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Cambial growth dynamics and climatic control of different tree life forms in tropical mountain forest in Ethiopia

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Abstract Munessa Forest is a mountain forest in southeastern Ethiopia experiencing seasonal rainfall variation. We investigated seasonal cambial activity and dormancy from increment rates of four different tree species belonging to varying life forms, namely, evergreen native conifer (*Podocarpus falcatus*), evergreen introduced conifer (*Pinus patula*), evergreen broadleaved tree (*Prunus africana*) and deciduous broadleaved tree (*Celtis africana*). Measurements of stem radius fluctuations were registered with the help of high-resolution electronic dendrometers. Daily amplitudes of stem diameter variations and daily and monthly net growth rates were determined and related to climatic variables measured at local climate stations. Thin sections of wood collected with a microcorer every 3–6 weeks allowed a visual control of newly formed wood cells during consecutive time intervals. Lack of water availability during the long dry season induced cambial dormancy of 5–7 months depending on life forms. After the onset of the short rainy season, stem swelling started quite synchronously with a variation of only single days in all studied species. Evergreen tree species were able to initiate wood formation during the short rainy season, whereas growth in the deciduous broadleaved species started in the long rainy season. The acquired data provide a basis for delineating the species-specific growth boundaries and the duration of the cambial growing season.

Introduction

Land use and climate change are potential threats for tropical mountain forests in equatorial Africa. In Ethiopia, the forest cover decreased from 40% in 1900 to only 16% in 1980 (Assefa 1986 and Taddesse 1995, in Nyssen et al. 2004). Recent remote sensing studies (Dessie and Kleman 2007) revealed a further reduction in forest cover to 3% in the vicinity of our study area. Population increases and demands to expand the agricultural area have exacerbated the rate of deforestation. On the other hand, climate variability with a high frequency of drought events, possibly aggravated by climate change, causes additional environmental stress. According to Nyssen et al. (2004), the driest decade of the twentieth century in Ethiopia occurred between the 1970s and 1980s. Therefore, understanding growth reactions of indigenous tree species to the changing environmental conditions is of great importance for a sustainable utilisation of the remnant natural forests. In addition, knowledge about the ecological behaviour of tree species is imperative to derive suitable adaptation management options under possible climate change scenarios, and for successful reforestation efforts.

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Knowledge of seasonal tree growth dynamics is the prerequisite for understanding annual wood formation in tropical regions. During recent years, a number of studies from different regions successfully detected annual growth cyclicity in tropical tree species (Worbes 1999; Biondi 2001; Schöngart et al. 2002; Brienen and Zuidema 2006; Bräuning et al. 2008). In contrast, other authors found a bimodal pattern of cambial activity as a result of distinct bimodal seasonal water availability (Gourlay 1995; Jacoby 1989; Borchert 1999). In Ethiopia, some tree species exhibit a variable wood anatomy due to regional differences in seasonal rainfall patterns (Wils et al. 2009). Hence, individuals of the same tree species (e.g. *Juniperus procera*, Cupressaceae) may show either clearly distinct ring boundaries or indistinct ring boundaries including many wood anatomical anomalies such as wedging rings, causing serious constraints for crossdating (Wils and Eshetu 2007; Wils et al. 2009; Sass-Klaassen et al. 2008). February and Stock (1998) stated that the indigenous tree *Podocarpus falcatus* is not useful for dendrochronological analyses because of its lobate growth and the formation of multiple rings per year in response to a double dry period.

Nevertheless, under certain climatic conditions, it may be possible to crossdate samples within a site and to construct chronologies that correlate with each other and with climate variables (Couralet et al. 2005, 2007; Sass-Klaassen et al. 2008). For example, several *Acacia* species from the Ethiopian lowland savannah have been successfully used for dendroclimatological studies (Eshete and Stahl 1999; Gebrekirstos 2006; Gebrekirstos et al. 2008, 2009). However, the seasonal growth characteristics of many Ethiopian tree species are so far still unknown (Sass-Klaassen et al. 2008), particularly in more humid mountain forests. Thus, our aim is to record cambial growth dynamics and seasonal variations of wood formation in tree species belonging to different life forms. The linkage of seasonally formed wood tissues and growth rates with weather conditions will provide a basis for the interpretation of wood anatomical structures and tree-ring formation in the Ethiopian highland forests.

Materials and methods

Study area and species

The study was conducted in the Munessa-Shashamene Forest, which is located at the eastern escarpment of the Main Ethiopian Rift Valley, 240 km south of Addis Ababa (7°26′N 38°52′E). The altitudinal gradient ranges from the traditionally termed Woyna Dega (mid-highlands; 2,100 m asl) to the Dega (highlands; 2,700 m asl; Fritzsche et al. 2006; Bekele-Tesemma 2007).

The regional climate shows two rainy seasons: a very erratic short rainy season from March to May and the major rains during July to September. Climate data registered (mean of 2006–2008) close to the study sites indicate an average annual rainfall of 1,121 mm with a standard variation of 217 mm and annual mean temperatures of 15.0°C (SD 0.3K). Relative air humidity varies between 45 and 75% during the dry season and reaches up to 90% during the long rainy season. According to the WRB System (World Reference Base for Soil Resources), the soils in the lower and higher parts of the study area were classified as Mollic Nitisol and Humic Umbrisol, respectively (FAO et al. 1998; Fritzsche et al. 2007).

Like many other regions in Ethiopia, the study site was affected by deforestation over the last few hundred years. The forest cover decreased from 16% to ca. 3% (Dessie and Kleman 2007). Consequently, the Munessa-Shashamene Forest today covers an area of about 23,000 ha of highly disturbed natural forest and plantations. The disturbance in the natural forest is due to selective logging by local people and cattle grazing. In addition, vast areas of the forest have been converted into plantations of *Cypressus lusitanica* Mill., *Eucalyptus saligna* Sm. and *Pinus patula* Schltdl. & Cham. The remnant semi-natural forest includes indigenous tree species of various life forms, namely evergreen conifers [*P. falcatus* (Thunb.) R.Br. ex Mirb. and *Juniperus procera* Hochst. ex Endl.], evergreen broadleaved trees [*Syzygium guineense* (Willd.) DC. and *Prunus africana* (Hook.f.) Kalkman] and deciduous trees (*Croton macrostachyus* Hochst. ex Delile and *Celtis africana* Burm.f.).

In this study, we selected four different species to investigate seasonal growth patterns of the co-occurring life form strategies: *P. africana* (Rosaceae), *C. africana* (Celtidaceae), *P. falcatus* (Podocarpaceae) and *P. patula* (Pinaceae). *P. falcatus* and *P. africana* are late successional, shade-tolerant species of the primary forest, whereas *C. africana* and *P. patula* represent pioneer tree species of secondary forests and exotic plantation species, respectively (Darbyshire et al. 2003; Abebe 2008).

According to the observations of Abebe (2008), the broadleafed tree *C. africana* sheds its leaves at the end of the long dry season. The peak of leaf fall is reached at the beginning of March and the peak of leaf flush follows 1 month later overlapping with the short rainy season.

Dendrometer data

Since March 2008, 24 electronic point dendrometers (Ecomatik, Germany) were installed in the natural forest divided to 6 on *P. falcatus*, 5 on *P. africana*, 5 on *C. africana* and 13 on 5 other species. Additional four dendrometers were set up in the plantation area on *P. patula* and *P. falcatus*. They were attached to the stems at 1–1.5-m

height. Radial stem changes were registered automatically in 30-min intervals to detect short-term stem diameter variations that mainly result from changes of the tree's water status. In addition, long-term growth trends are recorded that help determine the season of active cambial growth (Biondi et al. 2005; Bräuning et al. 2008, 2009; Volland-Voigt et al. 2010).

The diurnal cycle of stem diameter change can be divided into three distinct phases (Downes et al. 1999; Deslauriers et al. 2007; Drew et al. 2009; Volland-Voigt et al. 2010): (1) the contraction or shrinkage phase is the period during which the stem diameter decreases from the morning maximum to the daily minimum normally set in the afternoon; (2) the recovery or recreation phase is defined as the part of the cycle in which the diameter expands from the minimum until it reaches the value of the morning maximum again; and (3) the increment phase is the period in which the stem diameter exceeds the maximum of the morning to reach a new maximum. Afterwards, the stem starts to shrink again. Start and end time of each phase yield the duration (in h) and rate (in μm/h) of shrinkage, recreation and increment during one diurnal cycle (Downes et al. 1999). Here, we define 'increment' as a daily net increase of the stem diameter. It can result from stem swelling as a result of water uptake and saturation of the wood tissues, and from active growth by the formation of new wood cells. Daily radial change (dR) of the stem diameter is calculated from the difference between two consecutive daily stem diameter maxima.

The dendrometer data (dR) and the durations of the different phases of the diurnal cycle were correlated with precipitation and vapour pressure deficit. Results are documented in scatter plots indicating the levels of significance (p) and the coefficients of determination of linear regressions (r^2).

Wood samples

Cambial activity was additionally studied using microcores collected with a trephor microcorer from all 28 dendrometer trees at an interval of 3–6 weeks (Rossi et al. 2006). The 15-mm long and 2-mm wide wood samples were collected above the dendrometer with a changing sampling point and then embedded in polyethylene glycol (mixture of PEG 1500 and PEG 2000) to increase the stability of the important cambial cells (Gruber 1989). Thereafter, microsections of 20–35-μm thickness were cut with a sledge microtome and stained with solutions of astra blue and safranin red to distinguish living and non-lignified cells from lignified cells. In some cases, when the microcores were too short to show the former growth boundary, they were discarded from further analyses. The microsections were photographed by a Leica microscope system. The

different photographs of one sample were aligned automatically to one image and then edited by correcting intensity of colour and focus with the help of Adobe Photoshop software.

Climate data

Local temperature, precipitation and air humidity were measured in 30-min intervals within a distance of half a kilometre from the study sites. Vapour pressure deficit was calculated from the saturation vapour pressure of the air minus the actual saturation vapour pressure according to Häckel (1993).

## Results and discussion

Wood anatomy

We describe wood anatomical features following the terminology of Schweingruber et al. (2006). Cross-sections of the four studied species are depicted in Fig. 1. *P. patula* (Fig. 1a) forms distinct ring boundaries in the form of thick-walled latewood cells. Cells are aligned in radial rows with detached resin ducts located in the thin-walled earlywood. Furthermore, pronounced density variations within the earlywood located closely to the former growth ring boundary are occasionally found.

P. falcatus (Fig. 1b) shows similar wood anatomical structures as *P. patula*. However, the growth ring boundaries are not as distinct in *P. patula*. Latewood consists of rather narrow bands of radially flattened tracheids with slightly thickened cell walls and is sometimes difficult to distinguish from intra-annual density variations. Thus, tree-ring formation in *P. patula* is easier to study and might also help to understand wood formation in *P. falcatus*. Moreover, the occurrence of "false rings" in *P. patula* and *P. falcatus* is sporadic and also varies among the years.

The cross-sections of *C. africana* and *P. africana* revealed wood structures typical for hardwoods. *C. africana* (Fig. 1c) has small and thick-walled fibres and rays three to seven cells wide. Its vessel distribution is diffuse-ring porous; vessels are solitary or arranged in short radial rows of two to three. Vessel diameters slightly decrease towards the ring boundary. This decreasing diameter implements a construction of wood anatomy which is safer against cavitation during the dry period (Fonti et al. 2010). In addition, the growth ring boundary is formed by a thin band of marginal parenchyma cells. The paratracheal parenchyma is aliform to slightly confluent.

The ring boundary of the evergreen *P. africana* (Fig. 1d) is characterised by the presence of a hardly visible and thin marginal parenchyma band. Vessels of variable diameter

Fig. 1 Species-specific
anatomical structures showed
by cross-sections of *Pinus
patula* (**a**), *Podocarpus falcatus*
(**b**), *Celtis africana* (**c**), and
Prunus africana (**d**). *DV* density
variation, *EW* earlywood, *GRB*
growth ring boundary, *LW*
latewood, *PA* parenchyma band,
R ray, *RD* resin duct, *V* vessel
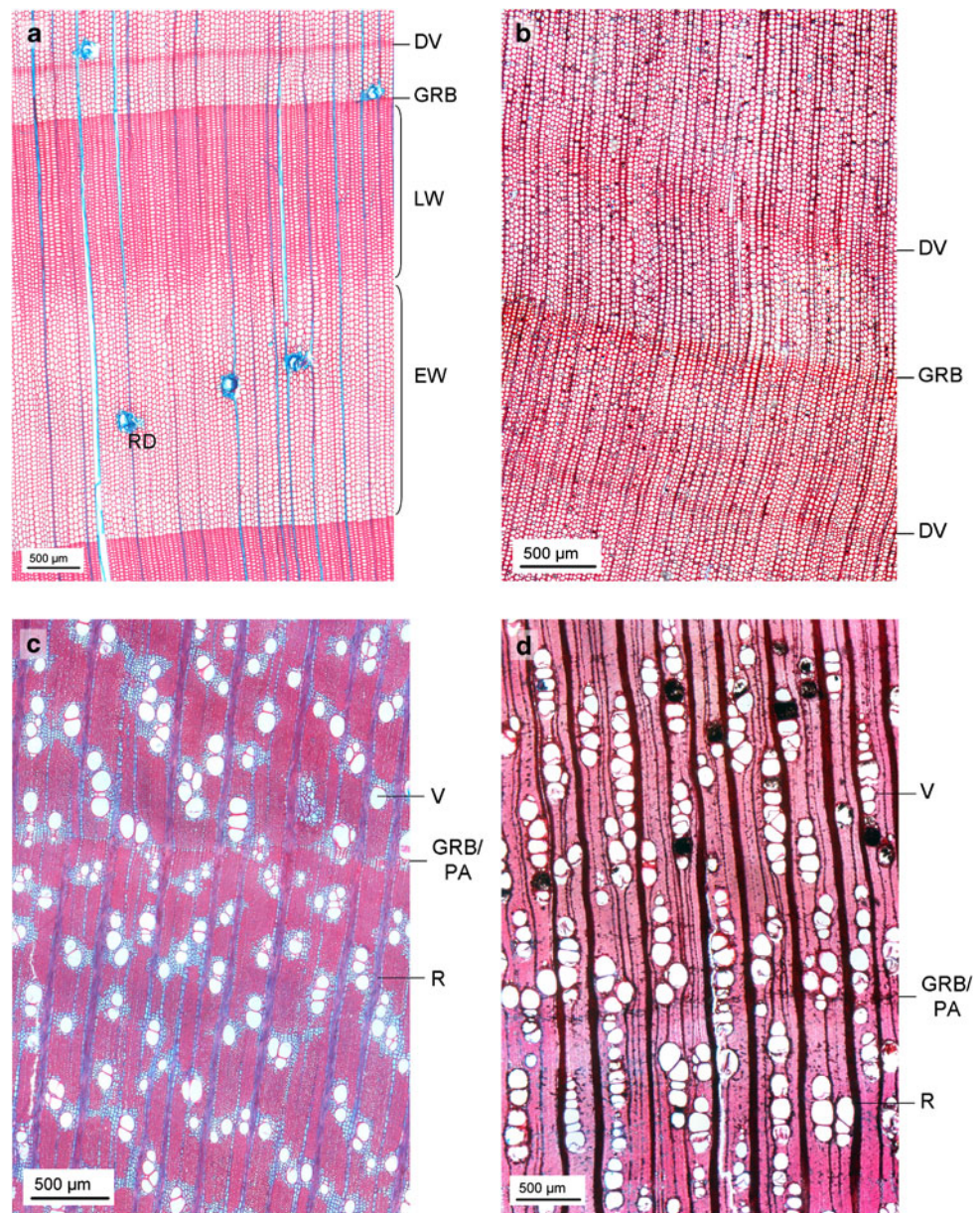
are arranged in radial rows of three to ten. Wood rays are
two to five cells wide. Both broadleafed trees do not form
false ring boundaries during the year.

Additional information about the cambial activity of the
four studied species was from coloured thin sections of the
microcores (Fig. 2). In the microsections of *C. africana*
and *P. africana* (Fig. 2a, c), no active cambium or even
juvenile cells are found in March 2009 and April 2009,
which would have been marked by blue colour. On the
other hand, this section of *C. africana* during the long rainy
season in July 2009 (Fig. 2b) shows several blue coloured
cells at the top, marking the area of active cambium (i.e.
cell wall is not yet lignified). The same mark is seen in
Fig. 2d, showing the microsection of *P. patula* collected in

March 2009. The lightly blue coloured cells below the bark
indicate the active cambium zone, whereas the blue cells
within the early wood are resin ducts. Finally, the thin
section of *P. falcatus* collected in June 2009 reveals a
density variation after a distinct ring boundary (Fig. 2e).

Dendrometer and climate data

As shown in Fig. 3, the short rainy season of 2008 started
at the end of March and lasted until the middle of May. In
comparison, the duration of the short rainy season in 2009
was short, lasting from the middle of March to middle of
April. Despite these differences in climate, the reaction of
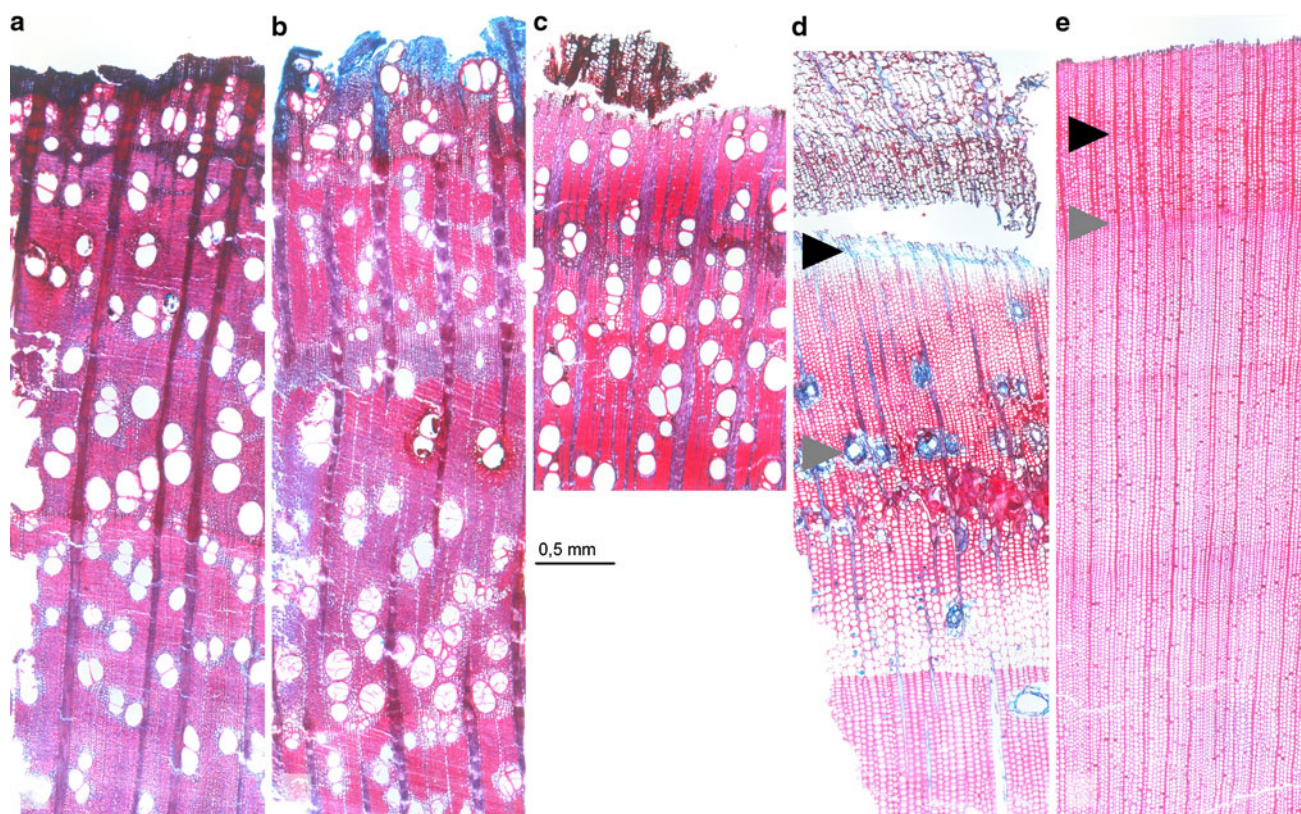the trees in both years was similar. Independent of life

Fig. 2 Thin sections of microcores extracted at different dates for detecting cambial activity: **a** *Celtis africana* March 2009; **b** *Celtis africana* July 2009, the blue coloured cells at the *top* mark the area of active cambium; **c** *Prunus africana* April 2009; **d** *Pinus patula* March 2009, the lightly blue coloured cells *below* the bark mark the area of active cambium (*black arrowhead*), whereas the blue cells at the end of the earlywood are resin ducts (*grey arrowhead*); **e** *Podocarpus falcatus* June 2009, the *grey arrowhead* marks a growth ring boundary, the *black arrowhead* marks a intra-annual density variation

form, the rising curve of cumulative radial diameter change depicts a swelling of all tree stems that occurred in concurrence with the onset of the short rainy season. During the short dry season, the stems shrank again. The main phase of cambial activity and radial stem increment of all different life forms is marked by the rise of the dendrometer curve shortly after the beginning of the long rainy seasons in June 2008 and end of June 2009, respectively.

The active growth period ceases at the end of the long rainy season. In 2008, the dendrometer curves indicate continuous growth until the end of September, when a data gap occurred. The registered dendrometer values after the data gap do not show considerable differences in stem diameters until the beginning of the short rainy season in 2009.

This visual concordance between precipitation and daily radial changes was investigated statistically. Best matches were found for pentads of cumulative daily diameter changes and 5-day sums of precipitation amount. Restricted to the short rainy season, we found these significant correlations for three of the four studied species. As shown in Fig. 4, the

pentads of daily radial changes of *P. falcatus* ($r^2 = 0.55$, $p < 0.01$) and *C. africana* ($r^2 = 0.50$, $p < 0.01$) are positively correlated with the precipitation amount of the preceding 5 days. Moreover, there is a lower correlation for *P. patula* ($r^2 = 0.36$, $p < 0.01$). In case of this exotic conifer, we found a higher correlation between daily radial change and precipitation amount of only one preceding day ($r^2 = 0.44$, $p < 0.01$). Stem diameter variations of *P. africana* were not significantly correlated with any climate variable.

Temporal patterns of shrinkage, recreation and increment phases

Daily values of stem diameter variation phases and precipitation during 2009 are shown in Fig. 5. In addition, Table 1 documents seasonally averaged daily duration of the three phases of the diurnal stem diameter variation cycle. According to the precipitation data, we divided the year into the long dry season (LD), the short rainy season (SR), the short dry season (SD), and the long rainy season (LR). Furthermore, the correlations between daily increment time and
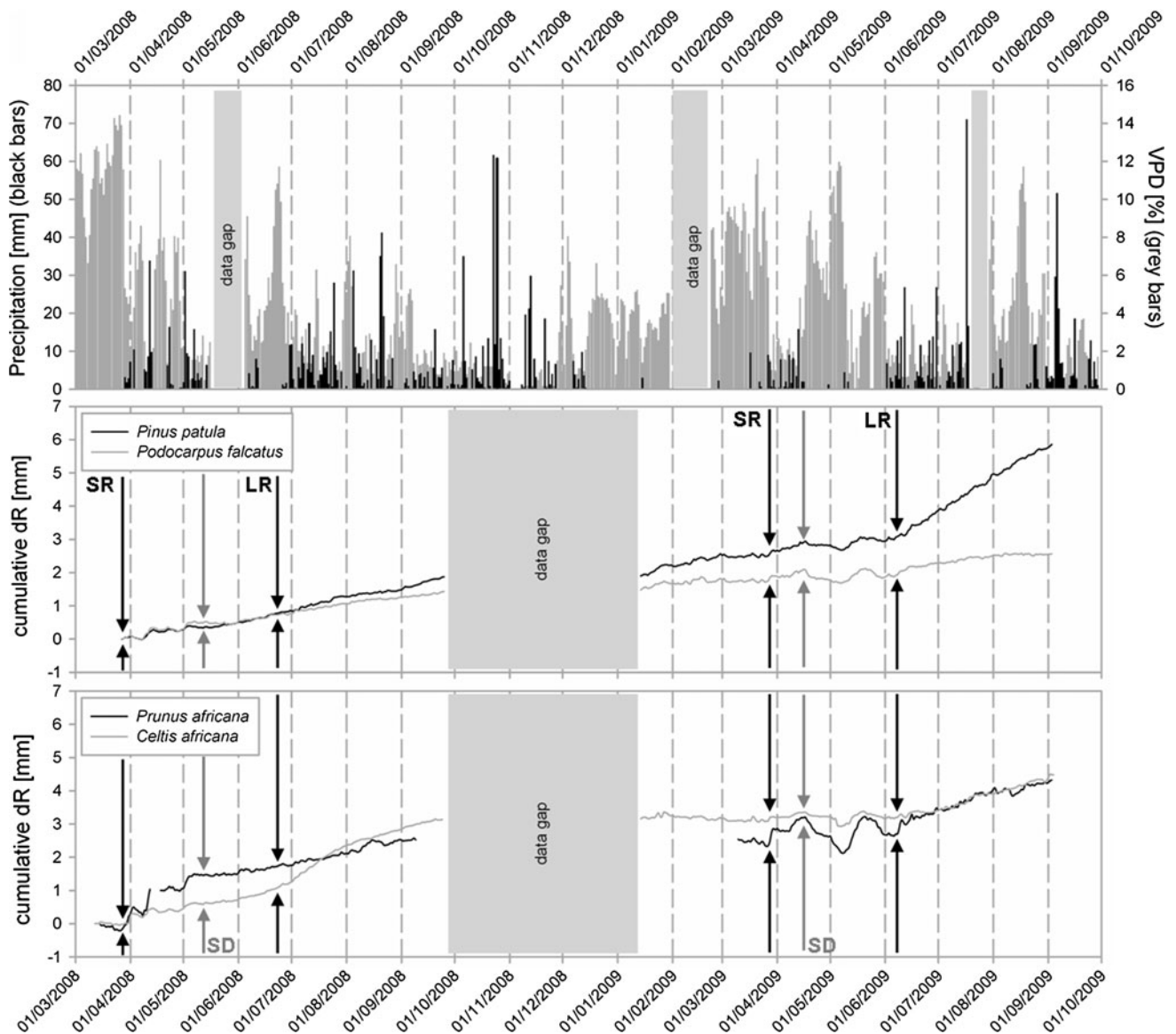
Fig. 3 Climate data (precipitation and vapour pressure deficit, VPD) and cumulative radial diameter change of evergreen exotic conifer *P. patula*, evergreen native conifer *P. falcatus*, evergreen broadleaved *P. africana* and deciduous broadleaved *C. africana* from March 2008 to October 2009. The *black arrows* indicate the rise of the dendrometer curve corresponding to the onset of the short rainy season (*SR*) and long rainy season (*LR*). The decrease of the dendrometer curve is initiated by the short dry season (*SD*) marked with *grey arrows*

precipitation amount of the day before growth are depicted in Fig. 6.

For *P. patula*, the average daily shrinkage phase during the LD and SR seasons lasts 8–9 h and is interrupted by a longer recreation time with an average duration of 14 h. The species responds to even small rain events and shows stem diameter increment during the days following rainfall events, lasting between half an hour to 10 h (1 h on average). For the SR season, we found a significant positive correlation (Fig. 6a) between the amount of precipitation of the preceding day and increment phase duration ($r^2 = 0.56$, $p < 0.01$). With the beginning of the LR season (1 June 2009), the daily pattern of the three phases

becomes more variable. On average, the duration of the recreation phase declines to 12 h while the mean duration of the increment phase extends to almost 3 h (Table 1).

Stem diameter variations of *P. falcatus* follow a similar seasonal pattern. Compared to *P. patula*, increment times show a lower difference between the LD and SR seasons. During the LD season, stem increment reactions on precipitation events are more intense than for *P. patula* and last up to 13 h (Table 1). Recreation time decreases during the seasons and is lowest during the LR season, whereas increment and shrinkage times show their maximum values during the LR season. The only significant correlation was found for the increment phase length of the SR season
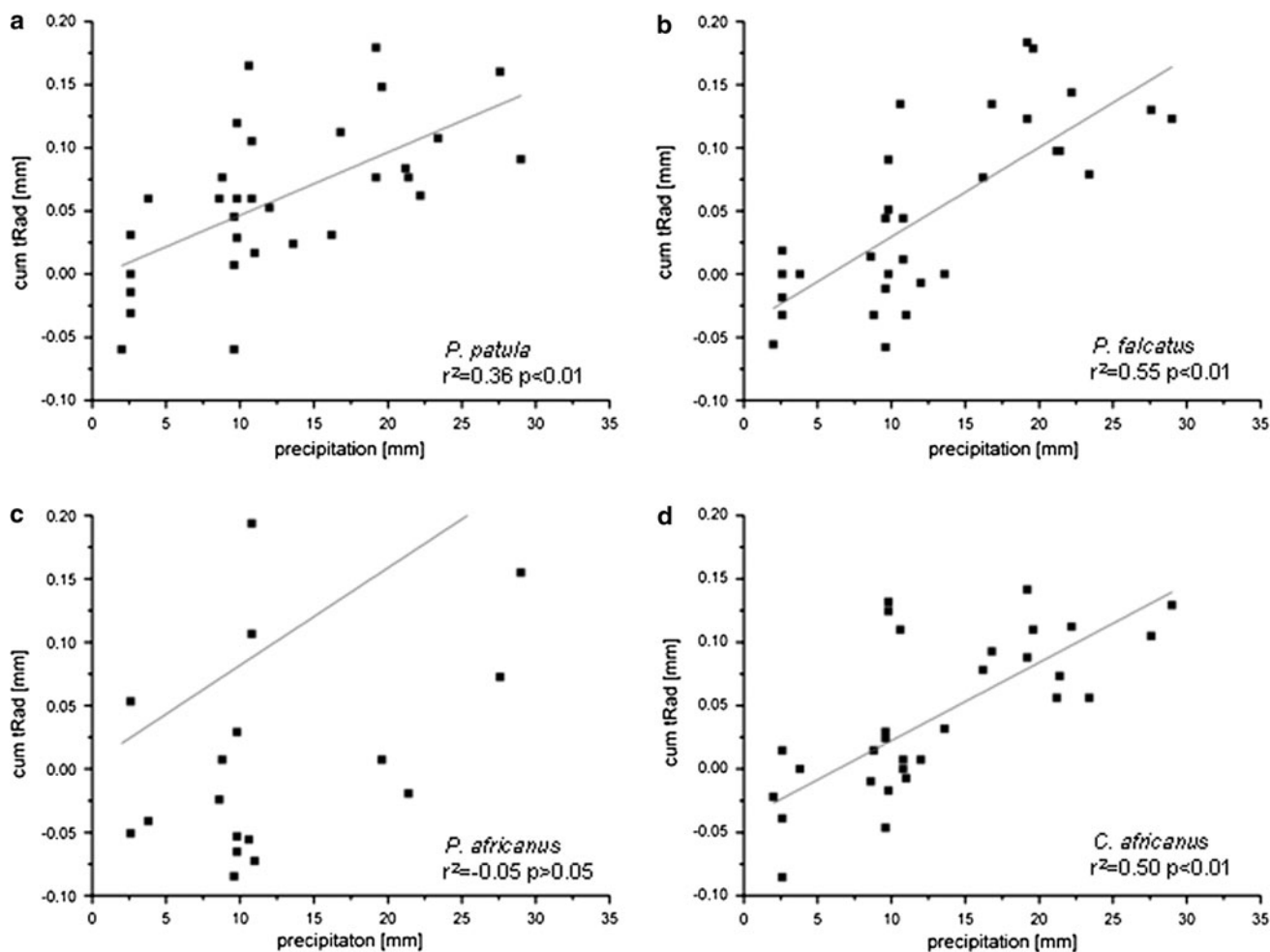
Fig. 4 Linear regression between pentads of daily radial stem diameter changes and pentads of precipitation sums during the short rainy season 2009 for *P. patula* (**a**), *P. falcatus* (**b**), *P. africana* (**c**), and *C. africana* (**d**)

(Fig. 6b) which responds positively to the precipitation amount of the preceding day ($r^2 = 0.35$, $p < 0.01$).

The pattern of the evergreen broadleaved *P. africana* displays diverse diurnal cycles. The duration of the three phases varies strongly between consecutive days, i.e. there are long recreation phases but no increment phases on dry days and long increment phases with short shrinkage phases during days with rain. This short-term variability is not reflected by the mean values that do not differ significantly from those of the conifer trees (Table 1). We found no significant correlation between precipitation and the increment phase during both dry and rainy season.

For the interpretation of the data of *C. africana*, its phenology has to be considered. *C. africana* sheds 80% of its leaves between February and April. Leaf flush starts at the end of March and leaf exchange is completed at the beginning of June (Abebe 2008). Hence, the daily mean increment time during the leaf exchanging period is considerably lower (LD 1.8 h, SR 3.8 h) than during the

freshly vegetated phase in the LR season (5.1 h). In addition, the pattern of the diurnal cycle gets more diverse during the freshly foliated phase (April to September 2009). Days which are dominated by a long increment phase and only a short or no shrinkage time alternate with periods without daily increment times. During the SR season, the correlation between daily increment time and precipitation amount of the preceding day was low ($r^2 = 0.29$, $p < 0.01$, Fig. 6c). However, we found a higher correlation between 5-day means of increment time and 5-day sums of precipitation ($r^2 = 0.60$, $p < 0.01$).

Increment rates for 2009

From the dendrometer data and wood microsections, we determined the seasonal periods with net stem growth and calculated daily increment rates by dividing net growth amounts by duration of increment phases. Hence, all species were expected to grow during the long rainy season. In addition, the conifer trees grew during the short rainy

Fig. 5 Climate data (precipitation and vapour pressure deficit VPD) and daily recreation, radial stem increment and shrinkage of the four studied species from January 2009 to September 2009
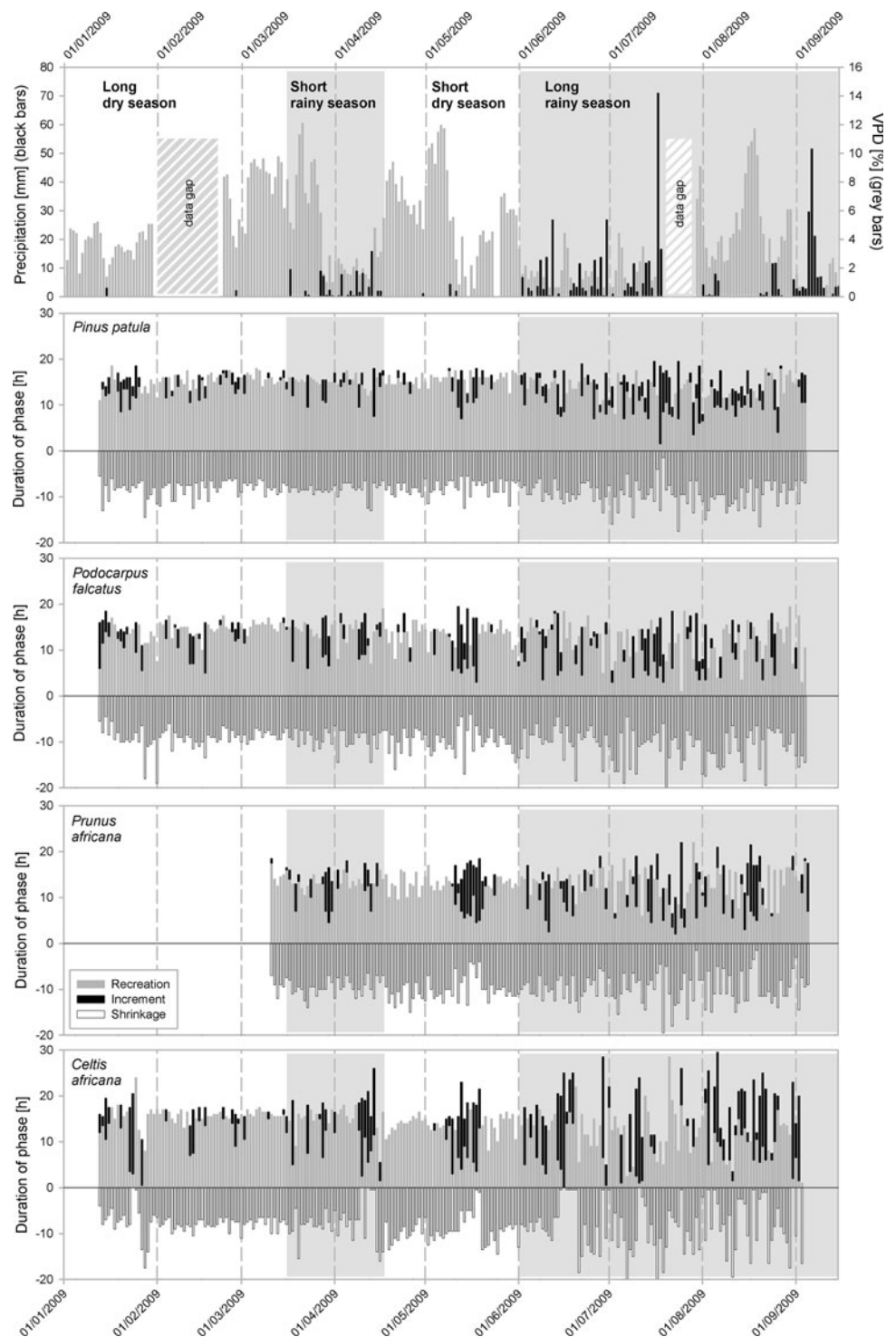
season. The numbers of days per month with increment and growth increment rates for 2009 are illustrated in Fig. 7.

In March and April 2009, *P. patula* showed higher increment rates (13 and 11 μm/h) than *P. falcatus* (8 and 6 μm/h, respectively). On the other hand, Fig. 7c and d does not indicate growth of the broadleaved tress during

March and April, since the broadleaved trees are not able to initiate cambial activity during the short rainy season.

Maximum increment rates of the evergreen trees coincided with the beginning of the long rainy season in June. *P. africana* reached the highest increment rate of all species (16 μm/h). Later in the rainy season during July until

Table 1 Mean duration in hours of the three different phases of a diurnal cycle during the long dry season (LD: 13 Jan. to 16 Mar.), short rainy season (SR: 17 Mar. to 16 Apr.), short dry season (SD: 17 Apr. to 31 May) and long rainy season (LR: 1 June to 5 Sept.)

Species	Recreation				Increment				Shrinkage			
	LD	SR	SD	LR	LD	SR	SD	LR	LD	SR	SD	LR
P. patula	14.3	14.0	14.8	11.6	1.3	1.6	1.1	2.9	8.4	8.5	8.1	9.4
P. falcatus	13.4	12.1	12.2	10.2	1.4	2.4	2.0	2.5	9.1	9.5	9.8	11.0
P. africana	15.0	12.0	11.7	11.2	–	2.2	2.2	2.8	9.0	9.8	10.1	9.9
C. africana	14.3	12.5	12.5	10.1	1.8	3.8	2.3	5.1	7.8	7.6	9.4	8.7
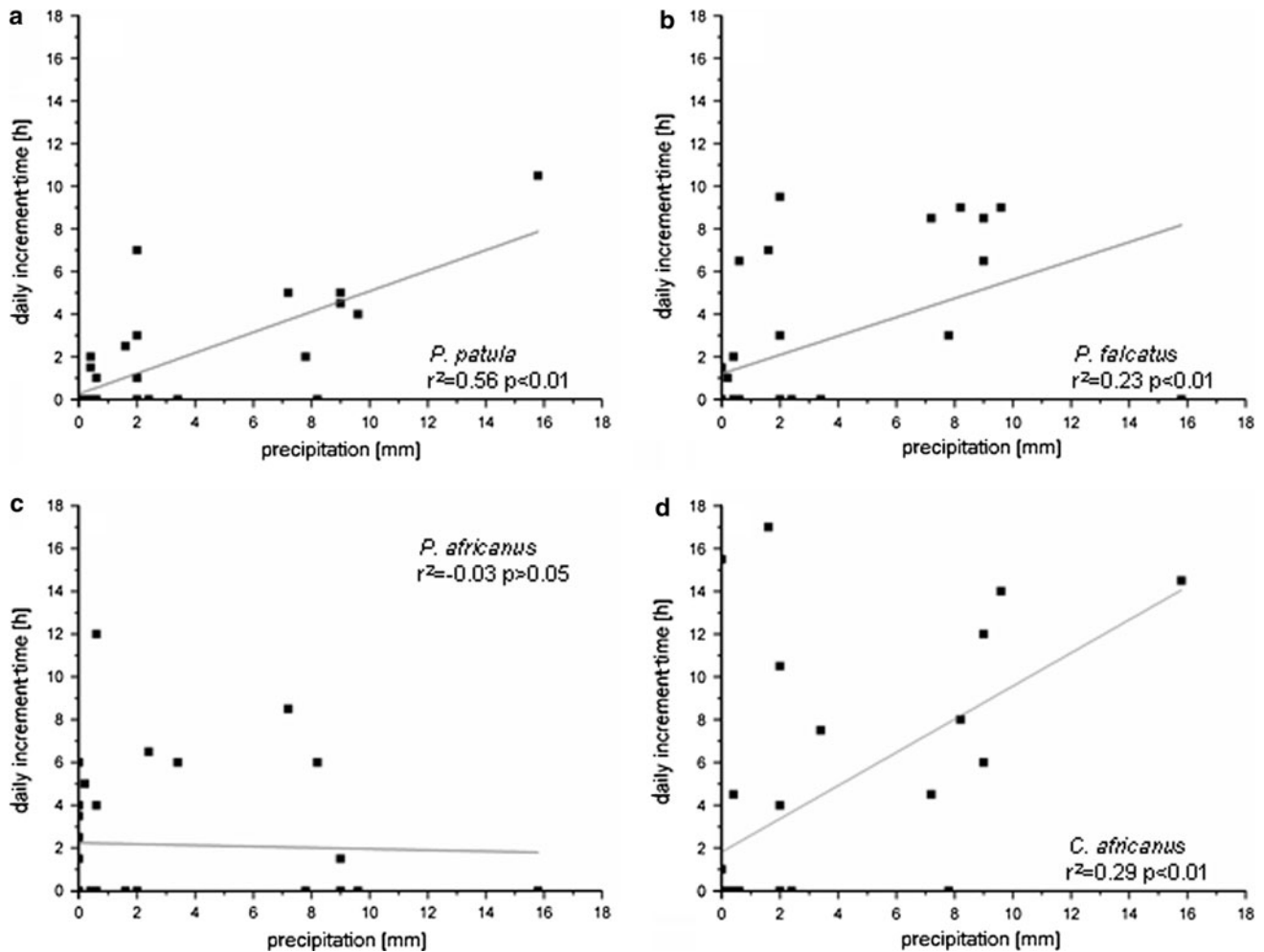
Fig. 6 Linear regression between daily duration of the increment phase and precipitation at the preceding day during the short rainy season 2009 for *P. patula* (**a**), *P. falcatus* (**b**), *P. africana* (**c**), and *C. africana* (**d**)

September, the evergreen trees reduced increment rates. In contrast, the broadleaved *C. africana* did not show high increment rates in June 2009 and growth rates during the long rainy season were constantly low. However, considering the high number of days with net increment (22 days in August 2009), *C. africana* seemed to compensate the low increment rates and gained similar stem diameter growth like the other tree species (Fig. 3).

Discussion

Cambial activity

Referring to the thin sections (Fig. 1), we suggest that in the course of the short rainy season and the following short dry season the conifers *P. patula* and *P. falcatus* are able to initiate and to interrupt growth within less than 1 month.
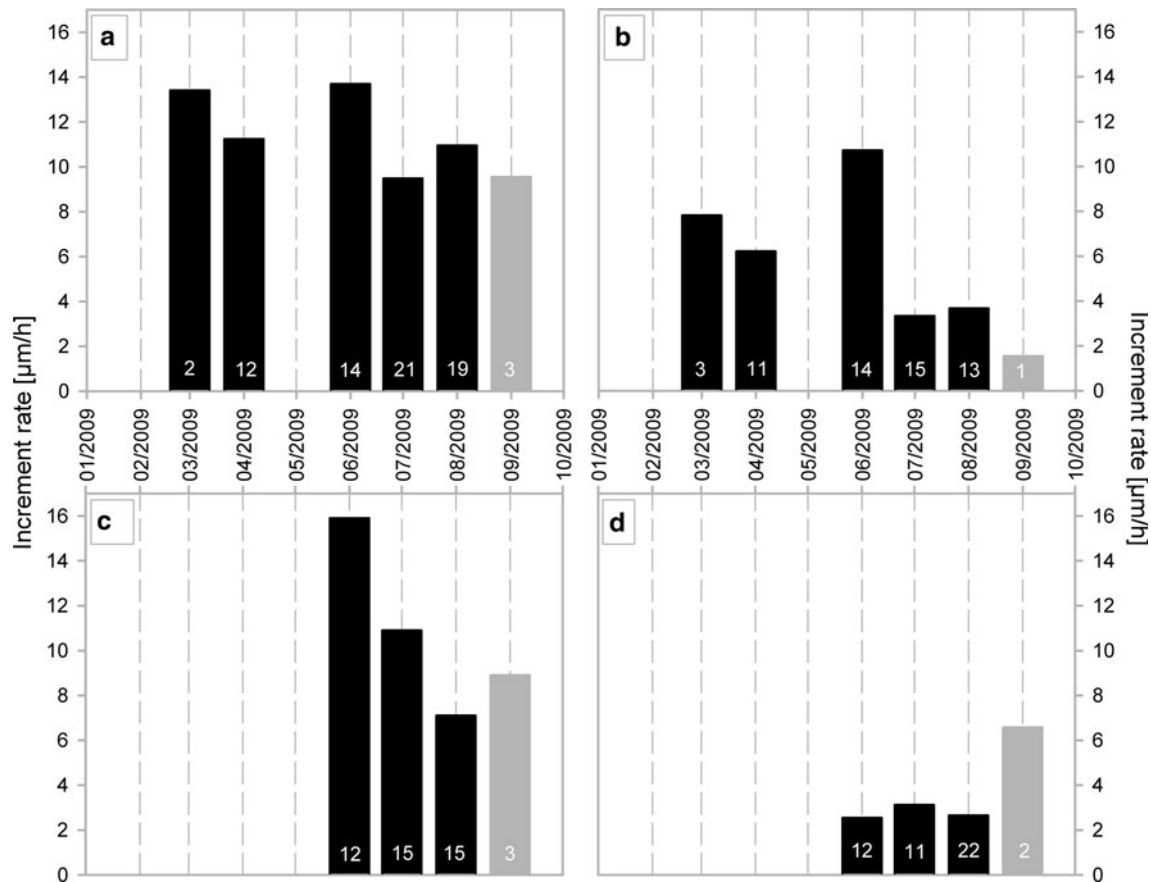
Fig. 7 Monthly mean growth increment rates and number of days with increment per month (*white numbers* in the *bars*) in 2009 of *P. patula* (**a**), *P. falcatus* (**b**), *P. africana* (**c**), and *C. africana* (**d**). Only increment rates during periods with cambial activity are shown.

Since the coniferous trees are able to initiate growth already during the short rainy season (March and April), there are additional bars for these species. September values do not represent the average of the whole month

Thus, the evergreen trees formed intra-annual density variations closely resembling annual growth ring boundaries. The occurrence of these "false rings" in *P. patula* and *P. falcatus* is sporadic and also varies among individuals, presumably based on changes in microenvironment. Studies about seasonal dynamics in the Mediterranean area revealed a similar dormancy period after the onset of cambial activity in spring (Liphschitz et al. 1984; Cherubini et al. 2003; De Luis et al. 2007). The dormancy period responds to intra-annual changes in climatic conditions varying from favourable to higher temperature and less precipitation. However, our study area shows almost constant temperature conditions around 15°C, so we conclude that the onset and interruption of cambial activity must be related to changes of water availability.

Additional evidence for the onset of cambial activity for the evergreen conifers is given by the thin sections in relation to the dendrometer data. The rise of the dendrometer curve of all four species (Fig. 3) during the short rainy season in 2009 was induced by an increment of stem diameter caused by water uptake or cambial activity. The thin sections of *C. africana* in March 2009 and *P. africana* in April 2009 (Fig. 2a, c) do not indicate a zone of active cambium. During this period, the deciduous species was exchanging its leaves, so that the tree might have used all its energy in forming fresh leaves instead of new wood cells (Abebe 2008). The sample of *C. africana* in July 2009 (Fig. 2b) shows blue coloured, freshly formed and non-lignified cells of an active cambium. At that time the tree was totally foliated started to grow at the onset of the long rainy season.

In contrast, the thin sections of the conifers *P. falcatus* and *P. patula* show evidence for active growth during the short rainy season. This can be inferred from the newly formed, blue coloured non-lignified cells of an active cambial zone in *P. patula* in March (Fig. 2d). The thin section of *P. falcatus* collected in June 2009 reveals a density variation (Fig. 2e), which must have been formed during a period of cambial activity during the short rainy season. In addition, the scatter positive correlations between daily radial diameter change and precipitation

amount of the preceding day (Fig. 6a, b) indicate that the cambial activity of *P. patula* and *P. falcatus* during the short rainy season depends on water supply.

The main growth period of all four species proceeds during the long rainy season until October. We estimate the beginning of cambial dormancy and formation of the main growth ring boundary after the beginning of the long dry season, since the registered dendrometer values did not show considerable differences in stem diameter after the data gap in autumn 2008 (Fig. 3).

In summary, we conclude that cambial activity of the evergreen conifer trees starts during the short rainy season and might cease again during the short dry season, depending probably on the intensity of precipitation during the short rainy season and the length of the following short dry season. Figure 1 and additional examinations of stem disks and increment cores of *P. patula* and *P. falcatus* revealed that the occurrence of density variations does not occur every year.

Species-specific stem diameter variations

The patterns of the daily diurnal cycle (Fig. 5) differ among the four studied species with *C. africana* showing the highest variability. During the long rainy season in 2009, the species experienced 15 days dominated by the increment phase with no or only short periods of shrinkage time. On the other hand, *P. africana*, *P. patula* and *P. falcatus* show only 2, 1 and no day without stem shrinkage, respectively. A day without shrinkage implies a long and intense increment phase. This is in agreement with the seasonal mean durations of the increment phase (Table 1), in which *C. africana* shows the longest increment period (5.1 h/day) among all studied species. Furthermore, *C. africana* showed the highest number of days with increment in August 2009 (Fig. 7d). This might imply that the deciduous tree is able to compensate its low growth rates during the vegetation period with longer increment times.

The long increment duration of *C. africana* during the short rainy season (Table 1) is not accompanied with new cell formation but rather implies stem swelling by water uptake. Comparable observations were made with another deciduous broadleaved tree species, *Bombacopsis quinata*, in the Amazon tropical dry forest. *B. quinata* shows a strong relationship ($r^2 = 0.81$) between phenology and water status (Worbes 1999). When *C. africana* sheds its leaves, the stem begins to shrink. During leaf flush, stem increment is significantly correlated with precipitation amount of the preceding 5 days ($r^2 = 0.60, p < 0.01$). In total, the growing strategy of *C. africana* is that of a pioneer tree with high growth rates.

Comparing the number of consecutive days without increment, we found that during the short rainy season, the conifer trees showed a maximum of 12 consecutive days

without increment phase, while *C. africana* and *P. africana* showed 17 and 24 days of this category, respectively. Since *C. africana* is not able to initiate cambial activity during its leave-exchanging time (see above), we may infer that a high number of days without increment phase implement cambial dormancy. Thus, the comparatively lower numbers of days without increment time of *P. patula* and *P. falcatus* (12 days each) might indicate that their cambium was active during the short rainy season of 2009. The wood anatomical evidence derived from microsections proved very useful to verify the interpretation of the dendrometer data (cf. Fig. 2a, b and Fig. 7a, b).

Finally, we tried to estimate the amount of wood formed in 1 day, month or during a complete season. For example, in June 2009, when *P. africana* showed its highest increment rate (15.90 μm/h) and longest increment time (12.5 h/day), the tree was able to form 0.19 mm of wood. The calculated net increment of *C. africana* in August 2009 (0.38 mm) matches well with the amount of increase of the dendrometer curve (0.41 mm). However, further expansion, cell wall thickening and lignification of the newly formed cells may take additional time that cannot be determined with this method.

Conclusions

By combining wood anatomy and dendrometer measurements, it is possible to differentiate between stem swelling by water uptake and cell formation in tropical trees. This is a prerequisite for the interpretation of tree-ring curves derived from ring-width measurements and subsequent dendroecological analyses. Nevertheless, it is still difficult to identify growth ring boundaries in *P. africana*. The terminal parenchyma band (Figs. 1d, 4c) is often indistinct and difficult to recognise.

It was possible to determine differences in the timing and length of the growing season of the studied conifer and broadleaved tree species. The conifers are able to form intra-annual density variations depending on the intensity of the short rainy season. Among the four studied tree species, the broadleaved *C. africana* responds most sensitive to weather conditions. The drought avoidance strategy by leaf shedding seems to be compensated by longer increment phases under favourable water conditions. *P. falcatus* and *P. africana* show less pronounced seasonal fluctuations of stem diameter variations, whereas *P. patula* is rather insensitive to climate seasonality.

When longer dendrometer data series and microsection series in years with different rainfall patterns are available, the relationship between weather conditions, the formation of density variations in conifer species and the exact length of the main growing season among different life forms will be further determined.

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