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NATURE AND PERIODICITY OF GROWTH RINGS IN TWO BANGLADESHI MANGROVE SPECIES

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SUMMARY

Nature and periodicity of growth rings were investigated in *Sonneratia apetala* and *Heritiera fomes*, two Bangladeshi mangrove species. From both species we collected three stem discs in the natural forest reserve of the Sundarbans. In addition, three discs were sampled from plantation-grown *S. apetala* trees of known age. Sanded stem discs revealed distinct growth rings but no periodic fluctuations in vessel variables (vessel density, vessel diameter, vessel grouping), which were measured at high resolution along a transect from pith to bark. The number of growth rings in plantation-grown *S. apetala* trees corresponded with the documented tree age, hence strongly suggesting the growth rings to be annual. Within species, the annual nature of the rings was further supported by a good match between the tree-ring series. The similar mean curves of *S. apetala* and *H. fomes*, growing at the same site in the Sundarbans, pointed to the presence of an external factor influencing their growth. A combination of precipitation and temperature was suggested influencing substrate salinity and phenological events. It became evident that tree-ring research in combination with the analysis of vessel patterns is a valuable tool to further investigate the complex interactions between tree growth and site ecology in mangrove forests.

Key words: Tropical dendrochronology, wood anatomy, growth ring, vessel variables, *Sonneratia apetala, Heritiera fomes*, Sundarbans, mangrove**.**

INTRODUCTION

The Sundarbans is the largest single tract mangrove forest in the world (0.57 million ha) and is situated at the south-western frontier of Bangladesh along the coast of the Bay

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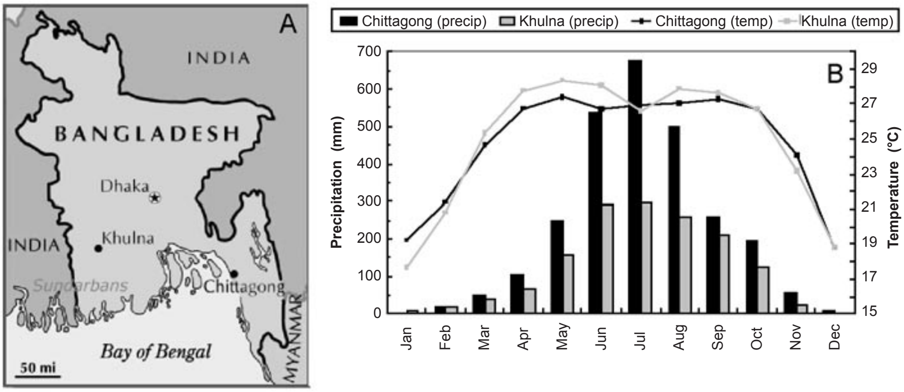

Figure 1. General characteristics of the study area. – A: Location of the two study sites in the natural forest of the Sundarbans and at a plantation near Chittagong (Adapted from Mapping Specialists, Ltd.) – B: Climate diagram of the study area.

of Bengal (Fig. 1A). In the period from 1960 to 2000 approximately 0.14 million ha of mangrove plantations, primarily *Sonneratia apetala* (Hoque & Datta 2005), have been raised under a number of coastal afforestation projects (Canonizado & Hossain 1998; FD 2006). However, nowadays Bangladeshi mangrove forests are declining mainly due to land reclamation for shrimp-aquaculture. In addition, river diversion causes a reduction in freshwater discharge into the mangroves, resulting in an increased salinity as well as changes in the sedimentation rate (Mirza 1998; Gopal & Chauhan 2005; Islam & Wahab 2005). Top dying started to affect *Heritiera fomes* (Rahman 2003) and is now recorded in 70% of the trees (Islam & Wahab 2005). It causes extensive economical losses since the species accounts for 73% of the total available timber in the Sundarbans (Mirza 1998). Furthermore, mangrove die-off triggers coastline vulnerability, which can have disastrous social impacts after storm events (Blasco *et al.* 1992; FAP 1993; Dahdouh-Guebas *et al.* 2005). To safeguard the future of the Sundarbans, water resource and forest management are of prime importance (Iftekhar & Islam 2004).

Tree-ring analysis can be used as a tool (*e.g.* Schweingruber 1996), to trace those environmental factors that mainly determine growth and vitality of mangrove trees. It offers a means for age and increment estimations, essential for calculating the annual allowable cut in a sustainably managed forest (Worbes 2002). The prerequisite for applying dendrochronological techniques is the existence of periodically formed growth rings, often absent in tropical trees (Worbes 1990; Sass *et al.* 1995; Schmitz *et al.* 2007). However, many tropical trees have been proved to be suitable for dendrochronological studies (*e.g.* Brienen & Zuidema 2005; Roig *et al.* 2005; Verheyden *et al.* 2005; Schöngart *et al.* 2006). Up to now, information about the periodicity of growth rings in mangrove species is restricted to only a few studies. Based on the relationship between diameter growth and rainfall, Duke *et al.* (1981) found a growth periodicity in *Diospyros* of 1.77 rings per year suggesting that about two rings form per year but only one ring every four years. Verheyden *et al.* (2004) identified annual growth rings in *Rhizophora mucronata* from Kenya resulting from a gradual change in vessel density, which they suggested was a response to changes in soil water salinity. Also in *R. mangle* from Brazil (Menezes *et al.* 2003) and *R. apiculata* from China (Yu *et al.* 2004) annual growth rings were reported. *Avicennia marina* has distinct but non-annual growth layers that are formed by successive cambia (Schmitz *et al.* 2007). The development of a new cambium and thus growth layer was proposed to be partly predetermined by mature tree height and partly controlled by environmental conditions such as soil water salinity (Schmitz *et al.* in press).

This study focused on two important mangrove species from Bangladesh, *Heritiera fomes* and *Sonneratia apetala*. The main objective was to check whether these two mangrove species produce annual growth rings. Therefore time series of both ring width and different vessel variables were tested for an annual periodicity. Vessel diameter, vessel density and vessel grouping were investigated since they are known to reflect external, mainly hydrology-related changes (*e.g.* Sass & Eckstein 1995; Gillespie *et al.* 1998; Pumijumnong & Park 1999; Corcuera *et al.* 2004; Verheyden *et al.* 2005; Schmitz *et al.* 2006).

MATERIALS AND METHODS

Study sites and study material

Three stem discs each were collected from *Sonneratia apetala* and *Heritiera fomes* growing at the Sundarbans, located in the Khulna district in the south-western part of Bangladesh. In addition, three stem discs of *S. apetala* were sampled from a plantation forest at the Chittagong district, about 250 km from the first study site (Table 1; Fig. 1A). This plantation was started under a coastal afforestation program in 1986 with the planting of two-year-old seedlings. Collected samples are now part of the xylarium of the Royal Museum for Central Africa (RMCA), Tervuren, Belgium (accession numbers Tw57952–57, Tw58370–72). Bangladesh has a monsoonal climate with one dry and one wet season (Shaman *et al.* 2005). Average monthly rainfall and temperature records for the period from 1952 to 2005 and from 1949 to 2003 respectively, were available from two meteorological stations located in Chittagong and Khulna (Fig. 1B; Bangladesh

Table 1. Overview of the studied stem discs, their size and their position in the tree.

Species	Location	Accession nr.	Diameter disc (cm)	Sampling height (cm)
Sonneratia apetala	Plantation (Chittagong)	Tw57952	8	50
Sonneratia apetala	Plantation (Chittagong)	Tw57953	10	50
Sonneratia apetala	Plantation (Chittagong)	Tw57954	10	50
Sonneratia apetala	Sundarbans (Khulna)	Tw57955	15	50
Sonneratia apetala	Sundarbans (Khulna)	Tw57956	13	50
Sonneratia apetala	Sundarbans (Khulna)	Tw57957	22	50
Heritiera fomes	Sundarbans (Khulna)	Tw58370	15	50
Heritiera fomes	Sundarbans (Khulna)	Tw58371	10	50
Heritiera fomes	Sundarbans (Khulna)	Tw58372	16	50

Meteorological Department, Abhawa Bhaban, Agargaon, Dhaka). Substrate salinity ranges between 5 ‰ and 25 ‰ (Hoque *et al*. 2006; Wahid *et al*. 2007) around Khulna and is somewhat lower around Chittagong with an average of 7‰ (SRDI 1998). At the two study sites, the mangrove forest is flooded twice a day.

Sample preparation and growth ring measurements

Stem discs were air dried and gradually sanded (100–1200 grit). Digital images were taken from pith to bark along two radii per sample, in an angle of 180° to each other, with a video camera coupled to a microscope and using the image-analysis software AnalySIS 3.2 (Soft Imaging System GmbH, Münster, Germany). Tree-ring width was measured on merged images ("Multiple Image Alignment", AnalySIS 3.2). First, the two tree-ring width series of each tree were compared by following the rings around the discs' circumferences to validate rings/missing rings. Then the two tree-ring series were averaged into a mean curve for each tree. These mean curves were compared per site and per species (Fig. 4). For the different trees growing in the natural forest, the mean curves were averaged into a grand mean per species and compared with the mean annual precipitation and a measure for the overall annual temperature (Fig. 5). This was calculated by reducing the maximum monthly temperature of 1949–2003 with the maximum monthly temperature for each year. Small values indicate exceptional warm years while larger values point to relatively cooler years.

Wood anatomical analysis

Vessel density, tangential and radial vessel diameter were measured directly on the polished wood discs (except for Tw57956) in successive measuring frames of 450–2133 μm along one transect from pith to bark. The width of the measuring frame was set arbitrarily to about three times the maximum radial vessel diameter. The percentage of solitary vessels was calculated as well as the vessel area using the formula of an ellipse and the number of vessels per group was counted.

RESULTS

Anatomy of the growth rings

Distinct growth rings were observed in both mangrove species. Growth rings were delimited by a marginal zone without parenchyma bands in *Heritiera fomes* (Fig. 2A) and a layer of flattened fibres in *Sonneratia apetala* (Fig. 2B). As illustrated for tree Tw57953 and Tw58372 (Fig. 3A, B), a negative age trend was observed in vessel density and a positive one in vessel diameter in the studied trees of both species. Near the ring border there was a slight tendency towards smaller but more vessels but none of the vessel variables showed a clear relationship with the detected tree-

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Figure 3. Time series of vessel density and vessel diameter with indication of the ring borders (dotted lines). – A: *Heritiera fomes* (Tw58372). – B: *Sonneratia apetala* (Tw57953). Note the decrease in vessel diameter (arrow) corresponding to a patch of red coloured wood as seen on the sanded stem disc and most likely caused by an insect attack.

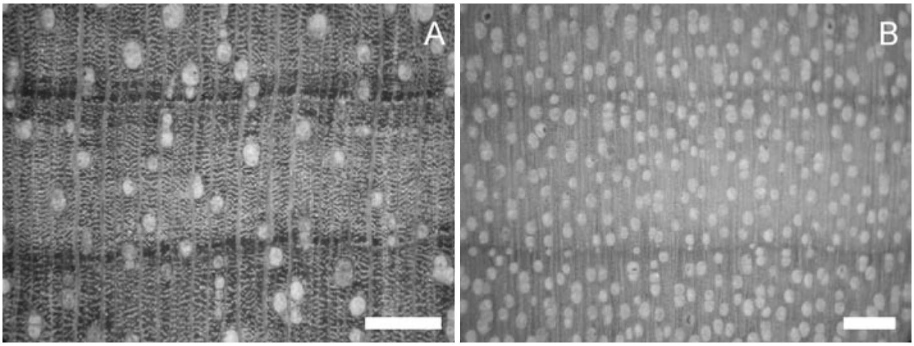
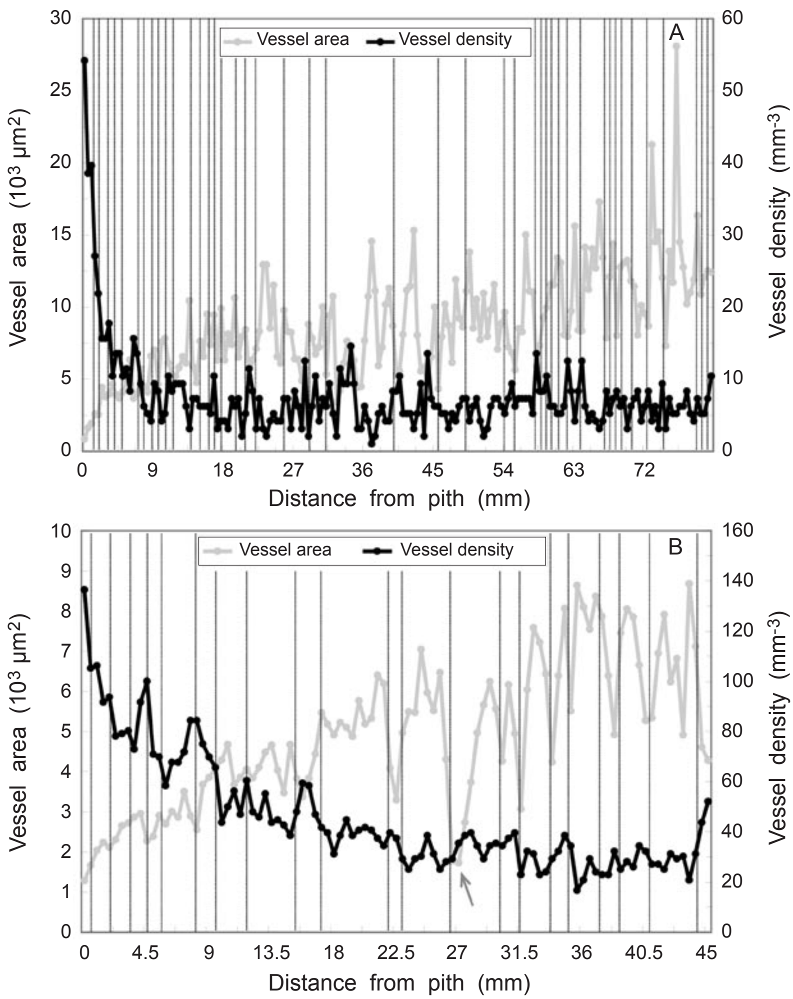


Figure 2. Detail of sanded stem discs showing the wood anatomical nature of the distinct growth rings. – A: *Heritiera fomes*. – B: *Sonneratia apetala*. — Scale bars = 500 μm.



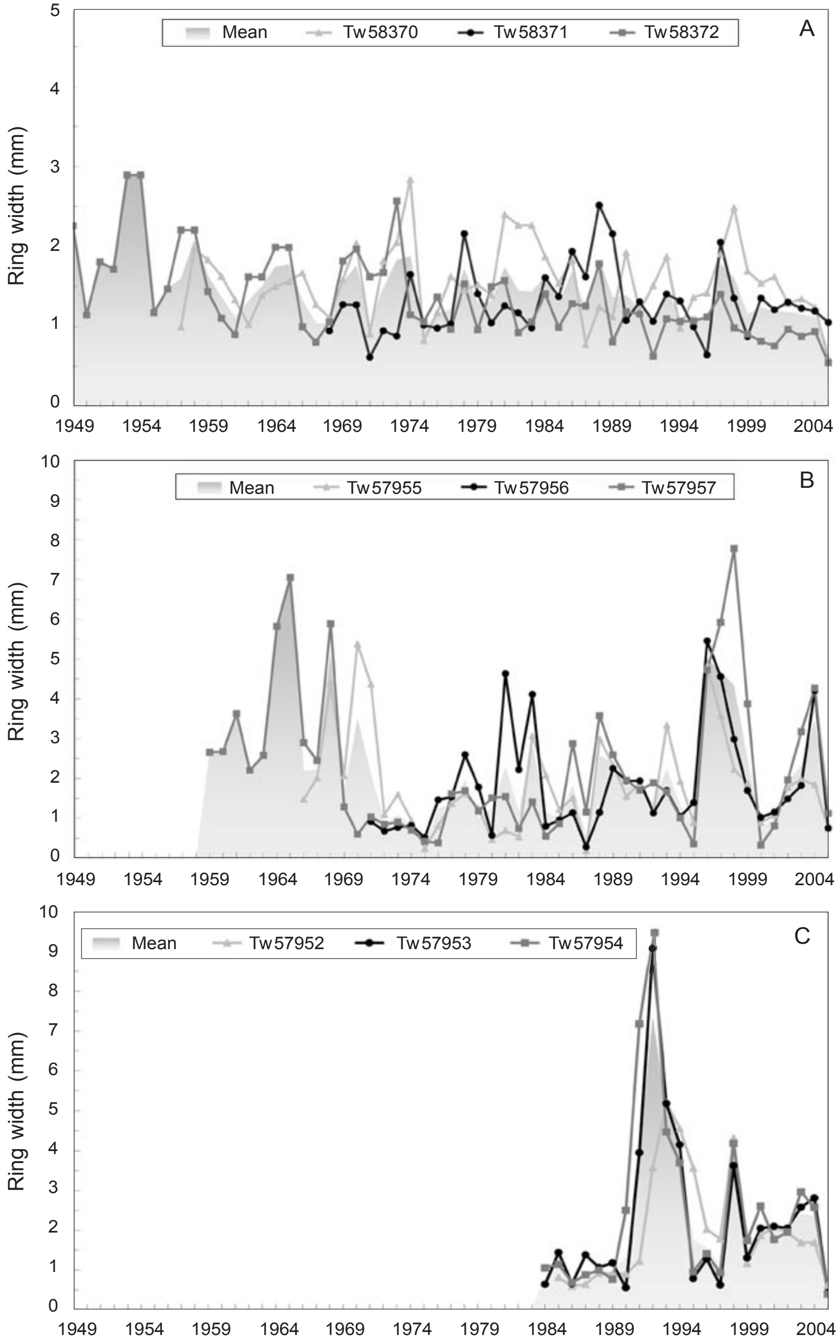


Figure 4. Ring-width series of the studied trees, averaged over the two radii per tree, together with their mean curve. – A: *Heritiera fomes*. – B: *Sonneratia apetala*, natural forest. – C: *S. apetala*, plantation.

Table 2. Description of the vessel variables of *Sonneratia apetala* (P, plantation; N, natural forest) and *Heritiera fomes*. Values are means of three trees, each time averaged over one transect from pith to bark, with range between brackets.

Species	Vessel density (mm^{-2})	Vessel diameter (µm)		Vessel grouping*	% Solitary vessels
		tangential	radial		
S. apetala P	42 ± 22 (16–136)	73 ± 15 (34–102)	86 ± 19 (40–129)	1 (1–4)	54 ± 15 (19–92)
S. apetala N	36 ± 23 (14–163)	67 ± 14 (32–100)	79 ± 19 (36–128)	1 (1–5)	47 ± 17 (10–91)
H. fomes	9 ± 6 (3–58)	100 ± 20 (34–153)	110 ± 26 (36–189)	1 (1–5)	48 ± 23 (1–93)

* Average number of vessels per group.

ring boundaries. Vessel density of *H. fomes* was considerably lower in comparison to *S. apetala* while the tangential and radial vessel diameter was much higher (Table 2). The degree of vessel grouping was similar in both species. On the stem disk of two *S. apetala* plantation trees (Tw57952–53) patches of red coloured wood could be seen that corresponded with a decreased vessel diameter (arrow in Fig. 3B). The ring width of *S. apetala* at the plantation ranges from 0.5 mm to 7.3 mm with an average of 2 ± 2 mm with similar results for the natural site (0.4–7.0 mm, average 2 ± 1 mm). *Heritiera fomes* had somewhat smaller rings ranging from 0.6 mm to 2.7 mm with an average of 1.4 ± 0.5 mm.

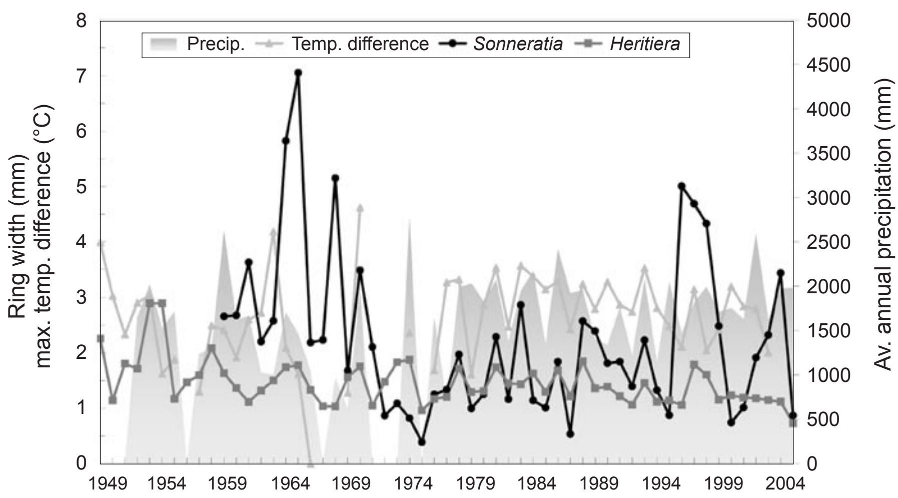


Figure 5. Mean curves of the three ring-width series per tree, averaged over two radii per disc, of *Heritiera fomes* and *Sonneratia apetala* from the Sundarbans in comparison with the average annual precipitation and the difference between the maximum monthly temperature of 1949–2003 and of each studied year. Missing data were converted to zero values.

Growth rings and periodicity

The number of growth rings in plantation-grown *S. apetala* trees corresponded with the tree age of 22 years taking into account a margin of uncertainty because of unclear growth ring margins around the pith. Within a site, the tree-ring series of both naturally-grown trees and plantation trees showed good visual agreement (Fig. 4B, C). The low sample replication and the short time span did not allow testing for statistical significance of these observations. The tree-ring series of the three *H. fomes* trees were less synchronous than those of the *S. apetala* trees (Fig. 4A). However, comparing the mean curves of *S. apetala* and *H. fomes* a similar annual variation throughout the whole 50-year period becomes obvious (Fig. 5). Although climate-growth relationships could not be calculated, a visual comparison of the chronologies with the average annual precipitation and a temperature anomaly time series (see Materials and Methods) showed a slight relationship (Fig. 5).

DISCUSSION

The distinct growth rings found in *Heritiera fomes* and *Sonneratia apetala* from Bangladesh correspond with earlier wood anatomical studies. In the Philippines, the growth rings of *H. littoralis* trees were occasionally seen to be marked by an initial band with a high frequency of vessels. However, absence of parenchyma bands at the margins was not observed (Panshin 1932), which might be attributed to inter-specific variations. Consistent with our data of *S. apetala* (Fig. 2B), Srivastava and Suzuki (2001) reported a combination of flattened fibres and narrower vessels at the ring borders of *S. kyushuensis* from Japan. Rao *et al.* (1987) observed flattened fibres at the ring boundary of 59% of the studied *Sonneratia* trees of four different species in the Bay of Bengal. In the Philippines, *S. caseolaris* and *S. acida* trees showed growth rings bordered by a band of flattened fibres, accompanied by smaller as well as fewer vessels (Panshin 1932).

The observation of distinct growth rings in *Sonneratia* and *Heritiera* species from different regions together with the seasonal climate in Bangladesh (Fig. 1B) points to the existence of annual tree rings in the studied species. In the plantation of *S. apetala*, this was confirmed by the agreement between the number of tree rings and the documented age of the trees. The existence of false or missing rings can, however, not be excluded because of the unclear tree-ring demarcations close to the pith. The slow growth during the first seven to eight years (Fig. 4C) possibly corresponds to a period of adaptation of the young planted trees to the new site.

In the natural forest of the Sundarbans, the annual nature of the growth rings was supported by the synchronized alternation of periods of good growth and abrupt growth depressions such as in 1972–1975, 1987 and 2000–2001 in all trees (Fig. 4B). Overall, the good visual correspondence of the tree-ring series within as well as between species (Fig. 4 & 5) supports the annual nature of their growth rings. In addition, it suggests that the growth of both mangrove species may at least partly be triggered by a common external factor.

Precipitation and temperature influence soil water salinity of mangrove forests making those promising candidates to explain at least part of the annual growth variations in the two mangrove species (Fig. 5). Although no long-term salinity data are available, it is supposed from earlier findings in Kenyan mangroves (Verheyden *et al.* 2005; Schmitz *et al.* 2006) that salinity as such might be an even better candidate. Not only rainfall and temperature but also river discharge, land run-off and tidal inundation (Mirza 1998; Fernández 2007) that extends up to 50 km inland (Gopal & Chauhan 2005) influence soil water salinity, resulting in considerable salinity variations in the Sundarbans both temporally and spatially (Gopal & Chauhan 2005). The seasonal variation in salinity due to the strictly seasonal climate (Hoque *et al.* 2006) may indirectly trigger growth ring formation (Lin & Sternberg 1992) via a peak in leaf flushing from March to May, at the start of the rainy season (*pers. observ.*; Wium-Andersen & Christensen 1978; Ochieng & Erftemeijer 2002; Mehlig 2006). Leaf shedding peaks in both evergreen species from December to February, which is during the dry season (*pers. observ.*). The growth of both species is in agreement with the relatively slow growth rate of other mangrove species studied in Kenya showing a range of 0–5 mm/yr in both *Rhizophora mucronata* and *Avicennia marina* (Verheyden *et al.* 2004; Schmitz *et al.* in press) with a maximum of 7.7 mm/yr and 4.7 mm/yr, respectively, in plantation-grown trees.

Next to the influence of substrate salinity on tree growth, the boring activity of an insect pest species was reflected in an abrupt decrease in vessel size around 1996 (arrow in Fig. 3B). This finding implies that the dynamics of the various insect pests that the *Sonneratia* plantations in Bangladesh are suffering from (Baksha & Islam 1997) can be investigated. In Kenya both planted and naturally-grown *Sonneratia alba* trees are also affected by a boring insect (pers. observ.; Mwangi 2001). The archiving of the insect outbreaks in the wood offers the possibility to study the striking sensitivity of *Sonneratia* species for pest attacks. Once the outbreak-to-anatomy relationship is established, it would be possible to use tree rings to go backwards in time and describe outbreak periodicity and intensity.

CONCLUSIONS AND FUTURE PERSPECTIVES

The potential for dendrochronological research was proven for two major mangrove species from Bangladesh, *Sonneratia apetala* and *Heritiera fomes*. It creates opportunities to clarify the effect of the complex hydrology of mangrove forests on tree growth, so far hardly understood. Tree-ring analyses of mangrove species can provide valuable information on forest productivity and changes of the local environment, extremely relevant in order to set up efficient management plans for the protection of these fragile ecosystems. The timing of growth-ring formation can be determined by repeated markings of the cambium (Verheyden *et al.* 2004; Schmitz *et al.* 2007, in press) that should be combined with dendrometer measurements in view of the slow growth rates that might hinder accurate measurements. Future dendrochronological studies should consider a larger sample size preferably in connection with ecophysiological analyses. In addition, the possibility of a complementary environmental signal in high-resolution time series of vessel characters should be explored.

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