Trees (2016) 30:227–239
DOI 10.1007/s00468-015-1292-2

ORIGINAL ARTICLE

Cambial dormancy induced growth rings in *Heritiera fomes* Buch.- Ham.: a proxy for exploring the dynamics of Sundarbans, Bangladesh

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Received: 19 April 2015 / Revised: 30 July 2015 / Accepted: 9 September 2015 / Published online: 23 September 2015
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Abstract

Key message **Cambial marking experiment and cambial activity analysis offer strong evidence on existence of annual growth rings in *Heritiera fomes* and revealing the potential of dendrochronological applications in Bangladesh mangroves.**

Abstract Despite enormous significance in coastal protection, biodiversity conservation and livelihood support to the local communities, mangrove ecosystems have been continuously degrading mainly due to anthropogenic disturbances and climate change. Time series based on dated tree ring is an option to identify the causes of forest dilapidation. In this study, we investigated the structure and periodicity of the growth ring in *Heritiera fomes*, the flagship tree species of the Bangladesh Sundarbans, combining cambial marking experiment and cambial activity analysis. Distinct growth rings were found which are delineated by a band of marginal parenchyma, predominantly one cell wide but up to three and occasionally interrupted with fiber. Of the 13 trees with cambium marking experiment, one growth ring was found in each tree during a year. The dormant cambium was characterized by the abrupt boundary between xylem and cambial zone, absence of enlarging or differentiating cambial derivatives, lower number of cambial cells and thicker radial walls in cambial cells. Growth ring anomalies, i.e., wedging and partially missing rings were also found. In most of the cases, the lower part of the eccentric discs had low radial increment (<0.75 mm) and therefore the growth ring in that area merged with previous one and produced wedging or partially missing ring. However, the existence of annual rings suggests its great potential for future dendrochronological applications to reveal the dynamics of vegetation and climate in Sundarbans.

Keywords Annual rings · Cambial marking · Cambial activity · Dendrochronology · *Heritiera fomes* · Mangroves · Bangladesh

Communicated by Y. Sano.

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Introduction

Sundarbans, the largest single tract mangrove forest in the world, is situated along the coast of Bay of Bengal (the estuary of the Ganges–Brahmaputra rivers) spreading over two neighboring countries (Bangladesh and India). It has enormous significance in coastal protection against natural calamities (Saenger and Siddiqi 1993), unique habitat for wildlife and fisheries (Islam and Wahab 2005; Gopal and Chauhan 2006; Loucks et al. 2010), supports socioeconomic activities (Walters et al. 2008), and maintains ecological balance (Kathiresan and Bingham 2001). Considering its uniqueness, the international communities, such as the Ramsar Convention and UNESCO have declared Bangladesh Sundarbans (covering 6017 km^2, Chaudhuri and Choudhury 1994) a Ramsar site and part of the forest (23 %) a world heritage site, respectively (Siddiqi 2001). Since 1893, the forest has been managed under e.g., 10-year management plans which have been prepared from the inventory data in which ages of trees were estimated from traditional girth measurements (Siddiqi 2001). However, depletion of the stock has resulted in over harvesting due to over estimation of growth increment from such kind of growth measurement (Canonizado and Hossain 1998). For example, the number of major tree species with diameter (>15 cm dbh) has been reduced at a rate of 0.27 % $year^{-1}$ during the 1926–1997 period (Iftekhar and Saenger 2008). Moreover, increasing deforestation and degradation of the forest by anthropogenic disturbances (Siddiqi 2001; Biswas et al. 2009), diseases (Rahman 1994), and disturbances related to natural calamities (IUCN 2003) and climate change such as sea-level rise (Agrawala et al. 2003; Loucks et al. 2010) demands for the establishment of new management plans for sustainable management of the Sundarbans. Since 1986, 120 permanent sample plots (PSPs) have been established in the Sundarbans (Rahman 1994) to obtain growth and demographic data e.g., age, growth rate, regeneration and survival. However, their contribution is very limited due to lack of systematic monitoring, such as trees are not properly marked and periodic diameter measurements are not documented for the respective trees. Tree growth data is crucial for understanding the underlying mechanisms of forest degradation, in addition to its applicability in designing sustainable forest management plan. Therefore, tree rings analysis (retrospective studies) might be an option for tree age and growth rate estimation.

Time series based on dated growth rings offer the opportunity for age and growth rate estimation (Worbes 1995, 2002; Rozendaal and Zuidema 2011; Groenendijk et al. 2014), fixing rotation and annual allowable cut (Brienen and Zuidema 2006; Schöngart 2008; De Ridder et al. 2013a), and to explore climate-growth relationships (D'Arrigo et al. 2011; De Ridder et al. 2013b; Vlam et al. 2014) for paleo-climate reconstruction (Borgaonkar et al. 2010; Song et al. 2014) as well as for the prediction of tree growth under future climate change (Brienen et al. 2010; Huang et al. 2013; Wagner et al. 2014). Compared to higher latitudes, tropical dendrochronology is challenging due to complexities of growth rings (Schweingruber 1988; Worbes 2002; Pumijumnong 2013; Gebrekirstos et al. 2014). Mangrove dendrochronology is even more challenging because of the very dynamic nature of the ecosystem that frequently inundated by the tides (Verheyden et al. 2004; Robert et al. 2011). Therefore, mangrove species received little attention in dendrochronological applications due to the assumption on indistinct tree rings (Van Vliet 1976; Sun and Suzuki 2000) or ambiguous rings (Amobi 1974; Rao et al. 1987; Srivastava and Suzuki 2001). However, existence of the distinct tree rings in few mangroves species has been reported from last few decades (Menezes et al. 2003; Verheyden et al. 2004; Chowdhury et al. 2008; Estrada et al. 2008; Robert et al. 2011) which explore their potential for future applications. However, the existence of distinct ring boundaries does not always guarantee the annual nature because the ring-width series do not always cross-correlate or show a clear relationship with the climate data (Chaudhary et al. 1999; Menezes et al. 2003). It is thus essential to determine the periodicity of the growth rings before exploring applications for dendrochronology.

Cambial marking experiment is an option to determine the periodicity of tree ring because a mechanical injury induces callus tissue as an artificial dateable scar in the wood (Mariaux 1967; Sass et al. 1995; Worbes 1995; Trouet et al. 2012). This method has been applied successfully to several mangrove species (Shiokura 1989; Verheyden et al. 2004; Robert et al. 2011). Analysis of cambial activity throughout a given period (Krepkowski et al. 2011; Volland-Voight et al. 2011; Al-Mefarrej 2014), combined with phenological observations i.e., leave shading and flushing (Borchert 1999; Rossi et al. 2012) and high-resolution meteorological data (Pumijumnong and Wanyaphet 2006; Trouet et al. 2012) is another approach for testing growth periodicity. The wood formation is a cyclic and gradual proliferation process of cambial cells where cell production and differentiation are linked with seasonality (Fahn and Werker 1990; Larson 1994; Rossi et al. 2006; Pumijumnong and Buajan 2013). The timing of cambial differentiation phases determine specific anatomical characteristics of the xylem (Oribe et al. 2003; Gričar et al. 2005; Begum et al. 2007; Chen et al. 2010; Dié et al. 2012). The cambial activity of mangrove species has not often been investigated unlike those of tropical terrestrial species (Priya and Bhat 1999; Venugopal and Liangkuwang 2007; Marcati et al. 2008). However, knowledge on the seasonal cambial dynamics in trees is extremely relevant not only for dendrochronologists but also for forest managers.

In this study, we aimed to elucidate the growth-ring structure and periodicity integrating cambial marking experiment and cambial activity analysis in *Heritiera fomes* Buch.- Ham., the flagship species in Sundarbans, Bangladesh. Moreover, the growth ring formation is discussed in relation to cambial characters, phenology and related environmental factors.

Materials and methods

Study site and climate

The current study was conducted in the Sundarbans, which is situated in the southwestern frontiers of Bangladesh

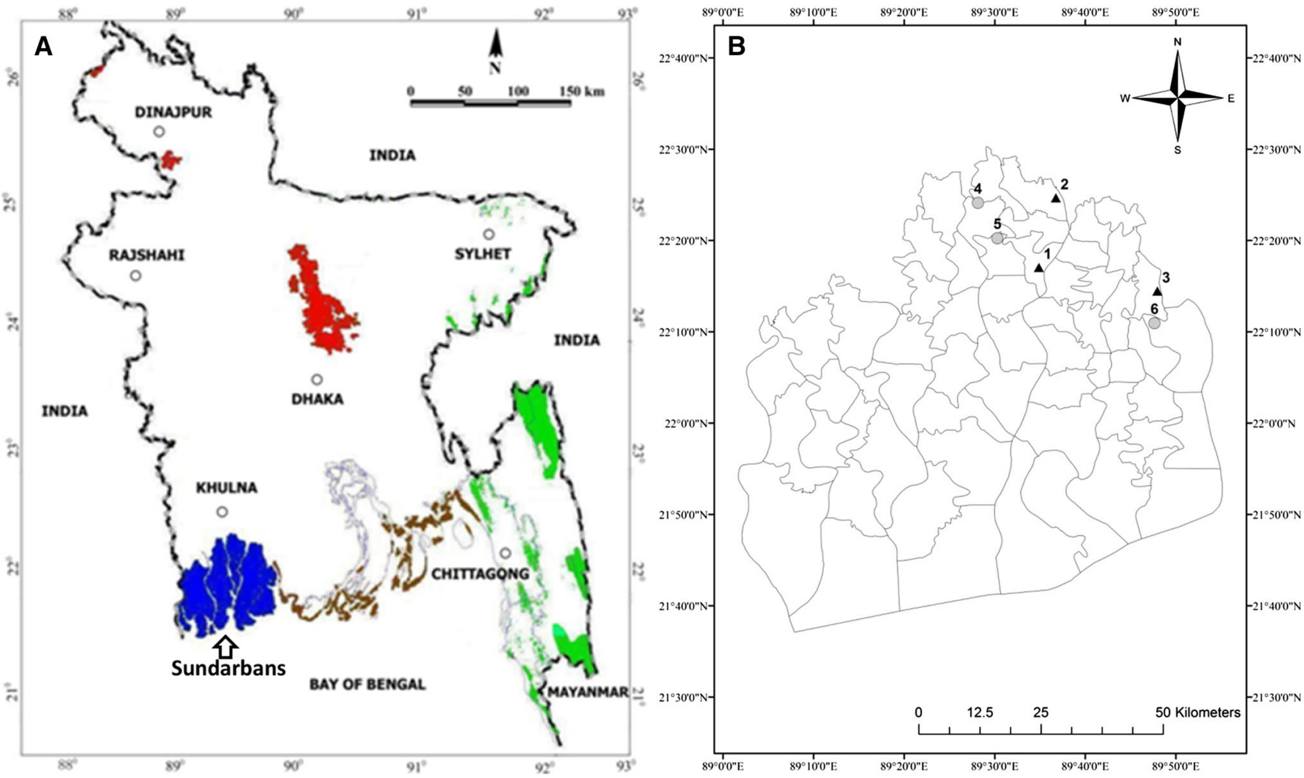

Fig. 1 Map showing distribution of forests in Bangladesh (**a**); *green color* indicates evergreen and semi-evergreen, *red color* deciduous, *blue color* natural mangroves (Sundarbans) and *brown color* plantation mangroves and sampling sites in the Sundarbans (**b**); *triangle* pinning site; *circle* sampling site for cambium analysis

(Fig. 1). The forest is regularly inundated by the tidal water and the amplitudes vary from 3 to 4 m throughout the forest (Ellison et al. 2000). Moreover, based on tidal amplitude, the forest can be divided into four zones, such as inundated by all tides (new accretions), inundated by normal high tides (covers most of the area), inundated only by spring high tides (mostly in the northern part), and inundated by monsoon high tides (northeastern part) (Siddiqi 2001). The salinity within the forest increases from the east to west direction (Islam and Gnauck 2011). The forest is also influenced by fresh water flows from the Ganges river through a branch namely Gorai river and within the forest water flow is distributed by a complex network of branching and meandering distributaries and rivers varying from a few meters to few kilometers (Wahid et al. 2007). In addition to spatial fluctuations, the freshwater discharges vary seasonally (decreases from December to April) within the forest and inversely regulate the salinity (Mirza 1998; Islam and Gnauck 2011). The average growth rate of tree species is lower in the higher salinity areas (Iftekhar and Saenger 2008). Species composition also varies along the salinity gradient (Siddiqi 2001). For example, in the less saline zone (eastern part), *H. fomes* forms pure stands in association with *Excoecaria agallocha* L., *Xylocarpus mekongensis* Pierre, *Bruguiera* spp., *Avicennia officinalis* Linn. etc. The high saline zone (western part) is mainly dominated by *Ceriops decandra* (Griff.) Ding Hou in association with *E. agallocha*, *X. mekongensis*, *X. granatum* J. König.

The study area is characterized by a monsoonal climate with unimodal distribution of precipitation (Fig. 2). The monsoon season ranges from June to September with an average precipitation of 276 mm which is preceded by a warm and muggy pre-monsoon (March–May) with sporadic precipitation (average of 92 mm). The post-monsoon

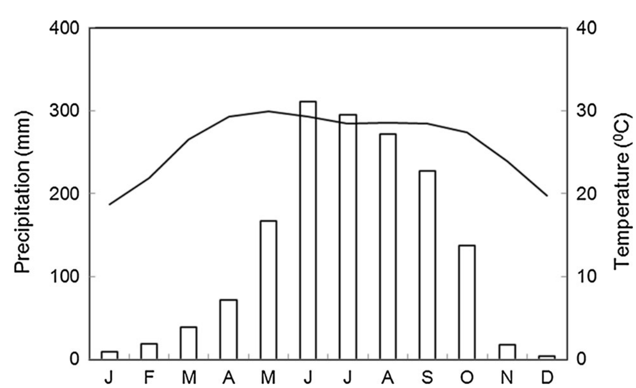

Fig. 2 Climate diagram of the study area. *Vertical bars* indicate precipitation and *solid line* indicates temperature

ranges from October to November (average precipitation of 76 mm) and the dry winter continues from December to February (average precipitation of 11 mm). The average temperature in pre-monsoon, monsoon, post-monsoon and winter is 29, 30, 26 and 20 °C, respectively. The average relative humidity throughout the year ranges from 69 to 83 %.

Site variables

Twenty soil samples were collected from each sampling site (during March) from a depth of 15 cm in polyethylene bags for analysis (Fig. 1b). The sand, slit and clay percentage was determined using the hydrometer method (Day 1965). The electrical conductivity (EC) was determined in a solution of 1:5 soil–water mixtures using a conductivity meter (Extech 341350A-P Oyster) and EC was converted to salinity (ECe; Shahid 2013). Variability among the sampling sites was analyzed separately for both experiments, such as cambial marking experiment (site 1, 2 and 3) and cambial activity analysis (site 4, 5 and 6) using ANOVA followed by a post hoc (Tukey HSD) test. Inundation classes were designated as I, II, III and IV where inundated by 100–76, 75–51, 50–26, 25–5 % of the high tides, respectively (Tomlinson 1994).

Cambial marking experiment and sample collection

Heritiera fomes is a flagship species in Bangladesh Sundarbans and widely distributed in the selected sampling sites. Fifteen trees in three study sites (five in each location, Fig. 1b) were selected for the cambial marking experiment and tagged for identification in the next year. Thereafter, cambium of the selected trees was marked on 6–8th January 2013, using a hypodermic needle (18G; 1.2 mm diameter) at 130 cm above the ground level. A total of 13 (5, 5 and 3 samples for site 1, 2 and 3, respectively) stem discs (Tw66289–66301) was collected after destructive sampling from the cambial marked trees on 30th March and 1st April 2014. In addition, fifteen stem discs were collected from another three sites (five in each site, Tw66320–66334) at the same height level for cambial activity analysis in March and April 2014 (Fig. 1b). These samples were immediately preserved in containers with 1:1 alcohol and glycerin.

Sanding and wound observations

Exact cambial marking positions were identified by a lenticel-like structure which is visible on the outer bark (Verheyden et al. 2004). The stem discs of the cambial marked trees were cut at few millimeters above the actual place of wounding and sanded (100–1200 grit) until reaching the wounding position. The wound tissue was carefully investigated to locate the position of the cambial initials at the time of pinning and the number of growth layers formed since marking the cambium was determined. For growth ring structure and wound observation, the images of stem discs (2.5× magnification) and wounding areas (4×) were taken using an opto-digital microscope (Olympus DSX–100, Tokyo, Japan).

Wood anatomical analysis

For anatomical characterization, images were taken (10×) before and after (restored wood) the wounding position of the stem disc using the same opto-digital microscope. Vessel density (number of vessels per mm^2) as well as average radial and tangential vessel diameters (mm) was measured using ImageJ software (Schindelin et al. 2012). Average vessel diameter was calculated from averaging radial and tangential diameters. Vessel grouping was measured by counting the number of vessel groups in the same measuring field (Schmitz et al. 2006). Number of rays per mm^2 was also calculated for both positions (before and after the wounding) on the disc.

Growth measurements after cambial wounding

Growth rings were observed after cambial wounding on the disc. However, the rings were discontinuous or partially missing in some samples. The stem discs from the cambial marking experiments also showed pith eccentricity which is expressed as the ratio of upper (tension wood) and lower part (opposite wood) of the disc (Sultana et al. 2010). Ring distinctness was categorized as I, II, III and IV where ring distinct by 100, 75, 50, 25 % of the concentric circle, respectively (Table 1). Radial increment after the cambial wounding was measured along the four intersected lines on the disc (Fig. 3). In case of distinct ring boundary, growth was measured in the respective line, rather used zero for locally absent ring. Finally, average growth rate was made from the four measurements for each tree.

Microtome sectioning and light microscopy

For anatomical characterization of the cambial marked samples, thin sections (transversal and radial) were prepared (near the area of cambial wounding) with a thickness of 20 µm using a sliding microtome (Microm, Fisher Scientific, Walldorf, Germany). The sections were stained with a 0.1 % safranin (Merck KGaA, Darmstadt, Germany) solution in 50 % ethanol and washed in an ethanol series (50, 75, 96 and 100 %, 5 min in each concentration). For the cambial activity analysis, each disc was cut into small blocks containing xylem, cambium and bark. These blocks

Table 1 Site characteristics along with tree diameter, ring visibility, eccentricity and radial growth after cambial marking

Sample number	Site	Salinity ± SD (ECe; dS m^{-1})	Inundation category*	Dbh (cm)	Distinctness category†	Eccentricity	Radial growth (mm)
Tw66289	1	24 ± 2^a	II	3.8	III	3.34	0.87
Tw66290	1			4.2	III	3.95	0.70
Tw66291	1			3.2	II	1.7	0.55
Tw66292	1			3.5	I	2.24	1.57
Tw66293	1			3.2	III	2.00	0.60
Average ± SD				3.6 ± 0.4			0.86 ± 0.41
Tw66294	2	20 ± 2^b	II	4.3	I	1.72	1.93
Tw66295	2			4.9	III	3.2	0.50
Tw66296	2			4.8	I	2.9	1.82
Tw66297	2			5.5	III	1.80	0.54
Tw66298	2			5.8	I	1.67	1.95
Average ± SD				5.1 ± 0.6			1.35 ± 0.76
Tw66299	3	18 ± 4^b	I	5.7	III	1.88	0.82
Tw66300	3			4.5	I	1.35	1.62
Tw66301	3			5.0	II	3.25	1.30
Average ± SD				5.0 ± 0.6			1.25 ± 0.40
Total average ± SD				4.5 ± 0.5			1.14 ± 0.53

Same letter indicates not significant and different letters indicate significant variation

SD standard deviation, *Dbh* diameter at breast height

* Inundation category according to Tomlinson (1994)

† Ring distinctness was categorized as I, II and III where ring is distinct by 100, 75, 50 % of the concentric circle, respectively

were embedded for 72 h with PEG1500 (polyethylene glycol) at 60 °C. Transversal and radial sections with a thickness of 20 µm and containing secondary xylem, cambial zone, phloem and bark were also cut using a sliding microtome. The sections were stained with a mixture of 0.1 % safranin and alcian blue solution. They were washed in an ethanol series (50, 75, 96 and 100 %) and mounted on microscope slides with Euparal (Carl Roth Gmbh + Co. KG., Karlsruhe, Germany). Observations were made with a microscope (Olympus BX60F-3, Tokyo, Japan), equipped with bright–field and polarized light optics, as well as epi-fluorescence using a mercury arc lamp and an Olympus WU filter cube (excitation 330–385 nm, long-pass emission 420 nm). By bright-field microscopy, red color shows lignified walls and blue color cellulosic walls. With the fluorescence microscopy, yellowish color indicates the lignified cell walls and violet or blue color shows cellulosic walls (Dié et al. 2012).

Results

Site variation

The salinity varied significantly among the sites ($F_{2,17} = 3.65$, $P < 0.05$) of cambial marking experiment. However, salinity variation between site 1 and 2 was not significant but varied significantly from site 3 (Table 1). Similarly, salinity of the soil samples from cambial activity analysis sites (site 4, 5 and 6) revealed significant ($F_{2,17} = 3.74$, $P < 0.05$) variation among the sites (Table 2). The inundation category did not show clear pattern in salinity variation but sites with higher inundation category (category I) showed lower salinity.

Observations of wound reaction and anatomical variation

The cambial mark appeared as moderate reaction in wood due to wounding (Figs. 3, 4a). The inserted needle produced puncture canal (up to 3 mm in length) in the xylem which is characterized by a combination of wood anatomical features, such as crushed cells, amorphous zone and oxidized xylem (see Smith 1988) (Fig. 4a). The dark layer was formed by the residues of crushed cells which are usually referred to as the 'stripes of cell wall residues' (Kuroda 1986; Nobuchi et al. 1995; Verheyden et al. 2004). The amorphous substances accumulated between the crushed cells and the oxidized wood (Fig. 4a). The oxidized wood produced around the puncture canal up to 1.5 mm distance after the amorphous zone. Above the layer of crushed cells, a large area of callus-like parenchymatous tissue was formed which indicating the actual wound response of the tree (Fig. 4a). Afterwards the wood

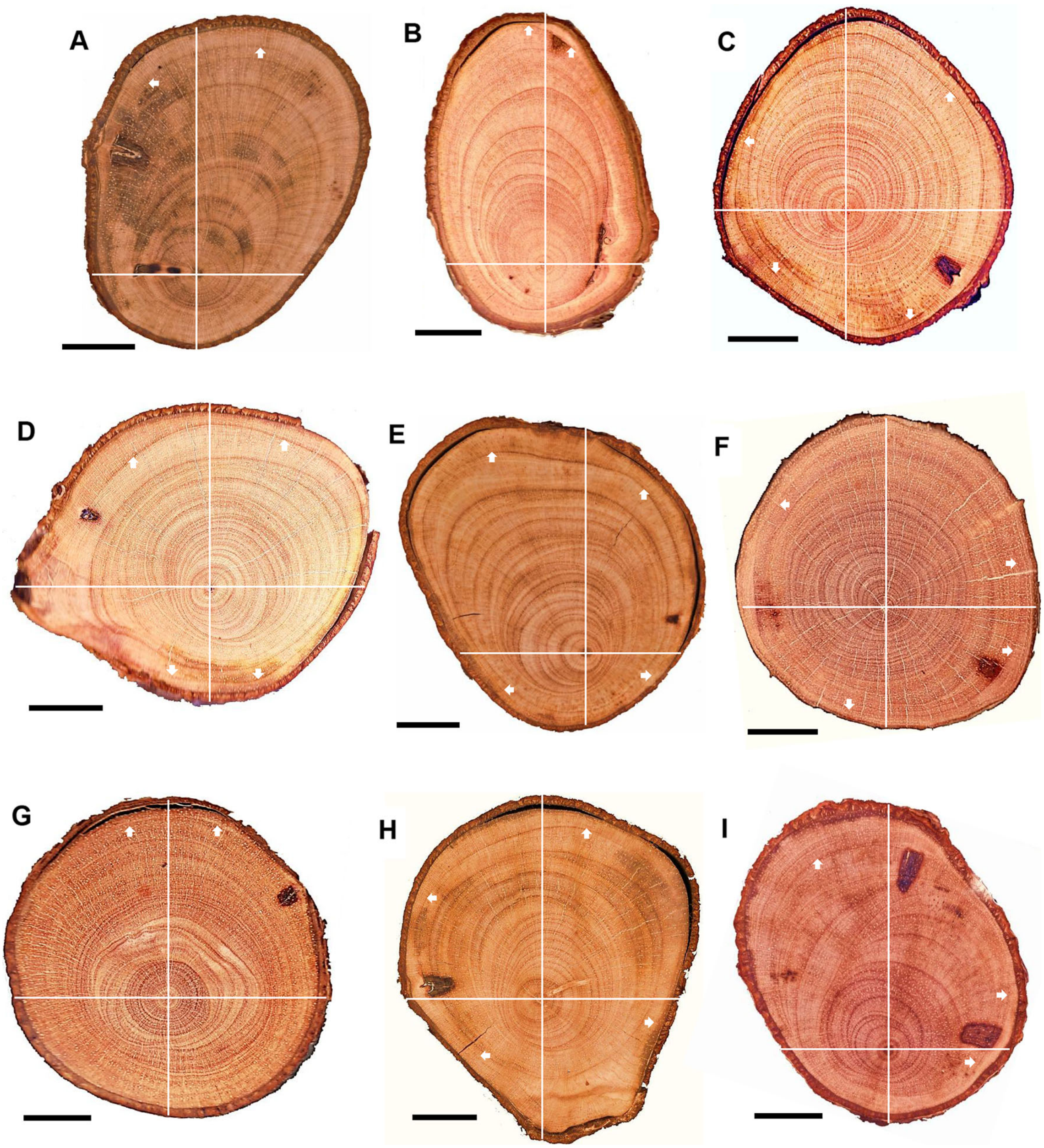

Fig. 3 Sanded stem discs with cambial wounding. **a** Tw66289; **b** Tw66290; **c** Tw66292; **d** Tw66294; **e** Tw66296; **f** Tw66298; **g** Tw66299; **h** Tw66300; **i** Tw66301. *Scale bar* 10 mm

production was restored. The newly formed wood produced a twofold higher vessel density and significantly (t test, $P < 0.01$) smaller size vessels after wounding (Figs. 4a, b; Table 1). Number of the vessel groups and ray density was higher in the post-wounding zone (Table 3). Moreover, most of the vessels in the oxidized wood were filled with gummy substances (Fig. 4b).

Growth ring characters and periodicity

Of the 13 samples collected from the cambial marking experiment, one growth ring was found after cambial marking in each tree (Figs. 3, 4). The ring is marked by a band of marginal parenchyma; predominantly one-cell wide but up to three-cell parenchyma and occasionally interrupted with fiber was also observed (Fig. 4). The ring boundaries, however, were not always concentric along the circumference of the discs (Fig. 3). In the studied samples, only 38 % showed category I, 16 % category II and 46 % category III ring on the discs (Table 1). Samples with category I ring showed low pith eccentricity compared to other categories. During 1-year experiment, trees formed a distinct ring when radial increments were more than 0.75 mm in the stem circumference. The average radial

Table 2 Site, cambial and non conductive phloem characteristics

Site	Salinity ± SD (ECe; dS m^{-1})	Inundation class*	Dbh (cm) ± SD	Cambial cells		
				Demarcation boundary	No. of cells	Enlarging/cell division
4	28 ± 4^{a}	III	4.4 ± 0.5	Abrupt	4–6	–
5	24 ± 2^{b}	II	5.1 ± 0.5	Abrupt	4–6	–
6	13 ± 5^{c}	I	4.4 ± 0.6	Abrupt	4–7	–

Different letters indicate significant variation

SD, standard deviation; –, absent; Dbh, diameter at breast height

* Inundation category according to Tomlinson (1994)

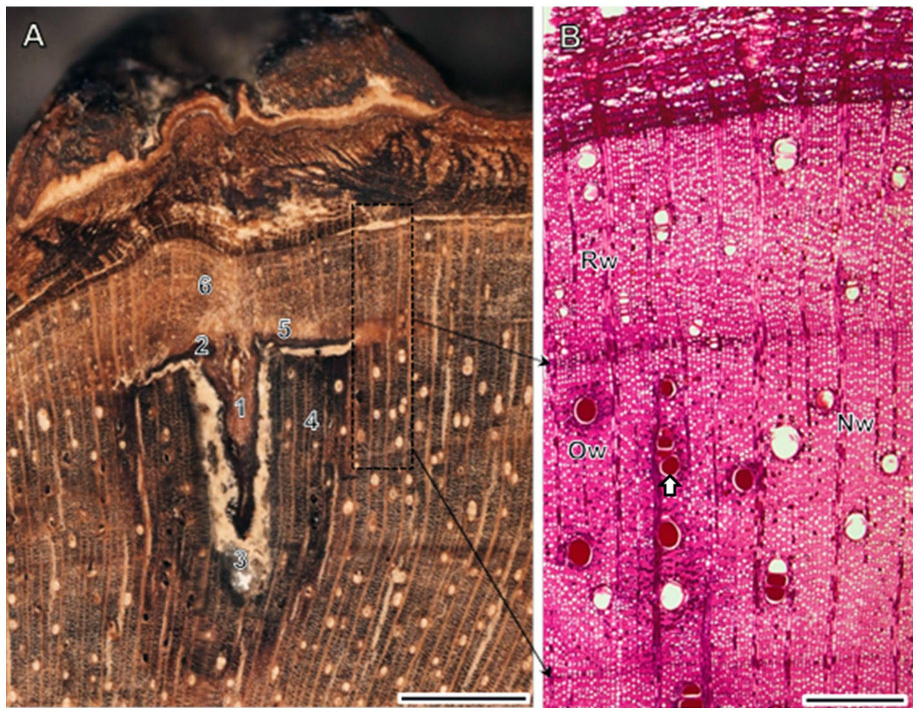

Fig. 4 **a** Microphotograph of the cambial wounding (Tw66289). *1* puncture canal; *2* crushed cambial derivatives; *3* amorphous layer; *4* oxidized wood; *5* parenchyma tissue; *6* restored xylem. **b** Anatomical characteristics of oxidized (*Ow*), normal (*Nw*) and restored (*Rw*) wood near the wounding. *White arrow* indicates gum deposited vessel and *black arrow* indicates the growth ring. *Scale bars* 2 mm (**a**), 500 μm (**b**)

growth after the last formed ring was 1.14 ± 0.63 mm. Trees from the higher salinity site (site 3) showed lower growth rate (0.86 ± 0.41 mm) compared to lower saline sites (Table 1).

Characteristics of the cambial zone

In this study, the term cambial zone applies to the entire region of secondary vascular tissue generation and includes intermediate cambial derivatives between the xylem and phloem (Rossi et al. 2006; Dié et al. 2012). The demarcation boundary between xylem and cambial zone was abrupt (Fig. 5). The cambial zone was characterized by 4–7 cambial cells with thin tangential and thicker radial walls. Moreover, there was no enlarging or differentiating cambial derivative. There was no site-specific variation in cambial zone characteristics (Table 2). These criteria firmly indicated that cambial was dormant in the studied samples.

Discussion

Wound-induced anatomical response

Shortly after wounding, the first stage of compartmentalization occurs to confine the wound injury within boundaries in the smallest possible area in the wood through anatomical and chemical changes (Shigo 1984, Smith and Lewis 2005), such as crushed cells, a zone with amorphous wood tissue and oxidized wood (Fig. 4a, b). The crushed cells originate from crushed cambial cells and cambial derivatives on both sides of the cambium (Kuroda 1986; Nobuchi et al. 1995; Verheyden et al. 2004). The

Table 3 Anatomical characteristics of pre- and post-cambial wounding

Sample no.	Vessel dia (μm) ± SD		Vessel density (no. mm^{-2})		No. of group vessels		Ray density (no. mm^{-2})	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Tw66289	104 ± 24	70 ± 15	8	19	2	5	4	6
Tw66290	88 ± 25	73 ± 23	9	14	2	4	5	8
Tw66291	95 ± 18	81 ± 17	10	17	1	3	5	6
Tw66292	99 ± 22	85 ± 20	9	14	1	3	4	7
Tw66293	102 ± 15	80 ± 21	11	17	1	3	7	9
Tw66294	100 ± 20	82 ± 16	8	12	2	3	4	6
Tw66295	105 ± 23	87 ± 20	9	24	2	4	7	9
Tw66296	89 ± 23	75 ± 13	13	20	1	3	5	8
Tw66297	98 ± 15	80 ± 20	10	14	2	3	4	5
Tw66298	110 ± 28	94 ± 18	9	11	1	4	5	6
Tw66299	99 ± 20	71 ± 23	8	13	2	4	5	7
Tw66300	112 ± 24	90 ± 12	8	12	1	4	6	9
Tw66301	107 ± 23	74 ± 15	9	17	1	3	4	6
Average	100 ± 21	80 ± 18	9	16	1	4	5	7

SD standard deviation

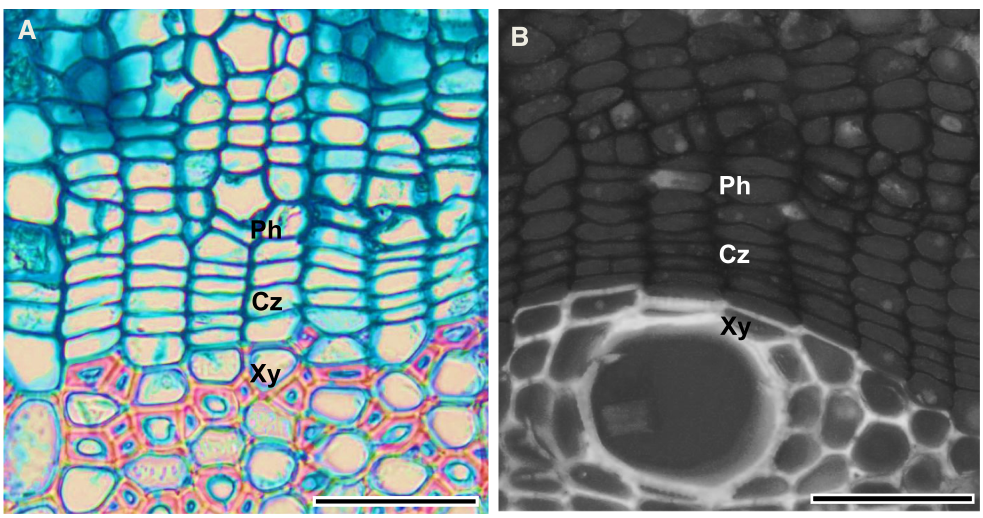

Fig. 5 Morphology of the dormant cambium. **a** Light micrograph of transverse section (Tw66330); **b** transverse section under fluorescence light (Tw66320). *Xy* xylem, *Cz* cambial zone, *Ph* phloem. *Scale bars* 50 μm

functional sapwood vessels around the wound were blocked with gummy substances (Fig. 4b) and the parenchyma cells might shift their metabolism from normal energy-yielding metabolism to the production of poisoning phenolic and terpene substances which are oxidized in the presence of available oxygen (Smith 1988). The oxidized products might be more toxic or inhibitory to the microorganisms (Pearce 1996). The cambium produced new (restored) sapwood in the second stage of compartmentalization (Figs. 4a, b) which is capable of energy storage and water movement (Smith 1988). The existence of higher amount of parenchyma above the wound (Fig. 4a) corresponds to a considerable effort for defense against pathogens and wound healing (Schmitt and Liese 1990). It is probable that the higher amount of spongy parenchyma cells decrease the mechanical strength which might be counter balanced by an increasing number of rays (e.g., Arbellay et al. 2012). Moreover, higher number of rays might have adaptive role in compartmentalization of decay (Shigo 1984). The wounding induced the formation of higher number of narrower vessels and mostly in groups (Fig. 4b). On the other hand, occurrence of few narrow vessels and higher number of rays after wounding has been reported in *Rhizophora mucronata* Lam. from Kenyan mangroves (Verheyden et al. 2004). Formation of higher number of narrow vessels and vessel groups in the restored wood might be therefore a trade-off between hydraulic safety and efficiency (Schmitz et al. 2006; Robert et al. 2009; Arbellay et al. 2014). However, the persistence of wound induced anatomical response and the nature of wound closure might vary according to species, tree vigor, and nature of wounding (Neely 1988; Delvaux et al. 2010).

Annual nature of growth rings

The studied samples displayed distinct annual growth rings delimited by a band of marginal parenchyma (Figs. 3, 4). Conversely, Mariam et al. (2012) reported that visibility of the growth rings is unclear in *H. fomes*. Chowdhury et al. (2008) also showed the presence of distinct growth ring in this species without parenchyma band using stereomicroscopic images. The discrepancies among the studies might be due to methodological difference in observations. However, the tree-ring periodicity tested in this study supports the results of Chowdhury et al. (2008) where the periodicity has been shown using synchronization of growth rings with annual precipitation. Another species of this genus, *H. litoralis* Aiton forms a ring boundary also with 2–4 cell layers of marginal parenchyma (Robert et al. 2011). Newly formed resorted wood was not found and the ring boundary also began instantly after the cambial marking (Fig. 4a). It can therefore be assumed that wood formation is ceased immediately before the cambial wounding. Of the 13 marked trees, 38 % trees developed a complete concentric growth ring (category I) after the cambial marking (Table 1). Our results suggest that growth ring anomalies are related to the reduced radial growth in the respected area of stem circumference (Fig. 3). In most of our samples, radial growth in the lower part of stems (opposite side of the tension wood) was minimum (<0.75 mm) and therefore the ring merged with the previous one forming wedging or partially missing ring. Similar conclusion was reached for *R. mucronata* from Kenya where trees also form annual rings where growth rate is greater than 0.5 mm year^{-1} (Verheyden et al. 2004). In addition, locally absent ring might be related to pith eccentricity of the stem. This phenomenon commonly occurs in the other tropical species (Sass-Klaassen et al. 2008; Trouet et al. 2012; Pumijumnong 2013). The collected samples were smaller in diameter (3.2–5.8 cm) and the occurrence of higher pith eccentricity encountered is due to asymmetrical growth stress during stem development (e.g., Fournier et al. 1994). In a highly dynamic mangrove environment, such kind of growth stress might be caused by frequent change of stem orientation due to inundation, sedimentation, erosion and seasonal storm events (e.g., Ellison et al. 2000; Robert et al. 2011).

The salinity variation between site 1 and 2 was not significant but varied significantly from site 3. The average growth rate was much lower in the higher salinity site (site 3) compared to other two sites (Table 1). The photosynthesis rate of *H. fomes* decreases with increase of salinity (Nandy et al. 2007), which might explain lower growth rate in the higher saline area. The average radial growth of this species is within the range of the earlier study (Chowdhury et al. 2008). Moreover, the slow growth of this species is similar to other mangrove species (Verheyden et al. 2004; Schmitz et al. 2007; Robert et al. 2011).

Cambial dormancy and growth ring formation

During cambial activity, the cambial derivatives alter gradually both morphologically and physiologically toward definite features (Larson 1994). Once their final stage has been reached, the cell walls complete their lignifications (e.g., Dié et al. 2012) and therefore in dormant cambial the boundary between xylem and cambial zone is abrupt (Fig. 5). The thicker radial walls of the cambial cells (Fig. 5) might relate to an increase of apoplastic translocation during dormancy through the cambial zone when storage materials accumulate in xylem and phloem parenchyma cells (Catesson 1990). There was no dividing or enlarging cell and the cambial zone comprised of four to seven cells in the three studied sites (Fig. 5). These are the typical morphological characteristics of cambial during the dormant season in the tropical species (Larson 1994; Priya and Bhat 1999; Venugopal and Liangkuwang 2007; Dié et al. 2012; Pumijumnong and Buajan 2013).

Heritiera fomes is an evergreen tree and sheds mature leaves immediately after emerging of young leaves in May to June (A. Rahman, Forest officer, Sundarbans; personal communication). From December to April, the precipitation is very low (nearly of 35 mm) which increases from May to September and again decreases from October (Fig. 2). The average winter (December–February) temperature (20 °C) increases around 29 °C in March to April while the maximum temperature is around 30 °C in rest of the year (Fig. 2). However, from December to April, the up-stream river flow decreases more than 75 % (Mirza 1998) while the water salinity increases around 80–90 % (Islam and Gnauck 2011). Thereafter a bigger drop in salinity occurs from late May due to monsoonal precipitation (Fig. 2) and increase of up-stream river flows with the network of streams and rivers criss-crossing the forest (Mirza 1998; Wahid et al. 2007; Islam and Gnauck 2011). There was no new restored wood and the growth ring boundary began immediately after the cambial marking (Fig. 4) which suggests the presence of dormant cambium in the samples (cambial marked in January). In addition, cambial activity analysis showed inactive cambium in the samples harvested in March to April (Fig. 5). It is thus assumed that cambial dormancy occurs in *H. fomes* from January to April in the Sundarbans. Conversely, in a similar monsoonal climate (Thailand), the cambial activity is not driven by climate in *Avicennia* spp. and *Rhizophora* spp. (Buajan and Pumijumnong 2012). It is noted that a dry season (<60 mm of monthly rainfall) lasting more than 3 months is sufficient to invoke a cambial dormancy to trigger the ring formation in tropical species (Worbes 1995, 1999; Trouet et al. 2012). In addition to a dry (low precipitation) period (January to April), increase of salinity creates physiological dryness in the Sundarbans (Parida and Das 2005) that might invoke dormancy in trees. On the other hand, decrease of salinity might induce cambial activity which is reflected by the leaf flushing (May–June). It is generally assumed that the cambial activity in tropical trees is induced by some time before leaf flushing (Borchert 1999). Tree produces a considerable amount of wood with a different anatomy through active cambium to form a distinct growth ring (Robert et al. 2011).

Conclusion and perspectives

The data presented here, using cambial marking experiment, as well as cambium activity analysis offer strong evidence for the presence of annual growth rings in *H. fomes* and showing their potential for analysis of tree age, carbon sequestration and reconstructions of forest growth dynamics and climate. Using stem discs will facilitate the visual detection of ring boundaries, allow for the identification of wedging and partially missing rings which are common in this species, as described in many other tropical species (Worbes 2002; Brienen and Zuidema 2005; Mbow et al. 2013; De Ridder et al. 2013b; Gebrekirstos et al. 2014). Due to these difficulties, using increment cores for this species may lead to errors even though this is considerably a nondestructive method (Rohner et al. 2013). *H. fomes* is still the most important species of the Sundarbans and covering over 67 % of the vegetated area (Iftekhar and Saenger 2008). Due to increase of anthropogenic disturbances (IUCN 2003) and reducing the allowable harvesting diameter in the successive management plans (Siddiqi 2001) might have decreased the large diameter trees in the Sundarbans. However, a recent forest inventory of the area using 68 PSPs (13.6 ha) shows that still there are trees approximately 50 cm diameter (around 200 years of lifespan) that might offer the opportunity to construct long chronologies.

Author contribution statement MQC and HB have designed the study; MQC has set up the experiment and sampled the wood materials and soils; MQC has analyzed site variables; MQC has also performed anatomical studies with the help of PK and CD; data analysis was done with the help of MD; and MQC has written the manuscript with the support of all co-authors.

Acknowledgments We thank Bangladesh Forest Department for the permission, Divisional Forest office of the Sundarbans (East and West Forest Division) for their generous support during the fieldworks and RIMS unit for the shape file of forest. We also thank SK Sarker, S Das, MM Hoque, N Das, HR Khan and H Murshed at SUST for their help during the fieldworks and site variable analysis. We acknowledge two anonymous reviewers for their constructive criticisms and comments on an earlier version of manuscript. MQ Chowdhury was supported by a mobility grant from the Belgian Federal Science Policy office co-funded by the Marie Curie Actions from the European Commission.

Compliance with ethical standards

Conflict of interest The authors have declared that no competing interests exist.

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