences in vessel area–diameter increment ratios between X_1 and X_2, X_5, and X_6 in the small-vessel class and between X_1 and X_2, X_4, and X_6 in the large-vessel class. The analogous values for *T. ciliata* show significant differences between X_1 and X_2, X_5, and X_6 and between X_1 and X_4 and X_6, respectively (table 3).

Discussion

Growth experiments were conducted to examine the responses of *Toona sinensis* and *Toona ciliata* in terms of phenological behavior, tree-ring formation, height and diameter growth, and vessel characteristics. The results show that the treatments were successful in both species in altering all these aspects, except for tree-ring formation, which was not affected in *T. sinensis*. However, the treatments had weaker effects on the phenological behavior of *T. sinensis* than on that of *T. ciliata*. Of the former species, 83% became leafless, 100% became semileafless, and 100% formed a ring boundary, while the respective values for *T. ciliata* were 17%, 50%, and 67%. During the entire experimental period, 33% of *T. ciliata* did not show any signs of deciduousness and did not form a tree ring, indicating that *T. ciliata* reacted more opportunistically to the optimum treatment than *T. sinensis*. This suggests that at least young trees of *T. ciliata* can adapt to favorite environmental conditions by suppressing dormancy, but *T. sinensis* seems unable to prevent entering it.

The experiment also illustrates that trees of both species that went through at least a semileafless phase during the experiment formed a tree ring as well. Obviously, leaflessness, whether partial or full, can be regarded as an indication of dormancy. In contrast, several leaf flushes without a period of deciduousness in between, as observed in *T. ciliata*, were not sufficient to induce a ring formation because the

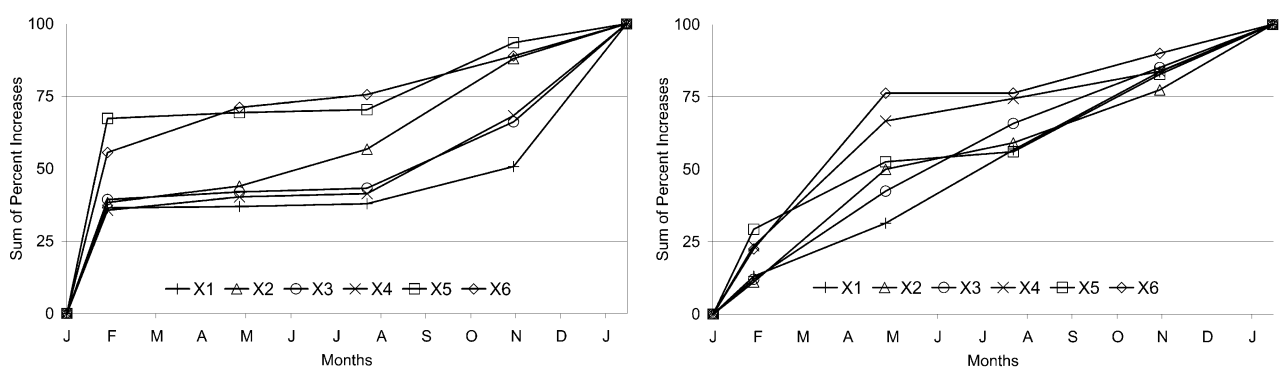

Fig. 5 Percentage diameter increases per treatment group of *Toona sinensis* (left) and *Toona ciliata* (right).

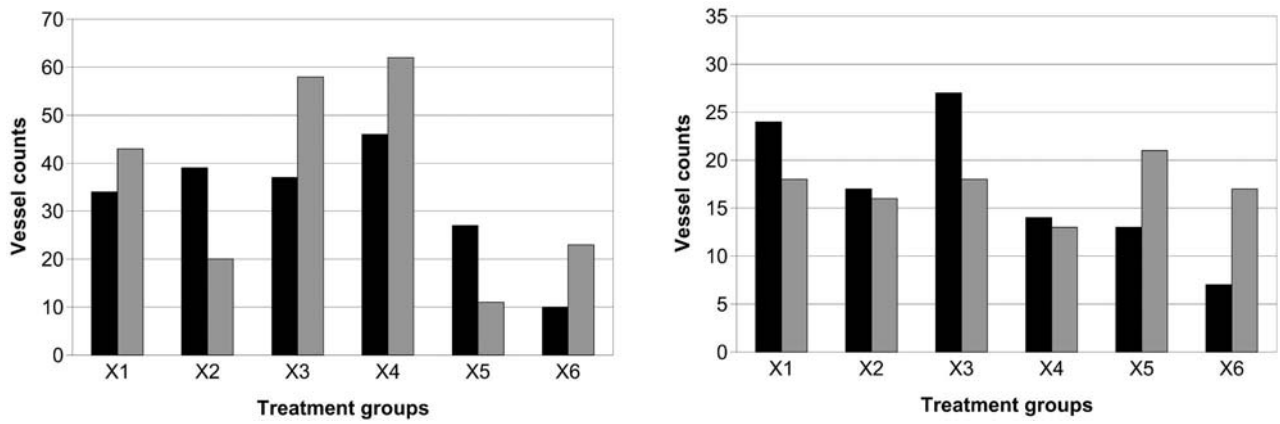

Fig. 6 Total numbers of large (black bars) and small (gray bars) vessels per treatment group for *Toona sinensis* (left) and *Toona ciliata* (right).

cambium noticeably did not become dormant between periods of leaf flushes. Furthermore, in shading experiments, specimens of *T. ciliata* produced multiple leaf flushes without forming tree rings (Heinrich and Banks 2006). This affirms results by Chowdhury (1958) and Tomlinson and Craighead (1972), who found that multiple leaf flushes did not result in the same amount of tree rings.

Insect attacks might sometimes result in loss of foliage followed by a leaf flush in order to immediately rebuild the photosynthetic apparatus. Although trees in group X_3 showed signs of wilting and shed some leaves, tree-ring formation and growth increments were not affected significantly. This indicates that the treatment in group X_3 was not sufficient to reduce diameter growth increments and hence that only heavy insect attacks might result in reduced diameter growth increments. Heinrich and Banks (2006) showed that only total defoliation of *T. ciliata* seedlings was successful in inducing a false tree ring that consisted of a line of vessels embedded in parenchyma cells. The vessels in the boundary of the false tree ring did not markedly differ in size from the vessels formed immediately before and after. Although a collapse of stem growth and formation of false rings might be expected in seedlings, this is less plausible for mature trees in natural forest habitats. Larger trees have the ability to

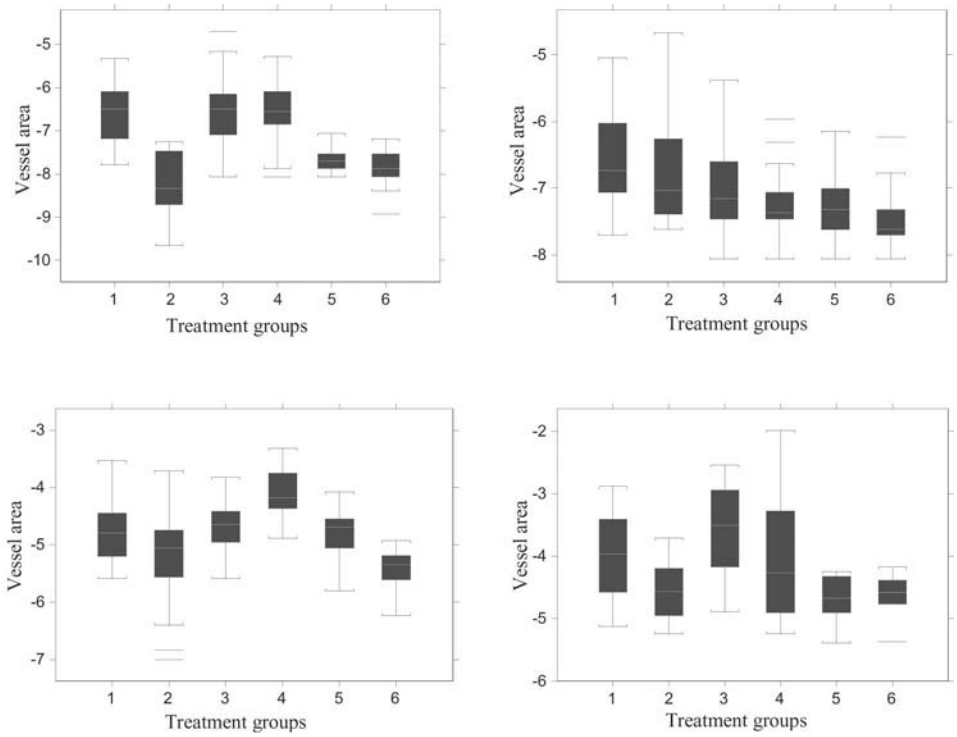

Fig. 7 Box plots of small-vessel (top) and large-vessel (bottom) area per treatment group for *Toona sinensis* (left) and *Toona ciliata* (right).

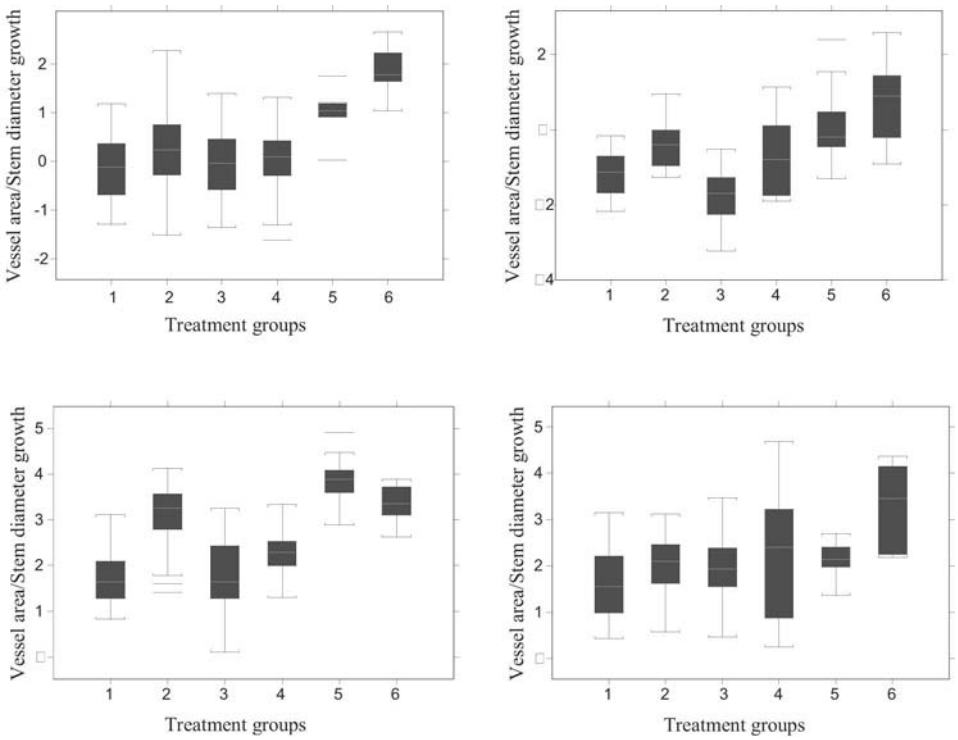

Fig. 8 Box plots of small-vessel (top) and large-vessel (bottom) area in relation to each distance between pinning wound tissue and cambium per treatment group for *Toona sinensis* (left) and *Toona ciliata* (right).

mitigate the detrimental effects because of their size. Additionally, especially young trees growing in light conditions or even open-grown trees have been reported to have significantly more borer infestations than mature trees in closed-forest habitats (Mo 1996).

The adjustment of the growth periodicity to water availability (Williams et al. 1997; Myers et al. 1998) and temperature (Paliwal et al. 1975; Iqbal and Ghouse 1982) has been observed in other tropical to subtropical tree species. In this study, the different treatments resulted in not only a general change of the phenology patterns but also the possibility of classifying the tree responses into three severity classes. The trees displayed longer periods of deciduousness and shorter periods of leaf flushes the more severe the treatments were; for example, in *T. sinensis*, the deciduous periods were short in the optimum group, longer when watering was limited, and even longer when the supplies of water and fertilizer were limited.

An overall comparison of the height and diameter growth data between the species demonstrates that *T. ciliata* generally grows faster than *T. sinensis*, except under low-temperature conditions, when *T. sinensis* exhibits larger height growth increments. The analysis also showed that the treatments exerting various forms of stress resulted in growth reactions according to the stress severities. Height increments of *T. ciliata* were smaller when temperatures (X_4) or supplies of fertilizer (X_5) were at a minimum than when water was at a minimum (X_2). This result is in agreement with Boland (2000) that the species is sensitive to both poor soil conditions and frosts. However, the comparison of the *T. ciliata* height and diameter data in the minimum-water group, X_2, and the minimum-temperature group, X_4, shows that height growth is relatively more limited by temperature, while diameter growth is more limited by the availability of water. The combination of the minimum-water and minimum-fertilizer treatments in group X_6 illustrates that both species have the ability to decrease height and diameter growth dramatically if environmental conditions worsen.

The intraseasonal diameter measurements show, as do the phenological observations, that *T. ciliata* reacts more opportunistically to optimum conditions than *T. sinensis*. All specimens of the latter species stopped growing for a prolonged period between February and August, while some trees of the former species did not stop growth at all. However, all *T. ciliata* specimens of groups X_2, X_4, and X_5 formed tree-ring boundaries, although the current data show slow but continuous growth throughout the normal dormant period between May and August. This suggests that they probably paused their growth for only a very short time, which might have not been detected by this study because the measurement intervals were too large. Since the experiment was conducted with young trees, the results cannot be simply generalized and applied to adult specimens. Coster (1928), Chowdhury (1961), Fahn et al. (1981), and Tomlinson and Longman (1981) found that younger trees have less distinct periodic growth patterns and that they continuously develop new shoots under good growing conditions, thereby keeping up plant hormone levels (Atwell et al. 1999). This inhibits the cambium from going into dormancy and might result in missing rings. However, the above studies also observed that false rings in older trees were less common. Therefore, during

future tree-ring analysis, young material of *T. ciliata* should be handled with care in this regard. Nevertheless, the results are encouraging for future dendroclimatological investigations of the species in tropical to subtropical Australasia because they suggest that the tree rings of both species are sensitive to precipitation and temperature, depending on appropriate site selection (Cook and Kairiukstis 1990).

As with phenology, height and diameter growth and the vessel characteristics of both species were also influenced in the course of the experiment. In all treatment groups and in both vessel size classes, samples of *T. sinensis* contained more but smaller vessels than samples of *T. ciliata*. Several studies (Carlquist 1966) have reported that water availability exhibits a positive correlation with vessel size and a negative correlation with vessel numbers. However, in the current data set, only the measurements for *T. ciliata* follow this pattern. In *T. ciliata*, large vessels are relatively more abundant than small vessels in the optimum groups, X_1 and X_3, than in the minimum groups, X_5 and X_6. In the medium-stressed groups, X_2 and X_4, total counts of large and small vessels are similar. Generally, *T. sinensis* contains relatively more small vessels than large vessels, except in groups X_2 and X_5. This pattern suggests that the species has adapted its physiology to somewhat drier climatic conditions compared with *T. ciliata*, which usually grows under more humid conditions.

The comparison of absolute vessel areas (fig. 7) with vessel areas in relation to intraseasonal diameter increments (fig. 8) shows a reversed distribution of the boxes in the box plots due to extremely reduced diameter increments in the minimum-supply treatment groups. This suggests that diameter growth changed relatively more than vessel dimensions. Trees in the minimum treatment groups adjusted to restricted growth conditions relatively more by reducing the amount of latewood formed. Phipps (1982) showed that latewood varied considerably more than earlywood in ring-porous trees from eastern North America. In ring-porous trees, the latewood portion of the annual tree ring is usually much larger than the part covered by the earlywood, and hence the effects of such an adjustment on the macroscopic occurrence of the tree-ring structure can be quite dramatic. The macroscopic impression is a highly porous wood of low density, implying that the tree grew under good conditions, while in fact the opposite was true. This phenomenon has been observed in a preliminary study of increment core samples taken from mature trees growing in tropical rain forests of Queensland, Australia (Heinrich and Banks 2006). The results imply that during a prolonged period of poor growing conditions, for example, extreme droughts in eastern Australia during the 1990s and in the early years of the twenty-first century, the wood anatomical result in *T. ciliata* would be several narrow rows of earlywood vessels, each representing one tree ring, with few to no latewood cells between. If such narrow ring patterns occur only occasionally because of extreme climate conditions, they act as pointer years and thus help during crossdating. However, if too many narrow tree rings are formed because of other nonclimatic restrictions, for example, competition or increasingly limited nutrient supply, crossdating will be hindered.

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