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The effects of watering on cambial activity in the stems of evergreen hardwood (*Samanea saman*) during the pre-monsoon season in subtropical Bangladesh

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Abstract

Water stress has a significant impact on tree growth. However, the effects of watering on cambial activity and its influence on tree growth in subtropical climates is poorly understood. The present study analyzed the cambial activity on the stem of evergreen hardwood *Samanea saman* in response to either high frequency or low frequency watering during the pre-monsoon season in subtropical Bangladesh. We used two groups of seedlings: one group of seedlings was watered daily (high frequency watering), while the second group of seedlings was watered at 4–5-day intervals (low frequency watering). Samples for sequential observations of cambial activity by microscopy were collected from the main stems of seedlings of both groups. At the start of the experiment on March 25, 2015, during the pre-monsoon season, the cambium was inactive with no evidence of cell division. After 10 days of high frequency watering, cambial cell division and xylem differentiation were initiated. New cell plates were formed in the phloem side of the cambium. However, the cambium was inactive when low frequency watering was supplied. Supplying water in high frequency reactivated the cambium with forming small to large vessels. In contrast, the cambium remained inactive when low frequency watering was supplied throughout the experiment. These results suggest that continuous supply of water to the soil is one of the most important factors for cambial reactivation during pre-monsoon season in subtropical trees. Furthermore, our findings of artificial watering treatments might help to better understand the response of cambium to changes in precipitation patterns under natural conditions, allowing us to learn more about how cambium of subtropical trees responds to climate change.

Keywords: Bangladesh, Cambium, Irrigation, Pre-monsoon, *Samanea saman*, Subtropical region, Tree growth, Water stress, Wood formation, Xylem differentiation

Introduction

Climate change and its impact on tree growth have received special attention in recent years, because, from an environmental, social, and economic perspective, trees play an important role in establishing a sustainable society [1, 2]. Trees will try to adapt to climate change by synchronizing their phenological events and physiological processes. It is assumed that global warming at the recently projected temperature rise of 3 to 6 °C within the next century would extend the tree growing season as a consequence of higher air temperatures [3–5]. In addition, the increased concentration of atmospheric carbon dioxide would enhance tree growth. However, higher rates of tree growth can only be sustained over time when excess water from the soil is available to the trees, as this is essential for photosynthesis and other physiological functions [6–9].

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Tree water status and phenology, such as leaf shedding, flowering, and shoot growth, are influenced by frequent precipitation or artificial watering [7, 8, 10–12]. Water stress influences radial growth of trees both directly, through cambial activity, and indirectly, through photosynthesis and the balances of plant hormones [13–16]. Cambium is a meristematic tissue that can divide and differentiate into secondary xylem and phloem and is responsible for the radial growth of trees [2, 17, 18]. Studies on temperate trees indicate that water stress can cease cambial activity and change the anatomical structure of the xylem [6, 19, 20]. It is important to note that climatic factors, such as temperature, precipitation, and day length, are the main regulators of cambial activity and, consequently, carbon allocation in woody parts of trees. The relationship between climatic factors and cambial activity has been studied in detail in trees in temperate climates [2, 21, 22]. However, less attention has been paid to trees growing in tropical and subtropical regions [23, 24].

It is assumed that temperature, precipitation, day length, or a combination of these factors influence cambial activity in trees growing in tropical and subtropical regions [7, 9, 23–32]. In tropical regions, temperature remains relatively constant throughout the year, but the patterns of precipitation often exhibit seasonal variations, which are known to be the most important factor for cambial activity [31, 33–36]. The absence (or less than 60 mm) of precipitation for 1–3 months during the dry season is responsible for a temporary cessation of cambial activity in tropical trees [34, 37]. However, in comparison with trees in tropical regions, the relationship between cambial activity and climatic factors of subtropical trees, is more complex because of the year-round variations of temperature, precipitation, and day length.

The factors that regulate cambial activity in subtropical trees are still unclear, because subtropical trees show contrasting findings of both decrease and increase in radial growth in relation to climate change [30, 32, 38, 39]. These differences are related to regional variances in main climatic factors, such as temperature, precipitation, and water availability, all of which control cambial activity. For example, precipitation affects cambial activity [40]; however, when soil water is abundant, cambial activity is associated with temperature rather than precipitation [25, 30, 32, 41]. We recently observed that, if precipitation continued regularly during the drier month, the cambium of *Acacia mangium*, *Tectona grandis*, *Eucalyptus urophylla*, and *Neolamarckia cadamba* trees remained active throughout the dry season in tropical Indonesia [31]. This investigation revealed that the pattern of precipitation is important for cambial activity, although it is unclear whether continuous or intermittent precipitation pattern is more effective [7, 31, 42]. So far, most studies on tropical and subtropical trees have focused on seasonal cambial activity and tree ring analyses. A sequential experimental setup involving intentional variations of environmental factors can provide more precise and detailed information on the climatic regulation of cambial activity in subtropical trees [30, 31].

Climate change potentially poses a very high risk to Bangladesh as a sub-tropical country. However, until now, little is known of how the cambium of perennial trees responds and synchronizes its activity under these uncertain climatic conditions. Dendrochronological studies of some tree species growing in Bangladesh have shown the formation of annual rings, indicating that cambial activity can cease and later resume [38, 43–47]. The width of annual rings drastically decreased and xylem anatomical features changed as a response to extreme drought [48, 49]. In particular, a slightly higher temperature during the pre-monsoon season (i.e., a hot spring) just before the monsoon season adversely affected the annual rings as well as the anatomical features of the xylem [45, 50]. Although tree ring analyses reveal a relationship between annual tree growth and precipitation, it is unknown how artificial watering during the pre-monsoon season affects the onset, continuation or termination of cambial activity [42].

The present study was designed to understand the response of the cambium on the stem at two different frequencies of watering during the pre-monsoon season in subtropical Bangladesh. We studied cambial cell division, xylem differentiation, and anatomical structure of xylem of the main stem of evergreen hardwood *Samanea saman* seedlings. We selected the *S. saman* tree species for this study because of its common use as an easily adapting and fast-growing tree in homesteads, along roadsides, and other places [51].

Materials and methods

Climate and soil status

Bangladesh has a warm and humid climate that comprises six seasons: summer, rainy, autumn, late autumn, winter, and spring. However, in practice, most of the six seasons overlap with each other. Based on meteorological climate data, Bangladesh is divided into winter (December to February), pre-monsoon (March to May), monsoon (June to September), and post-monsoon (October to November). The variation in monsoon rainfall depends on the easterly trade winds, southwest monsoon, and El Niño–Southern Oscillation (ENSO).

We set the experiment in a homestead area in the Dinajpur district of Bangladesh (25° 37′ 9.084″ N and 88° 38′ 49.2504″ E). This area is 42 m above sea level and located in the northern part of Bangladesh, which includes a

Fig. 1 Map showing the location of Bangladesh and of the experimental site (a yellow star; Source: Google, TMap Mobility, and Bangladesh forest department)

small tropical moist deciduous forest (Fig. 1). According to the Köppen climate classification, this area has a tropical wet and dry climate and falls under agro-ecological zone 1 (Old Himalayan Piedmont Plain). Sandy loam and clay loam soils are predominant with strongly acidic top-soil and moderately acidic sub-soils and comparatively higher soil organic matter content than other areas of Bangladesh [52].

The meteorological data for Dinajpur, Bangladesh for the years from 1901 to 2016 were obtained from the Climate Change Knowledge Portal [53], World Bank Group (Fig. 2a). The meteorological data for 2015 were obtained from the Meteorological Agency in Dhaka, Bangladesh (Fig. 2b).

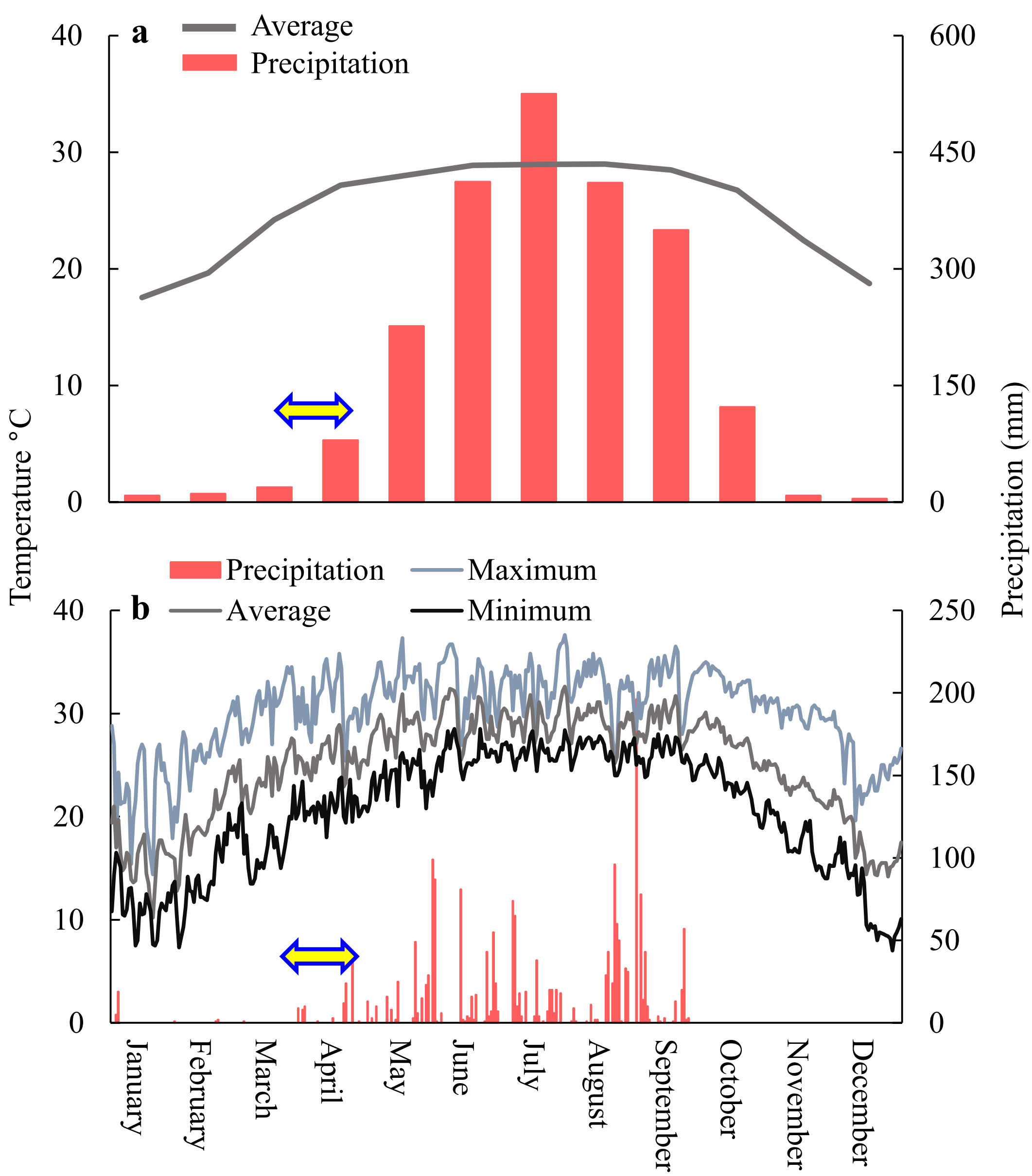

Fig. 2 Meteorological data showing average monthly air temperature and monthly (total) precipitation in Dinajpur, Bangladesh from 1901 to 2016 (**a**). The maximum, average, and minimum daily air temperatures and the daily precipitation of 2015 (**b**) at the experimental site in Dinajpur, Bangladesh (yellow arrow indicates irrigation period)

Plant materials

This experiment was designed for a total of 22 seedlings of evergreen *S. saman* (age, approximately 1.5 years; height, approximately 40 cm; average diameter of the sampled stems, 2 mm). The seedlings were grown in pots (diameter, 21 cm; height, 19 cm) that were filled with soil containing a mixture of two-thirds garden soil and one-third organic compost.

Treatments

Two treatments, namely, high frequency watering and low frequency watering, were applied to two separate groups from a total of 22 seedlings. In the "high frequency watering treatment", approximately 300 mL of water was applied to the soil daily. In the "low frequency watering treatment", approximately 300 mL of water was applied to the soil every 4–5 days. The experiment was started on March 26, 2015, and continued until April 25, 2015. We did not design an experiment without water treatment, because complete absence of watering during the pre-monsoon season would have likely resulted in dead plants and no additional data.

Collection of samples

Stem samples were collected 7–8 cm above the soil level of the main stem at 5-day intervals from all seedlings. Two seedlings were subjected to each condition on each sampling date and immediately fixed in 5% glutaraldehyde in 0.1 M phosphate buffer (pH 7.3) at room temperature (25–30 ℃).

Preparation for light microscopy

Fixed samples were washed in 0.1 M phosphate buffer, trimmed, dehydrated in a graded ethanol series, and then embedded in epoxy resin. Transverse sections with a thickness of approximately 1 µm were cut from the embedded samples with a glass knife on an ultramicrotome (Ultracut N; Reichert, Vienna, Austria). The sections were stained with a solution of 1% safranin in water for 30 min and washed five or six times with water to visualize cambial cell division and xylem differentiation. In addition, hand-cut transverse sections were prepared with a razor blade and double stained with Congo red and acridine orange to show cellulose in red and lignin in green according to Nakaba et al. [54], Rahman et al. [31] and Kitin et al. [55]. Thick hand cut sections were stained in an aqueous solution of 10 µM acridine orange for 10–15 min and washed four to five times with distilled water before they had been stained with 0.1% Congo red solution for 5 min and washed two times with distilled water.

All sections were examined under a light microscope (Axioscop; Carl Zeiss, Oberkochen, Germany) using three optical systems: bright field, polarized, and fluorescence as previously described [54–57]. Semi-thin sections were examined by bright field and polarized and hand-cut thick sections were examined by fluorescence according to Nakaba et al. [54] and Rahman et al. [31]. Using fluorescence filters set for green (Ex/Em, BP450–490/BP500–550) and red (Ex/Em, BP539–563/BP570–640), the Congo red stained for cellulosic cell wall and acridine orange stained for lignified cell wall were studied. The red and green color images were merged using the merge channels function of ImageJ (National Institutes of Health, Bethesda, MD, USA).

Cambial reactivation was determined by the occurrence of first cell division with thin tangential cell walls [5, 56, 58]. Active cambium is defined by the continuous division of cambial cells, while inactive cambium is defined by the absence of cell division in the cambium [5, 31]. Cambial cells were distinguished from newly differentiating xylem (expanding cells and secondary wall thickening cells) based on their smaller radial diameter, occurrence of division plates and cell wall birefringence, as visualized in epoxy-embedded 1-µm-thick transverse sections [5, 31, 56–61]. Under polarized light, cambial cells and expanding cells consist of only primary walls and exhibit no birefringence, whereas secondary wall thickening cells show birefringence. We separated differentiating expanding cells from cambial cells by measuring their size; if the cell size was nearly double that of cambial cells, we classified them as differentiating expanding cells. These differentiating expanding cells with primary walls were distinguished from differentiating secondary wall thickening cells by examining cell wall birefringence.

Results

Temperature and precipitation profiles

We observed identical variations of intra-annual seasonal temperatures and precipitation (Fig. 2). The 115-year record from 1901 to 2016 showed highest monthly precipitation (above 300 mm) from June to September; then, the monthly precipitation continuously decreased until it was very low or absent until the start of the rainy season in the following year from June onwards (Fig. 2a). The average temperature decreased in December and increased gradually from February. The changes in daily temperatures and precipitation in 2015 follows the same pattern as the 115-year record of temperature and precipitation profiles (Fig. 2b). The study area experienced six-to-seven drier months during the winter and pre-monsoon seasons.

Investigation of cambial activity

On March 26, 2015, before the start of the experiment, the cambium was inactive with no evidence of cell division (Fig. 3a–e). The inactive cambium consisted of three to five layers of radially narrow and compactly arranged fusiform cells that were located between the phloem and xylem cells (Fig. 3a, b). We observed some differentiating xylem cells between the compactly arranged cambial cells and completely developed xylem (Fig. 3b, c).

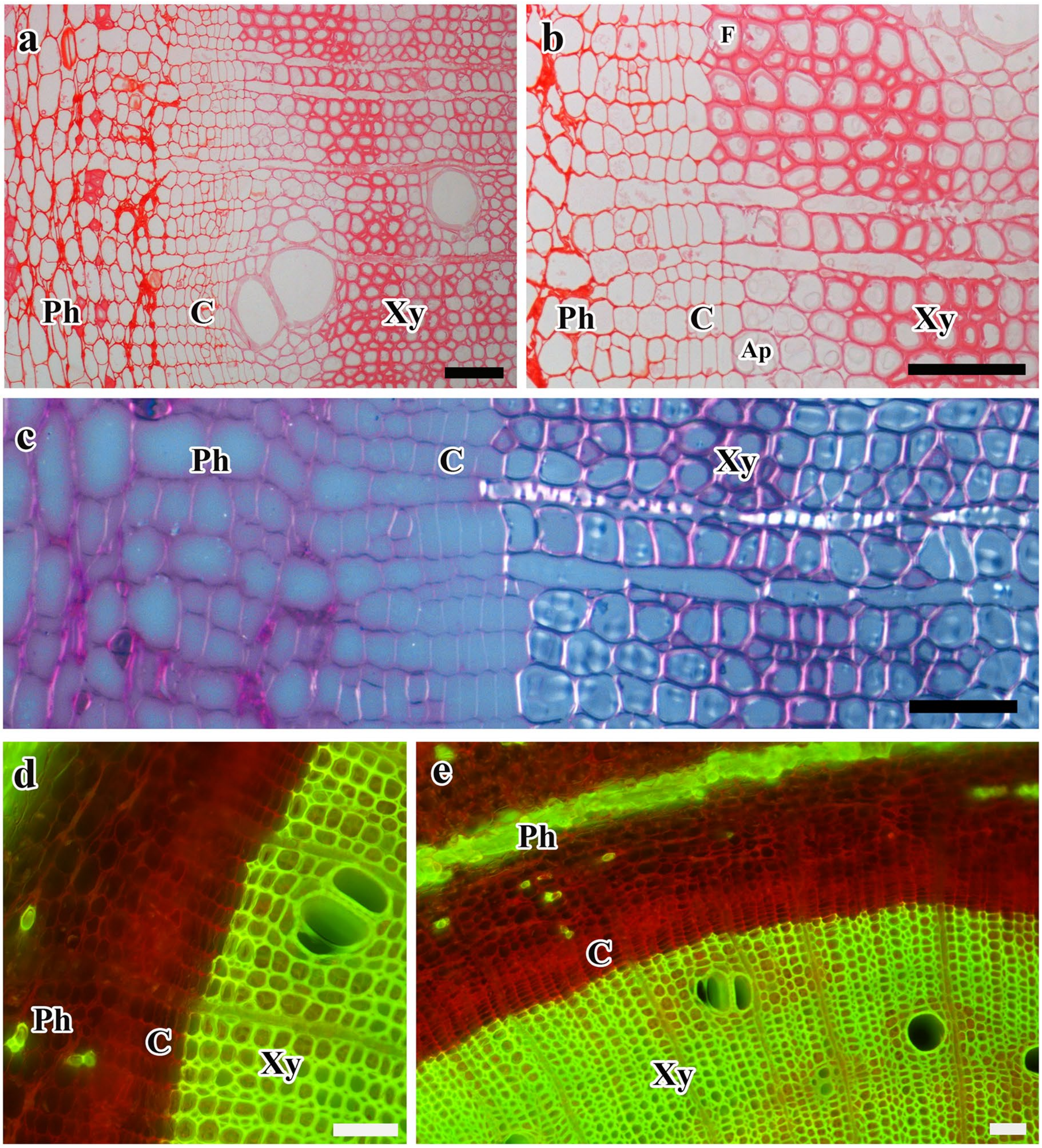

Fig. 3 Light, polarized and fluorescence micrographs showing transverse views of cambium before the start of the experiment on 26 March 2015 (**a**–**e**). On this date, three to five layers of fusiform cambial cells were arranged compactly with no evidence of cell division, indicating inactive condition of cambium on the stem (**a**, **b**). A polarized light micrograph of thin sections after staining with safranin showing the cambial region (**c**). Expanding and expanded xylem cells were separated by observing the birefringence of cell wall. Fluorescence micrographs (**d**, **e**) showing the phloem, cambium and xylem. The heterogeneous intensity of fluorescence in (**d**, **e**) indicates the less-lignified xylem adjacent to cambium. Merged green (Ex/Em, BP450-490/BP500-550) and red (Ex/Em, BP539-563/BP570-640) image. *Ap* axial parenchyma, *C* cambium, *Ph* phloem, *F* fibers, *Xy* xylem. Bars = 50 µm

On April 5, 2015, after the application of high frequency watering for 10 days, we observed the formation of new cell plates with thin cell walls in the cambium, which is an indication that cambial reactivation occurred on the stem (Fig. 4a). This newly dividing cambial cells were located near the phloem side of the cambium. Just below the dividing cambial cell layers in the xylem side, we observed differentiating xylem cells. In contrast, on the same date, cell division in the cambium was absent on the stems of those seedlings that had been treated with low frequency watering, indicating the inactive condition of cambium (Fig. 4b). Between these compactly arranged inactive cambium and completely developed xylem, differentiating xylem cells were observed.

On April 15, 2015, after the application of high frequency watering for 20 days, cambium was active and cell division in the cambium continued (Fig. 4c). We observed approximately 4–7 radial layers of dividing fusiform cells (Fig. 4c). Just below the dividing cambial cell layers in the xylem side, we observed expanding and secondary wall forming xylem cells that were differentiating into new wood fibers or parenchyma cells or vessel elements (Fig. 4c). By contrast, on the same date, the cambium was still in inactive condition with no evidence of cell division in samples when low frequency watering had been applied (Fig. 4d). Between the compactly arranged cambial cells and completely developed xylem, differentiating xylem cells were observed.

On April 25, 2015, after the application of high frequency watering for 30 days, the cambium was highly active with continuous cambial cell division and xylem differentiation (Fig. 4e). Just below the layers of newly dividing cambial cells in the xylem side, differentiating new wood fibers and vessels elements were observed (Fig. 4e). In contrast, on the same date, with the application of low frequency watering, cambium remained inactive with no evidence of cell division (Fig. 4f). On this date, we observed differentiating xylem cells between the inactive cambium and completely developed xylem.

The detailed anatomical characteristics of newly formed xylem cells, with the application of high frequency watering, were observed on the last date of observation on April 25, 2015 (Fig. 5a–f). We observed 4–5 layers of expanding and secondary wall forming xylem cells with large numbers of newly differentiating vessels located near the cambium (Fig. 5a, b). These newly formed vessels had variable diameters and thick cell walls (Fig. 5c, d). Thickening of vessel cell walls occurred ahead of the surrounding wood fibers and longitudinal parenchyma cells (Fig. 5b, e, f).

There were no identical differences in cambial activity among the individual seedlings from the same treatment on each sampling date. The low magnification image of the sample stem of high frequency watering treated seedling on April 25, 2015 showed no clear xylem growth ring boundary (Fig. 6).

Discussion

The application of high frequency watering during the pre-monsoon season induced cambial reactivation of inactive cambium on the stem of the diffuse-porous evergreen hardwood *S. saman*. In contrast, the cambium remained inactive when low frequency watering was applied. The results reveal that a continuous supply of water to the soil is one of the most important factors for cambial reactivation of the stem in the pre-monsoon season in trees growing in sub-tropical regions, such as Bangladesh.

Trees are more sensitive to temperature in comparatively cold regions. In contrast, they are more sensitive to water in hot and dry regions, and become increasingly temperature restricted with shortage of available soil water [9, 28, 62]. Studies in subtropical regions of China, India, and Mexico have revealed that cambial reactivation is closely associated with seasonal temperatures [25, 28, 30, 41]. In temperate and cool climates, an increase in temperature from late winter to early spring is widely recognized as a trigger for reactivating the process of cambial cell division and xylem differentiation in tree stems [56, 60, 61, 63–66]. Rossi et al. [64, 67–69] observed that cambial activity and xylem differentiation started above a certain threshold value of mean daily temperatures of 5–9 °C in temperate-grown *Larix decidua*, *Pinus cembra*, *Picea abies*, *Abies balsamea*, *Pinus sylvestris*, *Pinus leucodermis*, and *Pinus uncinata*. Cambial reactivation occurs when the daily maximum temperature exceeds the threshold maximum temperature of 10–15 °C for several days in deciduous hardwood hybrid poplar, evergreen conifer *Cryptomeria japonica*, and *Chamaecyparis pisifera* in Tokyo, Japan [5, 70, 71]. However, in subtropical China, cambial reactivation and xylem differentiation in *P. massoniana* Lamb. started in February, with a 7-day mean temperature of 12.2–16.1 °C [30]. Observations in subtropical regions in India showed that cambial reactivation and xylem differentiation started in March with monthly maximum, average, and minimum temperatures just above 20 °C, 15–20 °C, and 12–15 °C, respectively, in *Dillenia indica* and *P. kesiya* trees [25, 41]. In the present study, before the start of our experiment in March, the daily maximum, average, and minimum temperatures ranged from 27.0 to 34.5 ℃, 20.3 to 27.6 ℃, and 13.5 to 23.4 ℃, respectively. During our experiment from March 26 to the date of cambial reactivation on April 5, the daily maximum, average, and minimum temperatures ranged from 27 °C

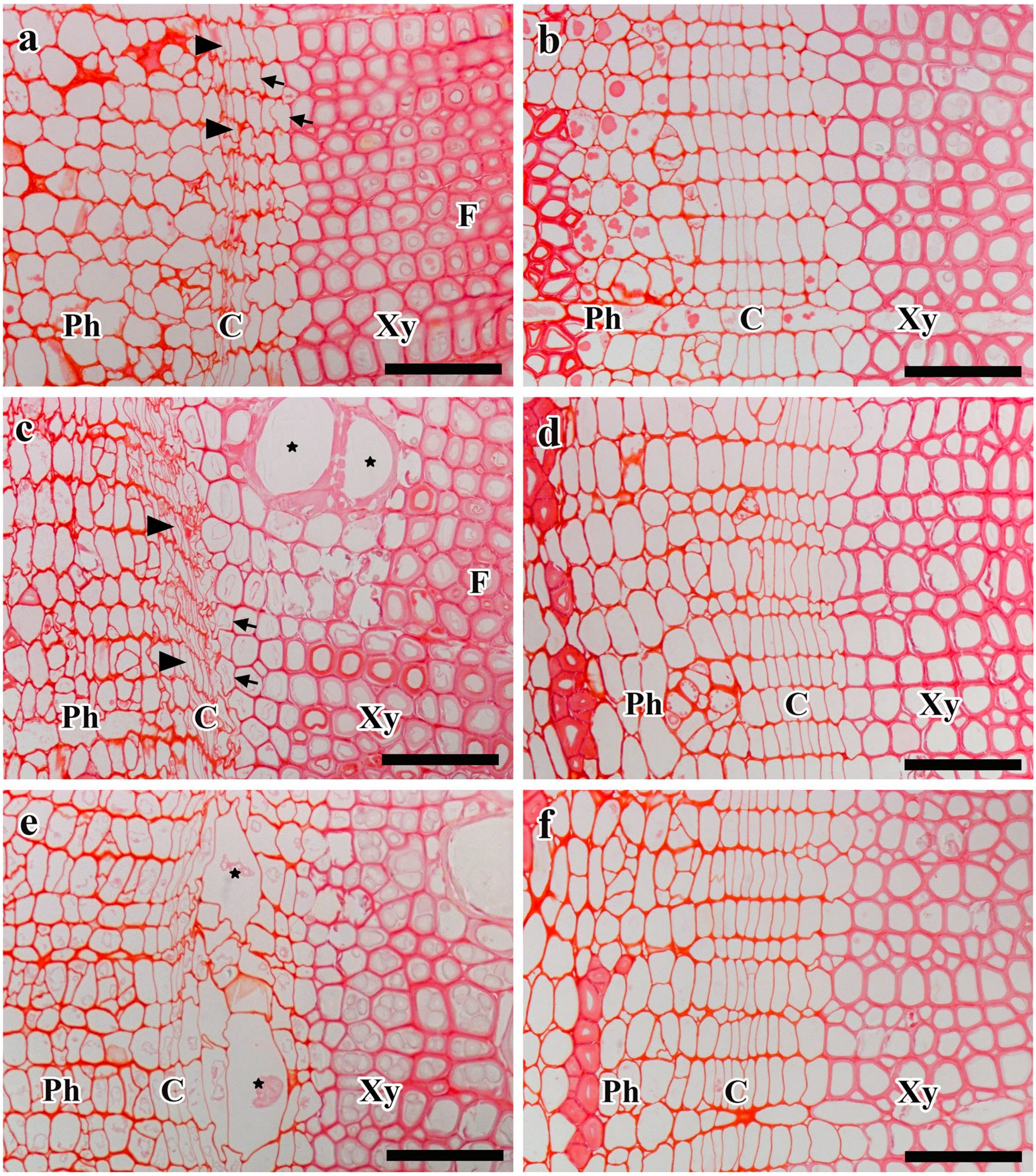

Fig. 4 Light micrographs showing transverse views of cambium from high frequency and low frequency watering treatments. On 5 April 2015, after 10 days of application of high frequency watering, cell division in the cambium was initiated and many cambial cells started to divide (arrowheads) and differentiate into xylem cells (arrows, **a**). On the same date, with the application of low frequency watering, the cambium was in inactive condition (**b**). On 15 April 2015 after 20 days of application of high frequency watering, cambial cell division (arrowheads) and xylem differentiation (arrows) were observed on the cambial zone (**c**). On the same date, with the application of low frequency watering, cell division was absent in the cambial zone (**d**). On 25 April 2015, after 30 days of treatment with high frequency watering, cambial cell division and xylem differentiation were continued (**e**). On the same date, after treatment with low frequency watering, there was no new cell division in the cambial zone (**f**). *C* cambium, *F* fibers, *Ph* phloem, * vessel elements, *Xy* xylem. Bars = 50 μm

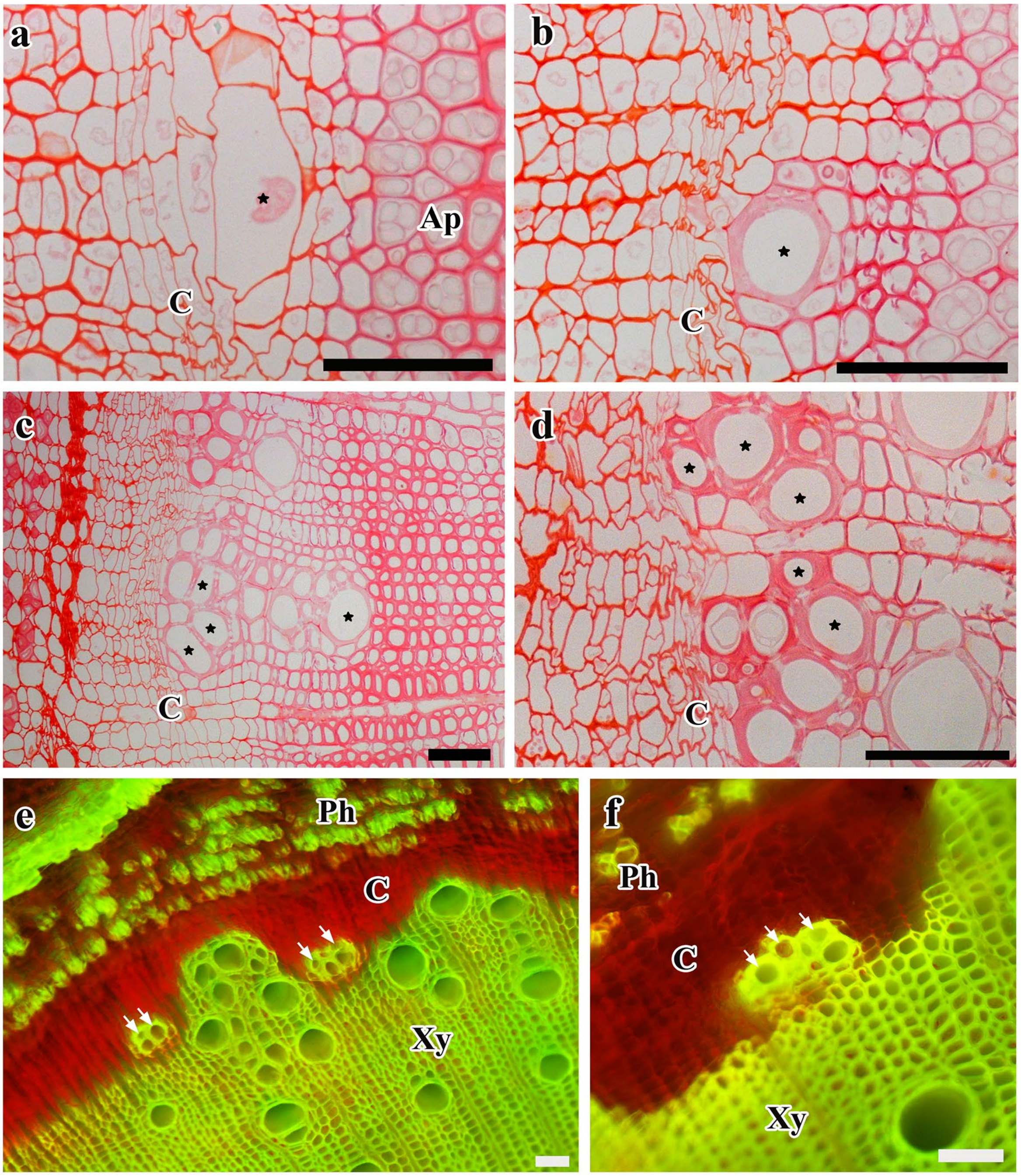

Fig. 5 Light and fluorescence micrographs showing transverse views of cambium and differentiating xylem cells after 30 days of application of high frequency watering on 25 April 2015. A newly differentiating vessel located close to the cambium consisted of large radial diameter and thin cell wall (**a**). The vessel located close to the cambium exhibited a narrow diameter and thicker cell walls than the surrounding wood fiber cells (**b**). Small vessels located close to the cambium exhibited thick cell walls (**c**, **d**). Fluorescence micrographs showing the phloem, cambium and differentiating (arrows) and differentiated vessel elements located close to the cambium (**e**, **f**). The heterogeneous intensity of fluorescence in (**e**, **f**) indicates the less-lignified rays and wood fibers adjacent to cambium. Merged green (Ex/Em, BP450–490/BP500–550) and red (Ex/Em, BP539–563/BP570–640) image. *Ap* axial parenchyma, *C* cambium, * *Ph*, phloem, *, vessel elements, *Xy* xylem. Bars = 50 µm

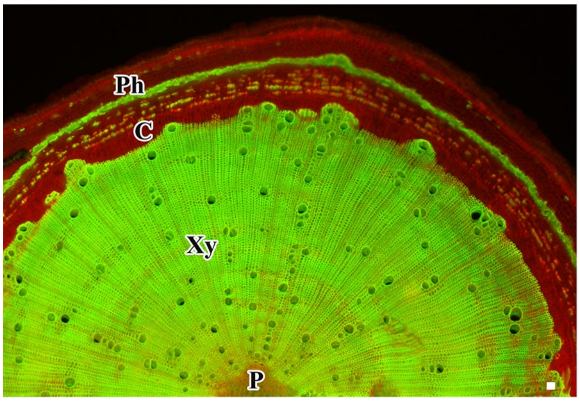

Fig. 6 Fluorescence micrograph showing low magnification transverse view of the stem sample consisting phloem, cambium and xylem after 30 days of application of high frequency watering on 25 April 2015. Absence of sharp boundary indicating xylem growth ring was not visible. Merged green (Ex/Em, BP450–490/BP500–550) and red (Ex/Em, BP539–563/BP570–640) image. *C* cambium, *Ph* phloem, *P* Pith, *Xy* xylem. Bar = 50 µm

to 33 °C, 23 °C to 27 °C, and 19 °C to 23 °C, respectively. Although the ambient air temperatures during our experimental period were sufficiently high in our study area to promote continuous cambial activity, the cambium remained inactive. Therefore, it was hypothesized that climatic factors other than temperature, for example, precipitation could influence the timing of cambial reactivation during the pre-monsoon season in Bangladesh.

Cambial reactivation occurred in deciduous hardwood *Tectona grandis* and evergreen conifers, *P. kesiya, P. latteri* and *Pinus merkusi*, and woody *Kielmeyera grandiflora* (Wawra) Saddi (Calophyllaceae) during the transition from the dry to rainy season or at the start of the rainy season when water was abundant in the soil [32, 34, 40, 72]. An exceptional precipitation or irrigation under natural condition during the mid-dry season caused bud flush in several tropical tree species grown in Costa Rica [73]. The first heavy rains initiate rehydration of the tree trunk and activate flushing, which in turn induce cambial activity [7, 72]. However, the observations of Trouet et al. [42], in *Brachystegia spiciformis* growing in tropical southern Africa, revealed that a substantial rainfall event, after the end of the seasonal cambium activity, did not induce xylem or false ring formation. Our observation in subtropical Bangladesh indicates that the application of high frequency watering for at least 10 days during the pre-monsoon season is required to produce new cell plates in the cambium and differentiation of cambial cells into xylem on the stem of *S. saman.* Our results suggested that cambial reactivation and the start of xylem differentiation may require a continuous supply of water to the soil for a specified duration of time during the pre-monsoon season.

Under the artificial water deficit condition, a small decrease in water potential in a tree can lead to the loss of cell turgor pressure and decline physiological strength of living cells around the cambium and ultimately restrict the cambial activity [6, 20]. In Bangladesh, an increase in pre-monsoon temperatures caused increased water stress, which eventually limited xylem growth ring width in *Chukrasia tabularis* [44]. In the present study, the application of low frequency watering did not initiate cambial reactivation on the stem indicating that low frequency watering was inadequate to reactivate the inactive cambium. However, with the application of high frequency watering, cambial cell division and xylem differentiation continued after the reactivation of inactive cambium. Our finding suggested that application of high frequency watering might provide a consistent osmotic flow to maintain the cambium cell turgor pressure which is needed for the continuation of cambial cell division and xylem differentiation.

Cambial dormancy is an important adaptive mechanism for tree survival under adverse climatic conditions. In temperate trees, a distinct period of cambial dormancy in winter represent compactly arranged cambial cells with no evidence of cell division [21, 22]. These cambial cells were located between the secondary phloem and thick-walled secondary xylem that had formed during the previous growing season. Such cambial dormancy in temperate trees consisted of two stages, namely, resting and quiescent [74–76]. The rest stage is the stage of dormancy imposed by internal factors, while the quiescent stage is the stage of dormancy imposed by external (environmental) factors, such as temperature [56, 58, 63, 76–78]. The adequate environmental conditions in the quiescent stage can initiate the formation of new cell plates in the cambium. However, these definitions are based on trees in temperate and cool climates, and it is not established whether subtropical and tropical trees respond with similar stages of dormancy. In subtropical China, a short inactive period of cambium was observed in *P. massoniana*, characterized by the cessation of cambial activity and the continuing lignification of the xylem cell wall near the cambium [30]. It was suggested that this shorter inactive period of cambium was imposed environmentally (quiescent), for example by a lower temperature and shorter photoperiod, when compared to the distinct cambial dormancy in temperate regions and defined as "semi-dormancy". The results of our study in the pre-monsoon season on subtropical *S. saman* show that the cambial cell division was absent at the start and cell division remained absent until the end of the experiment when low frequency watering was applied; however, application of high frequency watering could restart the cambial cell division immediately. Thus, we hypothesized that, during our experiment, inactive condition of cambium in *S. saman* seedlings might resemble the characteristics of semi-dormancy as like other studied tropical and subtropical tree species [30, 31] and it will reactivate immediately when adequate environmental conditions are met.

Artificial water stress during the active growing season induced deformed tracheids in *C. japonica* and vessel elements in *Populus* sp. [19, 20]. Under natural conditions, severe drought induced narrow tracheids in *P. kesiya* [79] and small vessels in *Chukrasia tabularis* as the number of vessels increased [48, 49]. In contrast to the results of water stress and severe drought, we observed that numerous vessels were produced with variable diameters and thick cell walls in the present study when we supplied high frequency watering for 30 days. Thickening of cell walls of vessel elements occurred earlier than the surrounding wood fibers and longitudinal parenchyma cells. A similar pattern of differentiation of vessel elements was found in the early growth season on temperate hardwoods, such as *Kalopanax pictus*, *Quercus serrata*, and *Robinia pseudoacacia* [80, 81]. It is plausible that the time required for xylem cells to mature vary according on their types and that temperate and subtropical hardwoods might have a similar tendency of xylem differentiation in the early growing season.

Cambial activity in tropical and subtropical trees are mostly studied by collecting samples seasonally or at regular intervals over a long period. To our knowledge, the present study is the first attempt to show that artificial watering induces cambial reactivation and xylem differentiation in subtropical trees over a relatively short period. Such an experimental setup might be particularly beneficial for studying the physiological and histochemical changes that occur during the cessation and reactivation of cambial activity in tropical and sub-tropical trees.

In conclusion, our results suggest that a continuous supply of water to the soil is one of the most important factors for cambial reactivation in the stem of *S. saman* during the pre-monsoon season. Our findings of artificial watering treatments on cambial activity might help to explain how variations in precipitation patterns affect cambial activity under natural conditions. The response of the cambium to water stress in subtropical Bangladesh offers valuable information which in turn may help us better understand how subtropical trees respond to climate change. Furthermore, in a country, such as Bangladesh, where natural forests are scarce, an efficient irrigation schedule could be a very useful practice for optimizing yield from commercial perennial fruit tree farms and artificial tree plantations.

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Author contributions
MHR: Conception and design of the study, sample collection, analysis and interpretation of data and manuscript writing. SB: Conception and design of the study, sample collection, interpretation of data. WDN: Analysis and interpretation of data. SN: Analysis and interpretation of data. RF: Final approval of the article.

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Declarations

Competing interests
We have no conflict of interest.

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