



ORIGINAL ARTICLE

Salinity drives growth dynamics of the mangrove tree *Sonneratia apetala* Buch.-Ham. in the Sundarbans, Bangladesh

Md. Saidur Rahman^{a,b,*}, Ute Sass-Klaassen^a, Pieter A. Zuidema^a,
Md. Qumruzzaman Chowdhury^{c,d}, Hans Beekman^c

^a Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

^b Forestry and Wood Technology Discipline, Khulna University, Khulna-9208, Bangladesh

^c Wood Biology Service, Royal Museum for Central Africa (RMCA), Leuvensesteenweg 13, Tervuren, Belgium

^d Department of Forestry and Environmental Science, Shahjalal University of Science and Technology, Sylhet-3114, Bangladesh

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ABSTRACT

Mangroves throughout the world are threatened by environmental changes apart from anthropogenic disturbances. Many of these changes may inhibit the growth and survival of mangrove species. To understand and predict the effects of global change on mangrove forests, it is necessary to obtain insights on the growth dynamics of mangroves in relation to environmental factors. This study was conducted on *Sonneratia apetala*, a mangrove species which grows under a range of salinity conditions across the Sundarbans in Bangladesh. We studied trees growing under respectively high, medium, and low salinity conditions based on the influence of freshwater discharge. First, the periodicity of radial growth across the year was detected by applying cambial analyses. Based on tree-ring analyses, we calculated the growth response of *S. apetala* to monthly variation in precipitation and temperature as well as river discharge, as a proxy for salinity. We found the cambium of *S. apetala* being active during the monsoon and post-monsoon period whereas it was dormant in the pre-monsoon. This periodicity in radial growth leads to the formation of distinct annual rings with ring boundaries being marked by radially flattened fibres. *S. apetala* trees growing under low salinity conditions generally show higher growth rates indicating the positive impact of river discharge, i.e. freshwater input on mangrove growth. Wet and warm conditions during the monsoon period positively affected *S. apetala* growth, especially in the low salinity zone. Our results show that salinity is the primary driver of growth dynamics of *S. apetala* in the Sundarbans. A gradual or seasonal increase in salinity, e.g. as a consequence of sea-level rise may therefore importantly alter the growth of this species, possibly leading to changes in mangrove forest dynamics and zonation.

1. Introduction

Mangrove forests are the most productive ecosystems across the globe (Woodroffe, 1982; Donato et al., 2011), and play an essential socio-economic as well as ecological role by providing a plethora of ecosystem services and products (Dahdouh-Guebas et al., 2000; Dahdouh-Guebas and Koedam, 2008; Himes-Cornell et al., 2018; Islam et al., 2018a). The Sundarbans, the largest continuous natural mangrove forest in the world, is located on the coast of Bay of Bengal (the estuary of the Ganges–Brahmaputra rivers) in Bangladesh (6,014 km²) and India (4,000 km²) (Chaudhuri and Choudhury, 1994). A portion of Bangladesh Sundarbans has been declared a Ramsar site under the Ramsar Convention in 1992 and UNESCO declared as a World Heritage

Site for its unique conservation value in 1997 (Siddiqi, 2001; Sarker et al., 2019). Historically, the anthropogenic disturbances, such as over-exploitation, shrimp and salt farming, oil spills, diseases, biological invasion, and natural calamities have been declining this ecosystem leading to diminishing growing stock (Iftekhar and Saenger, 2008). Besides, the Sundarbans has been experiencing a sea-level rise, and climate and environmental changes from the last century (McLeod and Salm, 2006; Gilman et al., 2008; Alongi, 2015). Based on the recent IPCC forecasts, this forest is under threat with the projected mean sea-level rise to 0.98 m in 2100, whereas the average elevation is 2 m (Church et al., 2013; Collins et al., 2013). It is a sea-dominated mangrove where precipitation and up-stream freshwater river flows used to modulate salinity and keep the ecosystem favourable for trees

* Corresponding author.

E-mail address: msrahman@fwt.ku.ac.bd (Md. S. Rahman).

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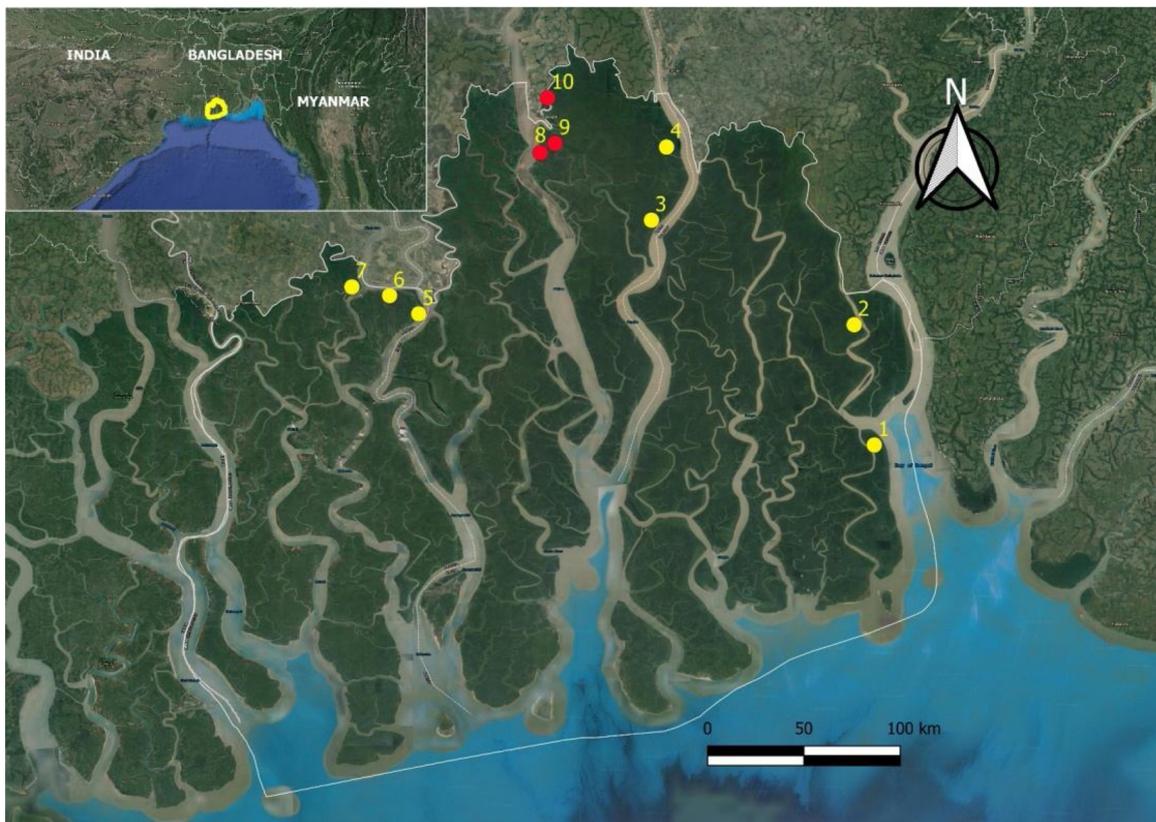


Fig. 1. Sampling locations in the Sundarbans. Yellow circle (1-7) denotes locations for the collection of stem disc for developing chronology, and red circle (8-10) indicates sampling sites for cambium studies. Locations 1 and 2 represent Low salinity zone (LSZ), 3, 4 and 8-10 represent Medium salinity zone (MSZ), and 5-7 symbolises for High salinity zone (HSZ).

(Chowdhury et al., 2016a; Sarker et al., 2019). Given the importance of the retrospective understanding of the growth dynamics of trees in natural forests in response to environmental changes, tree-ring research has proved to be a valuable tool. Besides tree age, it enables to detect growth-limiting factors for various tree species and through the calculation of climate-growth relationships enables to predict impacts of climate change on growth dynamics of mangroves (Menezes et al., 2003; Verheyden et al., 2004; Robert et al., 2011; Chowdhury et al., 2016b).

The application of tree-ring research is often limited in the tropics due to the complex anatomy of growth rings (Worbes et al., 2003; Rozendaal and Zuidema, 2010; Pumijumnong, 2013; Gebrekirstos et al., 2014; Groenendijk et al., 2014; Gaspard et al., 2018; Islam et al., 2018b) and lack of knowledge on the seasonality of growth-ring formation (e.g. Lisi et al., 2008; Morel et al., 2015). Mangrove species have received less attention due to absent or indistinct ring boundaries in many species (Amobi, 1974; Srivastava and Suzuki, 2001; Rozendaal and Zuidema, 2010; Robert et al., 2011). However, several studies confirmed the presence of annual growth rings in *Rhizophora mangle*, *R. mucronata*, *Sonneratia apetala*, *S. alba*, *Heritiera fomes*, *H. littoralis*, *Xylocarpus granatum* and *Lumnitzera racemosa* (Menezes et al., 2003; Verheyden et al., 2004; Chowdhury et al., 2008, 2016a, b; Robert et al., 2011). For many mangrove species, the timing of growth ring formation is not known which limits chances for the exact dating of ring-width series and hinders the analyses of driving environmental factors behind tree growth (Menezes et al., 2003; Verheyden et al., 2004). Studies on seasonal wood formation are essential to prove the presence of annual growth rings and allow for correct estimation of tree biomass formation (Mbow et al., 2013; Köhl et al., 2017), but also to understand the physiological background of calculated climate-growth relationships (Schöngart et al., 2006; Chowdhury et al., 2016a; Rahman et al., 2017; Martinez del Castillo et al., 2018), for predictions of tree growth under

future environmental change scenario's (Brienen et al., 2010; Huang et al., 2013; Wagner et al., 2014).

Growth rings are produced due to alternating periods of cambium activity in response to seasonal environmental changes, which are mostly driven by climate factors. Cambium dormancy followed by cambial re-activation and declining cambial activity across the growing season induces wood-anatomical changes that ultimately form ring boundaries (Fahn, 1982; Worbes, 1992). Investigating the seasonal cambial activity along with leaf phenology and environmental data is a fundamental approach to verify the annual character of growth rings of any species (Marcati et al., 2006; Pumijumnong and Buajan, 2013). Surprisingly, compared to species from boreal and temperate areas, very few studies on cambial activity have been conducted on tropical species (Priya and Bhat, 1999; Marcati et al., 2006; Venugopal and Lianguwang, 2007; Marcati et al., 2008; Dié et al., 2012; Pumijumnong and Buajan, 2013; Marcati et al., 2016). The number is even less for mangrove species which reflects a knowledge gap in mangrove studies (Schmitz et al., 2006; Buajan and Pumijumnong, 2012; Chowdhury et al., 2016b). Knowledge of seasonal cambial activity such as identification of the beginning of cambial cell production, cessation, and their duration is therefore essential for a better understanding of intra-annual wood formation in response to environmental changes.

Sonneratia apetala is an ecologically important tree species in mangroves of the Indo-Malayan region (Tomlinson, 1986). It is a light-demanding evergreen tree species belonging to the family of *Sonneratiaceae* (former *Lythraceae*) (Rashid and Rahman, 2012). In the Sundarbans, it mostly occurs in monospecific stands and often in association with *Avicennia officinalis* as a pioneer species in succession, preferably in moderate to high salinity zones (Iftekhar and Saenger, 2008). Considering the importance of conservation of the Sundarbans, a better understanding of environmental factors that may drive the

growth of *S. apetala* is essential. This study aims at investigating the growth dynamics of *S. apetala* in the Sundarbans by addressing the following research questions: i) do the trees produce periodic distinct growth rings? and ii) to which extent, do climatic (precipitation and temperature) and hydrology-related (salinity) factors affect radial growth?

2. Materials and methods

2.1. Study area and climate

The study was conducted in the Sundarbans which is situated in the south-western frontiers (21°35'-22°30' N, 89° 00'-89°55' E) of Bangladesh (Canonizado and Hossain, 1998) (Fig. 1). Out of its total area, about 69% is land, and the rest comprises rivers, small streams, and canals (Sarker et al., 2016). A significant portion of this forest is washed by the tide twice a day, and the salinity level is related to the combined effects of the tides in the Bay of Bengal and freshwater input from the Ganges through the Gorai river, the largest river connecting the Sundarbans to the Ganges. Islam and Gnauck (2009) found a significant negative correlation ($r = -0.86$, $p < 0.05$) between the Gorai river water discharge and salinity in the Sundarbans (Fig. 2A). To investigate the effect of salinity on the growth of *S. apetala*, we used monsoon (June–September) river discharge data of the Gorai river between 1985 and 2010 as a proxy for salinity due to unavailability of long-term salinity data (Anwar and Takewaka, 2014). Based on salinity, the Sundarbans is divided into three distinct zones: i) low salinity zone (LSZ) (salinity < 14 ppt), ii) medium salinity zone (MSZ) (salinity 14–25 ppt) and iii) high salinity zone (HSZ) (> 25 ppt) (Islam and Gnauck, 2009).

The climate of the study area is strongly seasonal with 87% of the mean annual rainfall (1500 mm) occurring between June to September,

representing the monsoon period (Fig. 2b) (Chowdhury et al., 2016a). The average temperature ranges between 26–29 °C in pre-monsoon and monsoon season, 26–27 °C in post-monsoon and 19–21 °C during the winter season (Fig. 2b). Precipitation and temperature records for the period from 1985 to 2012 were available from the Bangladesh Meteorological Department, Dhaka, and taken from nearby weather stations in Mongla (LSZ), Khulna (MSZ) and Satkhira (HSZ). The average monthly precipitation is significantly higher in LSZ than MSZ and HSZ (ANOVA, $F_{2,900} = 2.92$, $p < 0.05$). Similarly, a significantly higher average monthly temperature is prevailing in LSZ than MSZ and HSZ (ANOVA, $F_{2,924} = 65.335$, $p < 0.05$).

2.2. Sample collection and preparation

In 2014, a total of 17 wood discs were collected from small-sized *Sonneratia apetala* trees (Diameter at Breast Height (DBH) including bark ranges from 4 to 5 cm) for cambial analysis from the medium salinity zone (MSZ). Seven discs were collected in the last week of March (pre-monsoon), another seven in August (monsoon), and the remaining three in November (post-monsoon) in a way to represent the major seasons in the Sundarbans. The fresh wood samples were immediately preserved in a container with ethanol to avoid fungal contamination. In January 2013, 31 stem discs were collected from *S. apetala* trees from the three salinity zones ranging between 5 and 28 cm in DBH for tree-ring analysis. Among them, ten discs were collected from LSZ; six were from MSZ, and fifteen were from HSZ (Fig. 1). Wood discs were frozen for one week to prevent insect infestation. All discs were sanded using a sanding machine with gradually increasing grit from 100 to 1200.

2.3. Microtome sectioning and light microscopy

Each sample disc was cut into four small blocks containing xylem, cambium, and phloem. Transversal sections of 10 μm thickness were prepared using a GSL1 sledge microtome (Gärtner et al., 2014). The micro-thin sections were stained with a mixture (35:65) of 1% safranin and alcian blue solution (Jansen et al., 2004), subsequently washed with an ethanol series (50%, 75%, 96%, and 100%) and mounted on microscope slides. We used Roti®-Mount (Roth, Germany) for permanent fixation, and excess Roti®-Mount was cleared with Roticlear® (Roth, Germany). The micro-thin sections were observed under a light microscope (Leica DM 2500, Germany), equipped with bright-field and polarised light optics with a magnification ranging from 12.5 to 400 times. Polarised light was used to detect birefringence from crystals and developing secondary walls in the unstained section (Rossi et al., 2006; Gričar et al., 2007; Dié et al., 2012). Additionally, we used epi-fluorescence in a microscope using a mercury arc lamp and an Olympus WU filter cube (excitation 330–385 nm, long-pass emission 420 nm) to distinguish lignin-rich and cellulose-rich cell walls (Bond et al., 2008; Dié et al., 2012). The images were taken using a Leica camera (DFC 320) attached to the light microscope and the further image was stitched by Microsoft Image Composite Editor (ICE -2.0) and analysed using Fiji image J software (Schindelin et al., 2012).

2.4. Assessment of seasonal cambial activity

We distinguished four distinct zones on the thin sections: i) the cambial zone (CZ) consisting of undifferentiated cambial cells and derivatives and located between the xylem and phloem, ii) the expanding zone (EP) with differentiating, irregular shaped cells with primary cell wall showing and no birefringence (like the cambium and to a lesser extend living parenchyma cells) (Rossi et al., 2006; Dié et al., 2012), iii) the wall thickening zone (WT) with cells in various stages of developing the secondary cell walls and beginning to show birefringence (Gričar et al., 2007; Morel et al., 2015) and iv) the mature xylem (M) with fully developed and lignified cells with thick cell walls showing

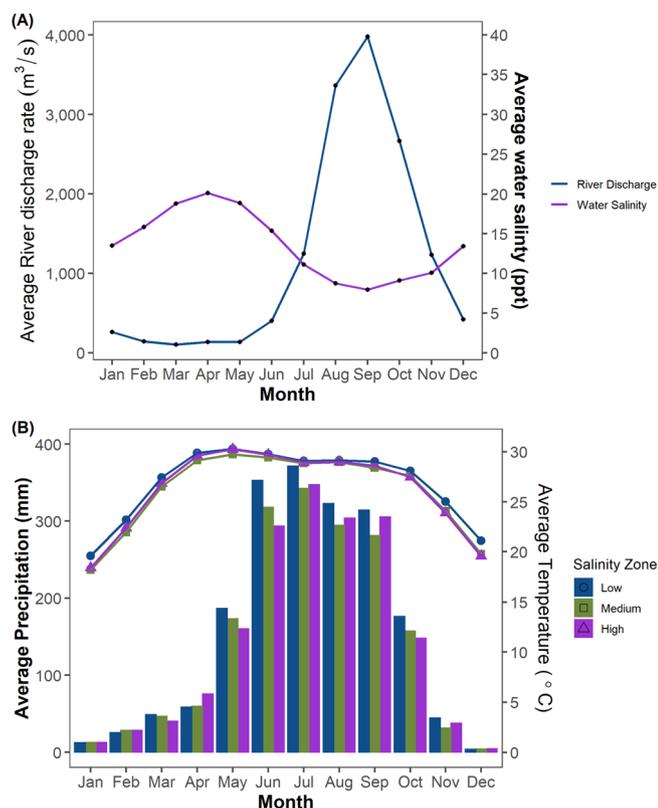


Fig. 2. (A) Monthly average river discharge rate and water salinity in the Sundarbans for the period 1989–1997. (B) Monthly average total precipitation and average temperature in three salinity zones of the Sundarbans for the period 1985–2012.

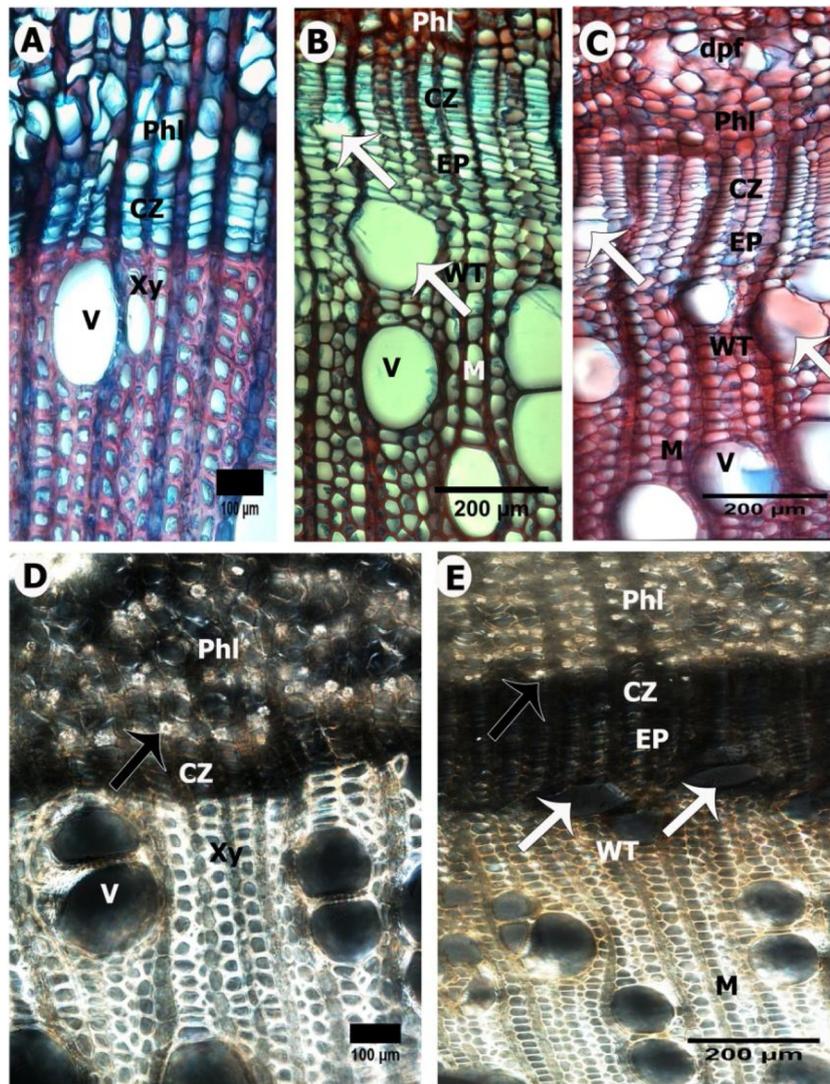


Fig. 3. Seasonal development of cambium and xylogenesis in *S. apetala*. (A&D) Dormant cambium in March, (B, C&E) Active cambium in August and November. Phl = Phloem, CZ = Cambium zone, Xy = Xylem, EP = Expanding zone, WT = Wall Thickening zone, M = Mature zone, V = Vessels, dpf = Developing phloem fibres. White arrow = Developing vessels, Black arrow = crystals. Methods: TS (A-E); BF (A-C) and PL (D-E), Where, TS: transverse section; BF: bright-field light microscopy; PL: polarized light.

birefringence. From each digital image, the number of radial cell layers, and width of the cambial zone in the radial and tangential direction were measured along with three continuous cellular files in each zone (Deslauriers et al., 2003; Rossi et al., 2006). Twelve counted values from each image were used for further calculations.

2.5. Compilation of growth ring chronologies

On the sanded discs, growth-ring boundaries were marked with a pencil under a stereomicroscope in three radii from pith to bark to check for ring anomalies (Fig. A1A). In the case of anomalies (false rings and particularly locally absent rings), every tree ring was followed along the tree circumference. Ring widths were measured with a resolution of 0.01 mm by using a stereomicroscope and a Lintab measuring device with TSAP-Win software (Rinn, 2003). To ensure assigning each tree ring to the exact calendar year, crossdating was done between individual tree ring series (Douglass, 1941). We cross-dated tree-ring series by visual comparison among the trees and using the Student's *t* (Baillie and Pilcher, 1973) and Gleichläufigkeit values (GLK) by TSAP-WIN software (Eckstein and Bauch, 1969). The cross-dating threshold was set in this study at a *t*-value of 2.0 ($p < 0.05$) and a GLK

of 60 % (Trouet et al., 2010; De Ridder et al., 2013). Crossdating of tree ring series per salinity zone was also done by averaging ring series into an individual tree series. Successful crossdating of trees thus indicates a common external factor influencing the growth of the trees (Cook and Kairiukstis, 1990; Worbes, 1995).

Each of the raw series were detrended by fitting a 10-year cubic smoothing spline with the degree of smoothing at 50% frequency response to eliminate or minimise the long-term and low-frequency variation due to age. Residual chronologies were calculated for the three sites, resembling salinity regimes, from the detrended ring width series by calculating a bi-weight robust mean (Cook and Kairiukstis, 1990) using dpLR package (Bunn, 2008) in R statistical software (R Core Team, 2019). The statistical parameters were calculated for each residual chronology. The first-order autocorrelation (AC1) was done to detect eventual persistence of growth variation after standardisation, and the mean sensitivity (MS) is an evaluation of high-frequency year-to-year variations in a tree ring width (Fritts, 1976). A mean sensitivity is considered as high when it is greater than 0.30, according to Ferguson's classification (Savva et al., 2006). As an indicator of the reliability of each chronology, the mean tree ring series correlation (RBAR) and the Expressed Population Signal (EPS) were calculated (Cook and

Kairiukstis, 1990). The EPS measures to what extent the sample chronology could be representative of the theoretical population (Wigley et al., 1984) whereas, RBAR is the mean inter-series correlation coefficient. A chronology with an EPS > 0.85 is often considered to be reliable (Cook and Kairiukstis, 1990). Signal to noise ratio (SNR) is an expression of the strength of the observed common signal among trees (Wigley et al., 1984).

2.6. Statistical analysis

All wood anatomical parameters were analysed by analysis of variance (ANOVA) and Welch's test after having examined the normality with the Shapiro-Wilk test and uniformity of variances with Leven's test using SPSS v.21.0. In the case of unequal variances, we used Welch's ANOVA (Quinn and Keough, 2002; Ruxton, 2006). The radial growth rate in three salinity zones was analysed by ANOVA with the General Linear Model (GLM), where diameter class was considered as a fixed factor. To investigate the effects of seasonal climatic and environmental factors on tree growth, the data were detrended by fitting a 10-year cubic smoothing spline method before analysis to focus on the drivers of annual growth variability. Therefore, all climatic parameters were expressed as deviations from the long-term trend. Furthermore, Pearson's correlation analysis was done for the chronologies from the three salinity zones (HSZ, MSZ and LSZ) with standardised monsoon season (June to September) precipitation, temperature, and river discharge, respectively.

3. Results

3.1. Seasonal variation of cambial activity

Apart from the phloem, four different zones, i.e. cambium zone (CZ), expanding zone (EP), wall thickening zone (WT) and mature xylem (M) were clearly detected on the thin sections under bright-field, polarised light and fluorescence microscopy in the samples taken in the monsoon and post-monsoon period, respectively in August and November (Figs. 3 & 4). The lack of the EP and WT zone in samples taken in March (Figs. 3A, D & 4 A), indicated the absence of cambial activity in the pre-monsoon period. Therefore, the demarcation boundary between M and CZ was gradual in the samples that were collected in August and November in contrast to the samples of March, where the transition from the mature tissue formed in the previous year to the cambial zone was abrupt. Recent cell divisions, as indicated by the presence of a thin cell wall in cells in direct vicinity to the CZ were visible in samples collected in August and November and lacking in the samples of March. The number of cells in the CZ ranges from 7 to 15, whereas the samples of March showed only 4 to 7 cambial cells (Table 1). The average number of cambial cells and the width of the CZ were significantly higher in the samples of August and November than those of March (for cambial cell number, Welch's ANOVA, $F_{2,65} = 394.5$, $p < 0.001$, for cambial width, Welch's ANOVA, $F_{2,65} = 111.2$, $p < 0.001$). Interestingly, the average radial diameter of cambial cells and the tangential width of cambial ray initial cells were significantly larger in the samples of March than those of August and November (for cambial cell's radial diameter, Welch's ANOVA, $F_{2,65} = 394.5$, $p < 0.001$, for cambial ray cell's tangential width, Welch's ANOVA, $F_{2,65} = 345.3$, $p < 0.001$). However, the average tangential diameter of cambial cells was significantly higher in the samples collected in August and November (Welch's ANOVA, $F_{2,65} = 90.4$, $p < 0.001$).

3.2. Growth ring characteristics

S. apetala has diffuse-porous wood with distinct growth ring boundaries that are marked by radially flattened fibres (Fig. A1). However, the distinctness of these growth ring boundaries varied between trees from the three salinity zones, with more conspicuous ring

boundaries occurring in trees from the higher salinity zone. False and locally absent rings complicated ring detection in trees from all salinity zones. The average radial growth rate ranges from 2.00 to 5.70 mm per year in all salinity zones and ANOVA test revealed that both salinity zones and diameter class had a significant effect on the growth rate of this species (for salinity zones, $F_{2, 68} = 22.3$, $p < 0.05$ and diameter class, $F_{2, 68} = 17.4$, $p < 0.05$). The higher growth rate was observed in higher diameter trees irrespective of the salinity zone. The corresponding LSD pair-wise comparison test showed that the average growth rate between LSZ and MSZ was not significant ($p > 0.05$); however, a significantly lower growth rate was in the HSZ ($p < 0.05$).

Despite having missing, locally absent rings and variable distinctness of ring boundaries, it was possible to crossdate the ring-width series visually and statistically and calculate ring-width chronologies for the trees in the three salinity zones covering a period of respectively 25 years (LSZ) and 28 years (MSZ and HSZ; Fig. 5). Pearson correlation test among the three chronologies reveals that all three chronologies correlated positively with each other (LSZ and MSZ, $r = 0.66$, $p < 0.05$, LSZ and HSZ, $r = 0.64$, $p < 0.05$, and MSZ and HSZ, $r = 0.7$, $p < 0.05$). The positive correlations among the chronologies indicate that there is a common external factor influencing the growth of this species. The *S. apetala* tree ring chronologies are representing the population signal as indicated by high intercorrelation as well as EPS values (Table 2). The lower first-order autocorrelation (AC1) in all three zones indicates the lower influence of external factors from the previous year to the current year's ring width. The similar average mean sensitivity (MS) ranged from 0.45 to 0.47 indicates that all the chronologies showed high-frequency inter-annual variations. Moreover, similar high average inter-series correlation (Rbar) and expressed population signal (EPS) indicating the existence of high common signals and poses the suitability of the chronologies for dendrochronological studies.

3.3. Relation of growth with climate and river discharge

The chronologies from all three salinity zones showed a significant positive correlation with river discharge rate during the monsoon season (June-September) (Table 3). Clear differences in response to monsoon precipitation and temperature can be seen between trees growing in the three salinity zones. *S. apetala* trees growing in the zone with lower salinity (LSZ) show a significant positive response to monsoon precipitation and a significant negative response to monsoon temperature. Trees growing under higher salinity regimes in the MSZ and HSZ still react positively to precipitation and negatively to temperature during the monsoon period, but the relation is much weaker.

4. Discussion

4.1. *Sonneratia apetala* forms annual growth rings

In this study, we found that the cambium of *S. apetala* is still dormant in March (starting month of pre-monsoon) but active during August and November, i.e. the period of monsoon and post-monsoon when precipitation, temperature and river discharge are quite high (Fig. 2). The distinction into zones defining the cell developmental stages worked well to assess seasonality in wood formation (Figs. 3 & 4). The lower number of cells with thicker radial cell walls, both in the cambium zone (CZ) was a clear indicator of dormancy (Table 1). The thicker radial walls of the cambial cells might be related to apoplastic translocation during the dormant period through the cambial zone from xylem to phloem parenchyma cells which usually stores food during the active period (Catesson, 1994). This together with the lack of enlarging cells and cells in cell wall lignification stage are widely used for characterisation of the dormant cambium in the tropics (Larson, 1994; Marcati et al., 2008; Dié et al., 2012; Pumijumnong and Buajan, 2013; Chowdhury et al., 2016b).

Conversely, active cambium was found in the samples of August

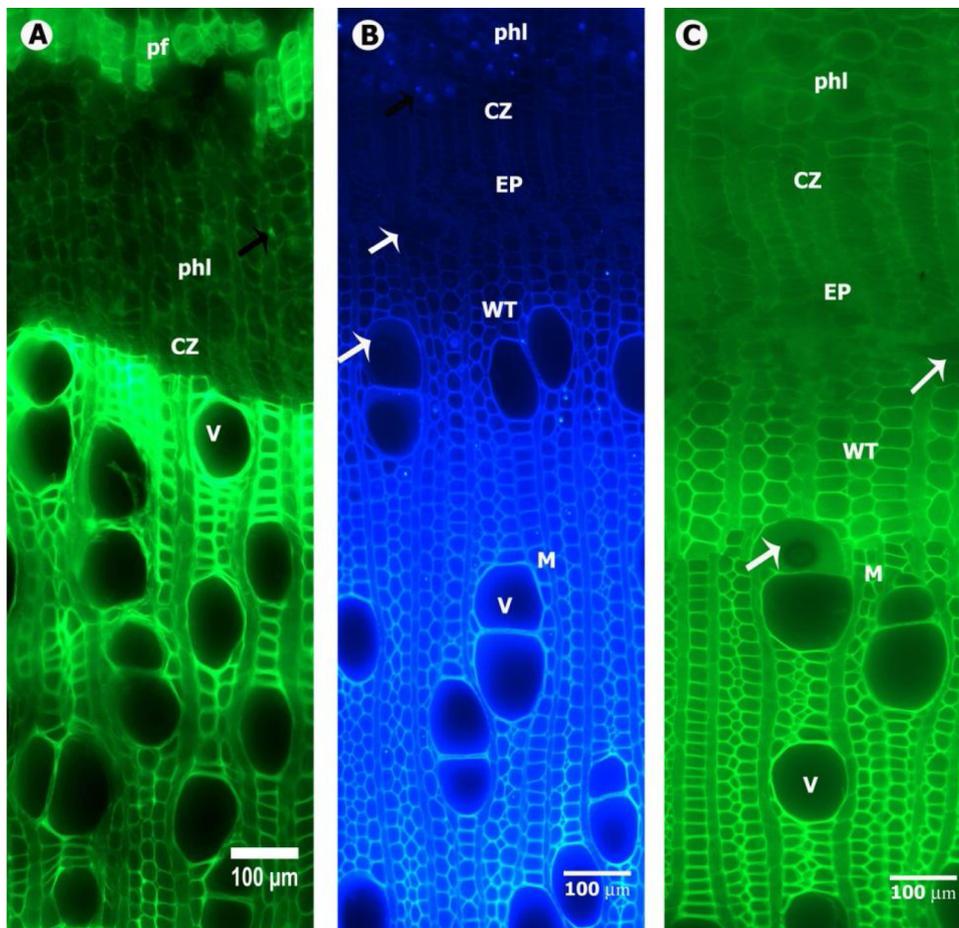


Fig. 4. Seasonal development of xylogenesis in *S. apetala*. (A) No cell differentiation in March, (B) & (C) Differentiation of xylem elements in August and November. Phl = Phloem, CZ = Cambium zone, EP = Expanding zone, WT = Wall Thickening zone, M = Mature zone, V = Vessels, pf = Phloem fibres, White arrow = Developing vessels, Black arrow = crystals. Methods: TS (A-C); FL (A-C), Where, TS, transverse section; FL, epi-fluorescence light.

(monsoon) and November (post-monsoon). The samples of both seasons show a gradual transition from the CZ to mature xylem (M) due to the presence of expanding zone (EP) and wall thickening zone (WT) (Figs. 3 & 4). The initial cells divided periclinally, producing xylem and phloem mother cells that divided through repeated tangential (anticlinal) divisions occurring on both sides of the radial file leading to an increased number of the cambial cells and wider cambial zone (Larson, 1994). The large size of the cambium, as well as other xylem differentiating zones in August, are related to the lower salinity during monsoon and the presence of mature leaves for active photosynthesis. From November to March (Fig. 2), the lower monthly precipitation (< 40 mm) and a decrease of up-stream river flows (57–69 %) leads to an increase in salinity (80 %) in the Sundarbans (Mirza, 1998; Wahid et al., 2007; Islam and Gnauck, 2011). Despite the on average lower precipitation in the post-monsoon period, the active cambium in November suggests that due to the effects of previous months and moderate river discharge, the salinity is still within the tolerance level for this species.

However, the lack of anticlinal division as observed in the cambium in November likely indicates the transition from an active to a dormant cambium (Iqbal, 1990; Venugopal and Krishnamurthy, 1994). It is also noted that an annual dry season lasting for 2 to 3 months with minimum precipitation (< 60 mm) triggering the cambial dormancy in the tropical species for the ring formation (Worbes, 1995; Trouet et al., 2010). The samples of March also showed that trees already produced three to five rows of flattened fibres as the dormant cambium (Fig. A2). The increase of precipitation might induce cambial reactivation during late pre-monsoon or onset of monsoon and trees to produce new xylem with the different anatomy, as evident in the samples of August and November. Although our cambium sampling scheme did not allow us a precise reconstruction of seasonal cambial activity throughout the year, it enabled to verify annual growth-ring formation and indicated the relevance of salinity for the growth of *S. apetala*. To precisely derive seasonal growth dynamics multi-annual and frequent, e.g. weekly or bi-weekly micro sampling or cambium marking campaigns are

Table 1
Seasonal variation of cambial morphology in the medium salinity zone (MSZ).

Months	Range of Cambial cells	Average no. of cambial cell	Average cambial zone width (μm)	Average cambial cells radial diameter (μm)	Average cambial cells tangential diameter (μm)	Average ray cambium cells tangential width (μm)
March	4–7	5.3 ± 0.1 ^c	79.9 ± 1.6 ^c	13.1 ± 0.2 ^a	38.9 ± 0.4 ^c	20.1 ± 0.3 ^a
August	7–15	10.3 ± 0.2 ^b	98.8 ± 3.5 ^b	8.9 ± 0.1 ^c	35.6 ± 0.3 ^b	12.2 ± 0.1 ^c
November	10–15	12.9 ± 0.2 ^a	146.9 ± 4.6 ^a	9.9 ± 0.2 ^b	40.2 ± 0.2 ^a	13.6 ± 0.3 ^b
Welch's test, F		394.5	111.2	134.8	90.4	345.3
p		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Note: Average values followed by different letters indicate significantly different means between different months. (Mean ± s.e.; Welch's ANOVA test followed by post hoc Games-Howell pair-wise comparison test at $p < 0.05$).

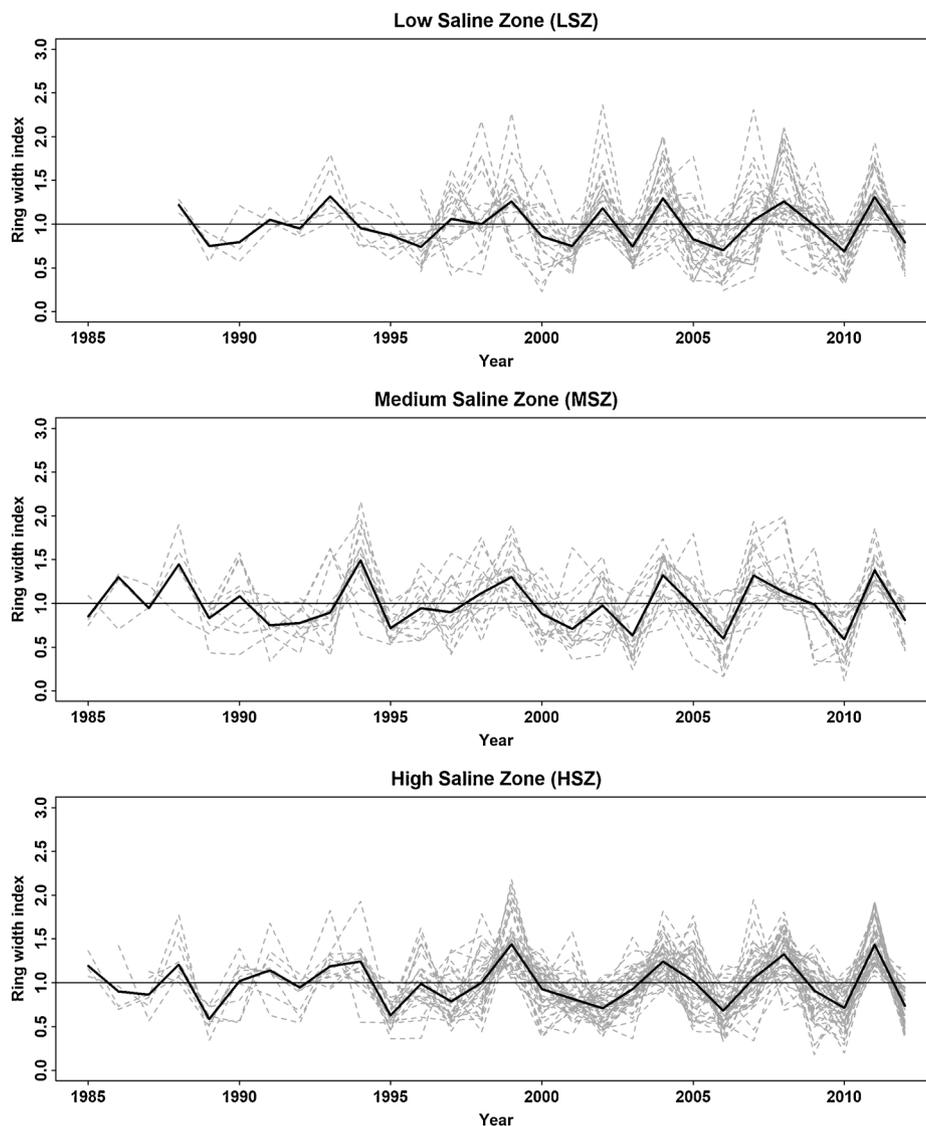


Fig. 5. Standard ring width chronology of three salinity zones (Top = LSZ, Middle = MSZ and bottom = HSZ). The horizontal dashed grey lines are the individual series and bold black line is their 10 year running average.

Table 2
Mean statistical attributes of crossdated ring-width series of *S. apetala* in three salinity zones.

Variables	Low salinity zone (LSZ)	Medium salinity zone (MSZ)	High salinity zone (HSZ)
Number of trees	10	6	15
Number of transects	30	18	45
Average stem diameter (cm)	13.11 (8.9–17.4)	21.4 (14.8–28.1)	9.85 (5.6–21.5)
Average age (years)	16 (11–25)	22 (16–28)	19 (12–28)
Time span (years)	1988–2012	1985–2012	1985–2012
Average ring width (mm) ± SD	3.11 (± 1.23)	4.39 (± 1.98)	2.39 (± 0.89)
1 st order autocorrelation (AC1)	0.32	0.18	0.18
Standard Deviation	0.38	0.42	0.37
Mean sensitivity (MS)	0.47	0.47	0.45
t-value BP (± SD)	5 (± 2)	6 (± 2)	8 (± 3)
GLK (± SD, %)	83 (± 3)	78 (± 3)	86 (± 3)
Expressed population signal (EPS)	0.96	0.95	0.98
The signal to noise ratio (SNR)	24.31	17.08	38.27
Mean interseries correlation (Rbar)	0.55	0.55	0.56

Note: LSZ = Low salinity zone, MSZ = Medium salinity zone and HSZ = High salinity zone. t-value BP = t-value Baillie Pilcher, GLK = Gleichläufigkeitskoeffizient. Value in the parentheses is range.

Table 3
Correlation coefficient of standard chronologies from all salinity zones with climatic and environmental factors.

Zone		River discharge rate	Precipitation	Temperature
Low salinity zone (LSZ)	Standard chronology	0.47*	0.57**	-0.49*
	River discharge		0.26	-0.18
	Precipitation			-0.13
Medium salinity zone (MSZ)	Standard chronology	0.44*	0.20	-0.26
	River discharge		0.14	-0.25
	Precipitation			-0.04
High salinity zone (HSZ)	Standard chronology	0.62**	0.27	-0.38
	River discharge		0.22	-0.20
	Precipitation			-0.20

recommended (Verheyden et al., 2004; Schmitz et al., 2007; Chowdhury et al., 2016b). Seen the considerable working load for collection, preparation and analyses of micro samples or cambial marks, the use of dendrometers is also recommended (Robert et al., 2014).

4.2. *Sonneratia apetala* growth is mainly driven by salinity

Although growth rings of *S. apetala* have found to be annual, the presence of false rings and locally absent rings categorises this species as indistinct to a distinct growth ring (Wheeler, 2011). These anomalies might be associated with phases of low growth rates or asymmetrical stem growth in mangroves (Chowdhury et al., 2016b), which is also common in other tropical species (Trouet et al., 2010; De Ridder et al., 2013; Mbow et al., 2013). Stem asymmetry can also be related to growth stress during stem development due to inundation, sedimentation, erosion, seasonal storms and anthropogenic disturbances (Ellison et al., 2000; Robert et al., 2011). The possibility to crossdate growth ring within and among the samples of *S. apetala* provides strong evidence that the growth rings are indeed annual driven by seasonality in climate and environmental factors as suggested in previous studies by Chowdhury et al. (2008) and Maxwell et al. (2018). When comparing growth ring series of *S. apetala* from the Sundarbans studied by Maxwell et al. (2018) with those of our trees from the low (LSZ) (Fig. A3) and high (HSZ) salinity zone, no match was found (for LSZ, $r = 0.01$, $p > 0.05$, and for HSZ, $r = 0.00$, $p > 0.05$); our MSZ chronology even showed a negative correlation ($r = -0.15$, $p > 0.05$). Although the sample collection site of Maxwell et al. (2018) originated from LSZ, they collected samples from the seaward side of the Sundarbans where there might be some external influence of the sea. On the other hand, our samples originated from the landward side- free from the direct influence of the sea. These differences, which can occur through short distances in the same study area indicate the importance of the specific environmental settings especially related to salinity for the growth of *S. apetala* and most likely also other mangrove species. This is supported by the chronology statistics yielded for the three salinity zones (Table 2), which indicates that the three chronologies show variable signals related to micro-climate variation of the three salinity zones or exogenic influences such as ocean El Niño oscillation or sea-level rise (Wigley et al., 1984; Maxwell et al., 2018).

In the low salinity zone (LSZ), the average radial growth of *S. apetala* is considerably higher than that those of medium (MSZ) and higher salinity (HSZ) zone (Table 2). The average radial growth rate (3.02 ± 1.20 mm) is within the range of the earlier study of Chowdhury et al. (2008), where the ring width ranges from 0.40 to 7.00 mm with an average of 2.00 ± 1.00 mm. The lower growth rate in the higher salinity zone indicates a negative influence on tree physiology (Siddiqi et al., 1989). Yan and Guizhu (2007) found a sharp decrease of the photosynthetic rate of *S. apetala* above 15 ppt (parts per trillion (10^{12})) salinity in a controlled experiment which likely has a negative effect on radial growth. The higher salinity stress due to lower freshwater input might be reflected as more unfavourable growth conditions for trees

(Menezes et al., 2003; Robert et al., 2011). The range of average growth rate of *S. apetala* corresponds well with *Rhizophora mucronata* ($0.50\text{--}4.81$ mm year⁻¹) from Gazi Bay, Kenya (Verheyden et al., 2004), but higher growth rate exhibited than *Avicennia marina* (1.00 mm year⁻¹) from Kenya (Schmitz et al., 2008), *Xylocarpus granatum* ($0.62\text{--}2.51$ mm year⁻¹), *Bruguiera gymnorrhiza* ($0\text{--}2.51$ mm year⁻¹), *Rhizophora mucronata* (0.94 mm year⁻¹) and *Sonneratia alba* ($0.31\text{--}1.25$ mm year⁻¹) from Micronesia (Devoe and Cole, 1998), *Heritiera fomes* (0.86 to 1.40 mm year⁻¹) from the Sundarbans (Chowdhury et al., 2008, 2016a, 2016b) and lower than *Avicennia marina* (4.84 mm year⁻¹) from Western Australia (Santini et al., 2013). Overall, the range of radial growth rate in different species from different continents shows that mangroves usually have a low growth rate in comparison to terrestrial tree species. However, for this type of comparison, confounding factors, such as environment, ontogeny, and inter-generic differences, are important to consider (Robert et al., 2011).

Irrespective of salinity zones, we could prove that river discharge during the monsoon season, i.e. from June to September, was positively related to the growth of *S. apetala* (Table 3). Several studies confirmed that the upstream river discharge rate is negatively correlated with salinity in the Sundarbans and a higher discharge positively affects the growth dynamics of mangroves in the Sundarbans (Wahid et al., 2007; Islam and Gnauck, 2009; Rahaman et al., 2014; Dasgupta et al., 2015, 2017). Our *S. apetala* trees in the lower salinity zone (LSZ) show, in addition to the positive relation to river discharge, a significant positive correlation with monsoon precipitation and a negative correlation with monsoon temperature. Similarly, Maxwell et al. (2018) also found a positive correlation between the growth and monsoon precipitation of *S. apetala* collected from low salinity zones. However, they concluded that the trees are not sensitive to salinity as they found a negative correlation with the dry season precipitation. An intolerance to salinity might hold for trees in low salinity areas, i.e. under conditions where the salinity is within the tolerance level of the species. This phenomenon does not hold for the trees in our sites as we found a strong relation with river discharge and climate factors prevailing in the monsoon period in all salinity zones. Mangrove physiology although adapted to salinity is generally favoured by lower salinity, but also lower temperature during the growing period as the high temperature increases water loss due to transpiration (Tomlinson, 1986; Reef and Lovelock, 2015). The fact that the relation with climate factors is strongest in the low salinity zone was surprising but highlighted the complex interaction between freshwater input from the river and the sky as well as evaporation and evapotranspiration loss triggered by high temperature.

Altogether, river discharge rate in combination with high precipitation and low temperature conditions during the monsoon season had a significant effect of reducing the salinity and in turn favour the growth of *Sonneratia apetala*. Besides, the growth variation of this species could also be linked with ocean oscillations as pointed out by Maxwell et al. (2018). The sensitivity to higher salinity, especially in the MSZ and HSZ, could be helpful to understand the ecology of this species in the Sundarbans, particularly with the rising sea level and the consequent rising salinity.

5. Conclusion

The analysis of seasonal cambium activity and the success of growth ring crossdating proved the existence of distinct annual growth rings in *S. apetala* driven by a distinct seasonality of salinity. The presence of annual growth rings provides a solid basis for age and growth rate determination which has necessary implications for understating the ecology of the species. The growth of *S. apetala* is mainly driven by freshwater input through river discharge and precipitation during the monsoon season. With the predicted sea-level rise and its consequences on rising salinity, our results suggest that *S. apetala* will likely experience adverse effects of climate change and global warming in the future with the declined growth rate. Besides offering the possibility to evaluate the impact of future changes in these factors on mangrove growth in the Sundarbans, the strong relationship between *S. apetala* growth and environmental factors provides the chance of reconstructing past climate and river discharge or salinity in this region provided that longer chronologies can be constructed.

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Conflict of interest

The authors agreed that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.dendro.2020.125711>.

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