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The number of days on which increment occurs is the primary determinant of annual ring width in *Callitris intratropica*

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DMD 30%; AER 25%; GDC 10%; GMD 10%; WG 15%; PB 10%

Key message:
The number of days on which a measureable increment occurred, and the average rate of stem growth, rather than the overall duration of the wet season, were the main determinants of ring width in young *Callitris intratropica* trees. These effects were amplified by competition.

Summary

Dendroclimatology of tropical tree species is an important tool for understanding past climatic variability at low latitudes where long-term weather records are often absent. Despite the growing number of published tropical tree-ring chronologies, however, still little is known of the factors that control annual ring formation in tropical tree species. In this paper we used an endemic Australian conifer, *Callitris intratropica*, to study the intra-annual dynamics of seasonal growth and xylem formation, and the effects of environmental conditions and competition, on growth ring formation. We combined high–resolution growth and climate monitoring (every 15 minutes for two years) with less frequent cambial sampling. Trees exhibited marked reductions in growth during certain periods within the rainy season when rainfall was not as regular and VPD was high. Overall, we found that ring width was most influenced by the number of days when increment occurred; regardless of how early the growing season began or ended, and by the rates of tracheid production. The effect of competition was also important. Trees growing in dense groves had narrower annual rings (4.6 mm) than trees that were growing in the open (6.7 mm), due to less active cambia, slower rates of xylem production and expansion and more increment days, although the overall growing season duration was also shorter in grove trees.

Keywords:

Tropical, dendroclimatology, drought, cambium, xylem, dendrometer, Cypress pine, savanna

Introduction

The savanna regions of sub-tropical and tropical Australia are characterised by seasonal monsoons that are strongly impacted by the El Niño-Southern Oscillation (ENSO) (D'Arrigo et al. 2008; Fensham R. J. et al. 2009), resulting in occasional extended dry seasons and low annual rainfall, while high cyclonic activity in other years can produce intense periods of elevated rainfall in the wet season (Cook and Goyens 2008). Variation in the widths of annual rings from forest trees has been successfully used to reconstruct past climate variability in the wet monsoonal tropics of Asia (Cook et al. 2010; Jones et al. 2009; Sano et al. 2009). Dendrochronolgy could also, therefore, be a valuable tool for interpreting historic variability in annual rainfall and length of the wet/dry season in northern Australian savanna regions, where long-term climate records are scarce. Uncovering historical variability in seasonal rainfall patterns is important for understanding the impact of future climate patterns on vegetation growth and ecology of tropical savannas in northern Australia. .

Species from the genus *Callitris* have emerged as having great potential to provide insight into past savanna climate variability because they are widespread and relatively abundant in northern Australia (Bowman et al. 1988; Russell-Smith 2006). *C. intratropica* and *C. collumelaris* have also been shown by a number of authors to produce clear rings, variation in which appears to contain a climate signal, and therefore to have significant dendroclimatological potential (Baker et al. 2008; Cullen and Grierson 2007; Cullen and Grierson 2009; O'Donnell et al. 2010; Ogden 1981; Pearson et al. 2011; Pearson and Searson 2002; Sgherza et al. 2010).

Despite these important findings, however, the mechanisms by which ecological and environmental conditions control short-term patterns of sub-annual growth and thus ultimately variation in tree-ring widths, remains poorly understood in tropical trees generally (Jones et al. 2009) and in *Callitris* spp. in particular (Cullen and Grierson 2007). The widths of annual rings are determined by the accumulation of multiple short-term growth responses to constantly varying climatic conditions, and by the duration of active growth in each season. Two annual rings of comparable width may have arisen from quite different conditions: one ring may have formed over a longer period, with slow average growth rates, whereas in another, average growth rates may have been high, but with a shorter growing season (Downes et al. 2008; Rathgeber et al. 2011). It is also possible that rapid rates of growth and a long overall growing season could still lead to a relatively narrow ring if there were one or more periods of suppressed growth at some time within the season. It is important to consider both the duration and rates of annual growth, as well as sub-annual temporal variability in the occurrence of growth, in order to understand the causes of ring width variation (Downes et al. 2008; Rossi et al. 2008).

It is also important to elucidate the contribution of other non-climatic environmental and ecological factors on ring width variation that affect the carbon or water economy of plants, thus limiting resources available for growth (Fritts 1976; Helama et al. 2004). Of these factors, the effect of competition is likely to be particularly important in *Callitris*, which often grows in dense groves and can survive in situations of intense intraspecific competition for many years (Ross et al. 2008), potentially affecting the environmental responses of the trees and the interpretation of information contained in annual rings (Lloyd and Fastie 2002; Wilmking et al. 2004). The influence of non–climatic drivers of variability in tree–ring width, such as competition from neighbouring trees, cannot always be removed from tree–ring series using statistical standardisation procedures (Cook 1987).

We hypothesized that annual ring width is determined to a large extent by the number of days on which growth occurred during the rainy season, and that this would be particularly critical in the case of trees experiencing severe competition. To test this hypothesis we aimed (a) to quantify, over two growing seasons, the effect of intra-annual variation in environmental conditions, growth patterns and the overall duration of the growing season, on the magnitude of annual growth (i.e. ring width), and (b) to test if competition affects tree growth responses and annual patterns of stem radial growth in *Callitris*.

Materials and methods

This study was conducted using the endemic Australian conifer *Callitris intratropica*, growing in a rare patch of *Eucalyptus tetrodonta*- and *Eucalyptus miniata*-dominated savanna near Darwin, Northern Territory, Australia (12.40ºS; 130.92ºE; 45 m AMSL). The site is rare in large part because it exists within the broader CSIRO campus in Darwin, which has not been burned for more than 40 years, having been protected from fire by a variety of mitigating measures on the property. Eight trees were selected from a population of *C. intratropica* that had self–seeded in approximately 1992 from a group of trees planted nearby. Four of the selected trees had recruited in isolation in an open grassy area (hereafter referred to as “isolated” trees). The remaining four trees were selected from a grove (hereafter referred to as “grove” trees) wherein the density was about 0.6 trees per m^2. Because the grove trees were growing under conditions of greater intra-specific competition, they had significantly ($p < 0.001$) smaller stem diameters (6.0 ± 0.6 cm), on average, than the isolated trees (9.9 ± 1.0 cm). Isolated trees were selected based on diameter measurements taken over the previous two years showing that the trees were still actively growing, to ensure that adequate growth would be recorded during the study period. Sampling was limited to eight individuals due to the logistical constraints of the sampling site (principally, the large distance between monitored trees and the data logger) and the intensive nature of the data collected.

Study site

The climate at the study site is strongly monsoonal. Of the circa 1700 mm of rain that falls each year on average, circa 90% fall during the wet season (October to April). During the dry season (May to September) little or no rain falls in any month (Cook and Heerdegen 2001). Soil at the site is classified as a PetroFerric Red Kandosol, with moderate water–holding capacity (Isbell 2002). The soil has a 10 cm deep A horizon (sandy loam) and a B horizon that is >0.5 m deep (sandy clay loam), with soil clay content 14–22%, silt 2–7 %, fine sand 44–49% and coarse sand 23–25% (McKenzie et al. 2004).

Measurement of radial growth

To characterise short-term radial growth patterns among the study trees, we installed high-precision electronic point dendrometers. In January 2009, a single electronic point dendrometer (Agricultural Electronics Corporation (AEC), Tucson, AZ, USA), using a small linear variable displacement transducer (LVDT) in concert with signal conditioning electronics, was installed on each of the selected trees at about 1.3 m above ground level (breast height). Dendrometers were positioned on the southwest, south or southeast side of the tree, depending on the presence of branches. Each unit was mounted on 2 mm diameter stainless steel threaded rods inserted approximately 2 cm into the wood, with the sensing head placed on the bark surface with loose bark having been removed. Data were logged every 15 minutes from September 2009 until May 2011. Total annual growth measured by the dendrometers over two full growing seasons correlated well with measured ring widths ($R^2 = 0.95$; $p < 0.001$). We used the detailed data on stem size variation from the point dendrometers to assign the date of growth initiation and cessation each year. We defined the date of growth initiation to be the day, each year, on which the trees returned to a zero tree water deficit (see Drew et al. 2011), and the date of growth cessation to be the first day after which there was no stem growth increment. When measured with high precision, tree stems exhibit a daily shrinkage, recovery and increment phase (Drew et al. 2008; Drew et al. 2011) (Figure 1).

We define "increment" here as an increase in stem size (as measured by the dendrometers) above a previously measured maximum. "Increment" will be used in this paper strictly in this sense (in regard to relative dendrometer measurements), while "growth" will be used more generally in reference to the overall and irreversible increase in stem size by wood production. Inevitably, large measured "increment" events will correspond closely with actual short-term "growth": this issue is discussed further in the manuscript. The observed daily pattern of increment can be resolved clearly into three components (Downes et al. 1999), which provide a powerful means of estimating and quantifying patterns of growth in relatively fast growing trees such as those in our study:

(a) its magnitude (by how much did the stem exceed a previous maximum on day *d* (µm)?),

(b) its duration (how many hours did the stem exhibit increment on day *d* (h)?) and

(c) its rate (magnitude/duration = µ h^{-1}).

Wood and cambial samples

Samples of developing and mature xylem were taken on several occasions during the study using a Trephor microcorer (University of Padua, Italy) (Rossi et al. 2006) and also at the end of the study using a 5-mm diameter wood corer. Samples were not taken more often because of the small size of the trees and the likelihood of compromising the health of the trees and damaging the cambial tissue.

The 2-mm core samples were fixed in a solution of formalin/acetic acid/alcohol/water (FAA) after removal and trimmed to small blocks incorporating the cambial zone. These were dehydrated in an ascending acetone series and embedded in Spurr's resin (Spurr 1969). From each block 4µm sections were cut, and stained using toluidine blue. Images of the mounted sections were captured using a Zeiss research microscope and subsequent measurements of tracheid and cambial dimensions were made using Axiovision (Carl Zeiss MicroImaging, Germany) image analysis software. Cells were distinguished as being in the cambial zone, or alternatively, in the zone of enlargement, based on measurements of radial diameter. Cells in which radial diameter was increasing were considered to have begun the stage of enlargement, and ceased to divide. Cells were considered to have entered the stage of secondary wall thickening if birefringence was observed in the cell walls when view through cross polarisers.

Cores taken at the end of the study were allowed to air dry before being mounted. The transverse end was sanded with increasingly fine grades of sand paper, to achieve a highly polished surface. Images were then captured using a Zeiss dissecting microscope at 100× magnification and ring widths were measured from images of each core sample using Axiovision software.

Cambial dynamics were calculated using cambial samples taken in February 2010. The rate of cell production was determined by calculating the amount of growth equivalent to the sum of the radial diameters of the last ten cells produced. Cell production rate was thus equal to ten divided by the number of days required for the stems to grow radially by that amount. The duration of the cell cycle was calculated by dividing the number of cells in the cambial zone by the rate of cell production. Similarly, the number of days for cell growth to occur was calculated by dividing the number of cells in the zone of cell enlargement by the rate of cell production. The rate of tracheid enlargement was calculated as the difference between the average radial diameters of the last three fully enlarged tracheids and the average diameter of cambial initials, all divided by the duration of tracheids' radial enlargement (see Drew and Pammenter 2007 for more information on this approach).

Soil water content

Relative soil water content in the upper 10–20 cm of soil was measured using capacitance probes (AEC, Tucson, AZ, USA) from January 2009 to May 2010. Due to a system failure, these were replaced with soil water content reflectometers (CS616, Campbell Scientific Inc, Logan, Utah, USA) which were used from September 2010 to May 2011. In both cases, two sensors were placed in the open area and two were placed amongst the trees in the grove. The AEC sensors were inserted horizontally into undisturbed soil at a depth of approximately 10 cm. The CS probes were inserted vertically to a depth of about 20 cm. Measurements were made every 15 min for 28 months, although there were periods of missing data. The AEC sensor data were rescaled using expected dry season minimum (8%) and wet season maximum (30%) values for this soil type based on Duff et al. (1997) and values measured subsequently at the site (A. Richards, unpublished data; D.A.J Lindsay, unpublished data). To provide an indication of soil water content variation over periods of missing data (February – August 2010), we developed a simple soil water balance model (Equation 1).

$$\mathrm{SWC}_d = \begin{cases} \mathrm{SWC}_{\mathrm{min}} & \mathrm{SWC}_d < \mathrm{SWC}_{\mathrm{min}} \\ \mathrm{SWC}_{d\,-1} + \mathrm{rainfall}_d \ - \alpha{*}(1{*}(\mathrm{RH}_d/100))^{\beta} & \\ \mathrm{SWC}_{\mathrm{max}} & \mathrm{SWC}_d > \mathrm{SWC}_{\mathrm{max}} \end{cases} \quad \text{….Eqn 1}$$

Where SWC_d is soil water content on day d, $\mathrm{rainfall}_\mathrm{d}$ is total rainfall on day d (mm), α is a parameter that determines the rate of movement of water out of the soil profile, RH_d is average relative humidity on day d and β is a parameter that corrects for canopy interception and evaporation of rainfall. $\mathrm{SWC}_\mathrm{min}$ and $\mathrm{SWC}_\mathrm{max}$ are parameters that specify the maximum and minimum possible SWC for the soil.

Soil water potential (Ψ_S) was then calculated from volumetric water content using the function of Williams et al. (1983) (Equation 2). This equation assumes a soil texture of 22% clay, 43% fine sand and 16% coarse sand, which corresponds closely with soil textural properties at the study site.

$$\ln|\Psi_S| = -3.3 - 4.7\ln(\theta) \quad \text{……………………………………………Equation 2}$$

Where Ψ_S is soil matric potential (kPa) and θ is volumetric soil water content ($\mathrm{m}^3\ \mathrm{m}^{-3}$).

Environmental data

Temperature, humidity and solar radiation data used in this study were obtained from the Australian Bureau of Meteorology (BOM) automatic weather station at Darwin airport, approximately 5 km from the study site (12.42° S; 130.89° E; 30 m AMSL). Rainfall data were obtained from a manually checked rain gauge (from July 2008 to July 2010) and a subsequently installed automatic weather station (July 2010 onwards) at the study site. The first three months of 2011 were the wettest on record for Darwin, coinciding with the occurrence of tropical cyclone Carlos, which crossed the coast of Darwin between the 15th and 17th of February 2011. The much wetter conditions meant that mean incoming solar radiation at the site was 1.6 MJ m^{-2} lower in the 2010–2011 season than the long-term average. In 2009–2010, by contrast, mean daily solar radiation received at the site was close to the long term average. During the 2010–2011 wet season, the site received 1.5 h less sunshine per day than average, while in 2009–2010, the site received 0.2 h per day more sunshine than average (Table 1).

Data analysis

Differences between treatments and the two growing seasons in various parameters were assessed using a linear mixed effects model, with tree number as a random effect. A simple linear model, with standardized coefficients, was used to assess if, and to what extent, growth rate, frequency of growth events and season duration contributed to ring width in individual trees.

Results

Ring width and stem growth

Average ring width was significantly ($p < 0.001$) lower in the grove trees (3.2 mm) than in the isolated trees (6.7 mm), but the 2009 – 2010 ring (4.6 mm) was not significantly ($p = 0.103$) smaller than the 2010 – 2011 ring (5.3 mm) (all trees).

The average duration of the growing season (i.e., the period of time between the onset of growth until the final cessation of growth) was about 10% shorter ($p = 0.009$) in the grove trees (189 d) than in the isolated trees (215 d) (Figure 2). This difference was caused by the later onset of growth ($p < 0.001$) and earlier cessation of growth ($p = 0.060$) in the grove trees. Overall, the length of the growing season did not differ between years ($p = 0.278$). Although there were no large changes in measured soil matric potential (except early in the season), trees nevertheless exhibited marked stem shrinkage events (and reductions in growth) in association with certain mid-season periods characterised by low rainfall and high VPD in both years, particularly March – April 2010 and January – February 2011. The effect on growth of the record-breaking rainfall associated with cyclone Carlos in February 2011 was limited (Figure 2).

The average rate of daily stem increment was significantly ($p = 0.0092$) lower in the grove trees (53.0 $\mu m\ d^{-1}$) than in the isolated trees (82.2 $\mu m\ d^{-1}$) (Figure 2). The average daily stem increment rate also differed significantly ($p = 0.010$) between years (2009 – 2010: 75.0 $\mu m\ d^{-1}$ vs. 2010 – 2011: 60.6 $\mu m\ d^{-1}$).

There were significantly ($p = 0.020$) fewer days of increment in the grove trees (67 d) compared to the isolated trees (100 d). Overall, there were also significantly ($p = 0.002$) fewer days of increment in the 2009 – 2010 growing season (73 d) than in the 2010 – 2011 growing season (94 d). Rainfall events typically led to marked stem increment (short-term swelling), but there was no consistent relationship between the amount of rainfall received and the measured increment.

Both the average daily increment magnitude and the number of measured increment events, contributed significantly ($p < 0.001$) to an overall model of seasonal growth (Table 2). Season duration (period between growth onset and cessation) was not, however, a significant (p = 0.541) predictor of total growth (i.e. annual ring width). There was no evidence of any interactions between variables. Overall, a change of one standard deviation in the number of increment events had a 60% greater impact on ring width than a one standard deviation change in daily increment magnitude (an indication of daily growth). In 2009 – 2010, a change in the number of increment events had a 150% greater impact on ring width than a change in daily increment magnitude.

Characteristics of the cambial zone

Although rapid stem expansion was observed following rainfall in early September 2010, the trees did not resume continuous growth activity (i.e., the production of xylem) before early October (Figure 2 and Figure 3). By this time, trees had begun cambial re-activation with a wider cambial zone (p = 0.042) that had more cells in that zone (p = 0.005), compared with samples taken in September (Figure 3). In samples taken in October, a tangential cell plate, indicating active periclinal cell division, as well as incipient cell enlargement in cells pith-ward of the cambial zone, was evident in many cases.

By mid-May 2010, radial growth had ceased in most trees (no more increment events were recorded by the dendrometers) (Figure 3). Based on analysis of cambial samples taken at that time however, it was evident xylem differentiation was not yet complete. In fact, there were on average still 5.2 and 3.5 cells per radial file, in isolated and grove trees respectively, in which secondary wall thickening had not yet commenced, and an extensive zone of cells in which secondary wall thickening was ongoing.

In February 2010, when growth rates (increment magnitudes) were high, the grove trees had significantly (p = 0.012) fewer cells in the cambial zone, a significantly lower rate of tracheid production (p = 0.001) and a significantly longer cell cycle (p = 0.006) than the isolated trees (Table 3). The grove trees had two fewer cells (p = 0.028), on average, in the zone of enlargement, a lower (p = 0.009) rate of tracheid enlargement and a longer (p = 0.023) duration of cell expansion than the isolated trees. Overall, the average daily increment magnitude during January 2009 and February 2010 was significantly correlated (overall model R^2=0.66, p=0.008) with the number of cells in the cambial zone (p = 0.039), and the average rate of tracheid radial expansion (p = 0.017) (data not shown).

Discussion

The width of an annual ring, or the cumulative radial stem growth during a season, is a function of the interaction of multiple developmental dynamics (Downes et al. 2008). In the tropical context, a wide ring may be formed, for example, in a longer-than-normal wet season (giving it more time to form), or due to overall rapid growth during the season. It is also possible that even in a long wet season (i.e. an early start or a late finish, or both) variability within the season could result in several periods when conditions are less conducive to high rates of growth (shown in our study to be affected by both tracheid production and expansion), leading to a narrower ring. These growth dynamics will be continually modulated by the conditions under which the tree is growing, including competition for resources from neighbouring trees.

In our study, because conditions were variable during both seasons, the most important determinant of ring width was not the overall duration of the season, but rather the number of days, within a growing season, on which increment occurred. That is, even if the growing season started earlier, or ended later, the annual ring was not necessarily wider. This was effectively because growth was somewhat limited on one or more occasions within that season. Although measured daily stem increments will be driven to varying extents by the replenishment of water in tissues that experienced a prior period of shrinkage (Zweifel et al. 2001), the frequency of increment events in these trees provides a good indication of the potential for 'real' growth (i.e. the production of new, differentiated xylem tissue leading to the widening of the annual ring). Measurable (over-bark) increment events will be associated with conditions conducive to rapid xylem production and irreversible growth (Zweifel et al. 2006) . Trees with fewer days on which a measurable increment were detected will also be trees in which actual growth is suppressed by limitations that reduce the potential for cell growth, division and differentiation.

All of these environmental controls, and the resultant processes and dynamics that determine ring width, were amplified under the effect of competition. Trees growing in the grove, experiencing greater competition, had shorter growing seasons and fewer days of increment, than isolated trees. They also had lower daily increment magnitudes than isolated trees, partly because the latter maintained wider zones of cambial cells, but also because tracheid expansion was reduced in grove trees.

In addition to the number of days of increment, the magnitude of increment events (a function of both the potential for tracheid production and the rate of tracheid expansion) also contributed significantly to annual radial stem growth (i.e. ring width). Importantly, the interplay between the number of increment days in the season and the magnitude of the increment events on those days explains why there was no significant difference, overall between the ring widths in our study trees between the two years. Although in 2010 – 2011, trees exhibited more frequent increment events than in 2009 - 2010, the rates and magnitudes of daily increment were, on average, lower than in 2009 – 2010.

Certainly, it was surprising that the difference in average ring width between 2009 – 2010 and 2010 – 2011 was not larger, given that previous research has shown close correspondence between ring width variation in *Callitris*, and total growing season rainfall (Baker et al. 2008; Cullen and Grierson 2009; Ogden 1981); our study site received nearly 900 mm more rainfall in 2010 – 2011 compared to the prior season. This can be understood, at least in part, because the rain in 2011 fell with great intensity over a very short period, in association with Cyclone Carlos, and prior to that the site had already been relatively wet (with the trees actively growing). Furthermore, average daily growth rates in 2010 – 2011 may have been damped by reduced incoming solar radiation that year, an effect well documented in tropical forests (Graham et al. 2003). Overall, it would seem that ring width variation in *C. intratropica*, growing in conditions such as in our study, may not be a very sensitive indicator of the differences between ‘average rainfall’ and ‘very wet’ years. Narrow rings may well, however, provide information about ‘dry’ compared to ‘average’ or ‘wet’ years, and data from below average rainfall years would be needed to test this assumption.

Potential for understanding signals in wood properties

Variation in wood properties, rather than just ring widths, may yield additional or different information about climate in these trees (Drew et al. 2013). Our findings show that the ecological conditions experienced by *Callitris* may also affect wood properties. For example, while grove trees stopped growing earlier than isolated trees, duration of growth did not necessarily equal duration of secondary wall development. Our data suggest that any variation in maximum wood density in tropical *Callitris* would be more a function of conditions in the early weeks of the dry season, rather than the last weeks of the wet season, and that this effect is even more marked in isolated trees. Even though seasonal growth may be complete, with no further ring width adjustment, processes of wall formation may still continue for some weeks (Denne 1971; Skene 1969; Skene 1972). Accordingly, these processes will be influenced by environmental conditions that have no impact on growth and ring width. Such a consideration is important for work using wood properties for making climate inferences with *Callitris* and other species. Latewood or maximum wood density, for example, is a commonly measured wood property in dendroclimatology (Briffa et al. 2002), and one that is primarily determined by wall properties in the latewood (Carlquist 1988).

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Tables

Table 1: Summary of climate at the study site, and weather over the two years of the study

Table 2: Summary of models of ring width (seasonal growth) predicted by the average rate of daily stem increment, the number of increment days in the growing season, and overall season duration. The table shows the standardized coefficients of each variable, and the significance to the model.

Table 3: Cambial characteristics in February 2010 in grove and isolated trees

Table 1

Data	2009–2010 growing season	2010–2011 growing season	Long-term average (70 years)
Total rainfall (mm)	2137	3000[†]	1685
Average temperature (°C)	28.6	27.5	28.6
Average relative humidity (%)	75.6	79.5	69.5
Average hours of sunshine per day	7.7	6.0	7.5
Average number of rain days	15.4	21	14.1
Average daily incoming solar radiation (MJ m^{-2})	19.7	17.9	19.5

[†] Rainfall may be slightly under-estimated due to overflow of the on-site rain gauge during the 2011 cyclone event

Table 2

	Increment rate	Increment days	Season duration	Adjusted R^2
Overall	0.41 ($p < 0.001$)	0.66 ($p < 0.001$)	0.07 ($p = 0.998$)	
Isolated trees	0.82 ($p = 0.028$)	1.15 ($p = 0.029$)	0.11 ($p = 0.705$)	0.80 ($p = 0.020$)
Grove trees	0.36 ($p = 0.05$)	0.67 ($p = 0.003$)	0.18 ($p = 0.293$)	0.94 ($p = 0.002$)
2009 - 2010	0.27 ($p = 0.010$)	0.68 ($p < 0.001$)	0.14 ($p = 0.100$)	0.99 ($p < 0.001$)
2010 - 2011	0.75 ($p = 0.003$)	0.82 ($p = 0.006$)	-0.53 ($p = 0.056$)	0.98 ($p < 0.001$)

Table 3

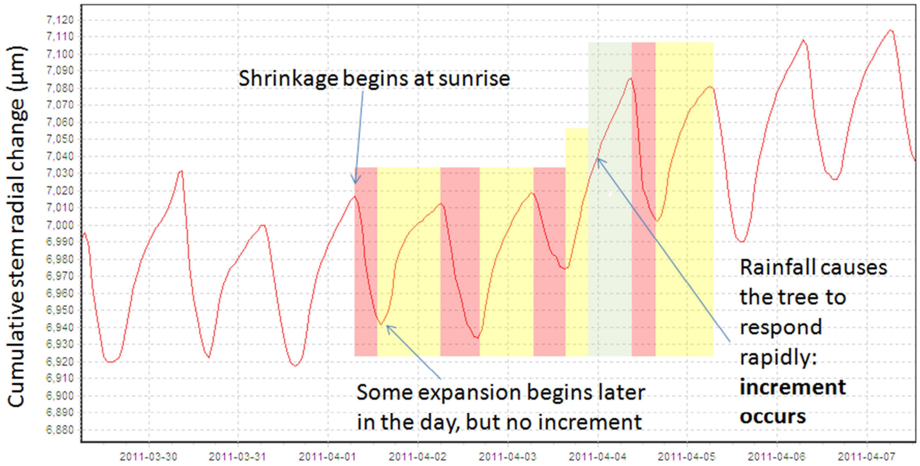
	Grove	**Isolated**
	2010	**2010**
Number of cells in the cambium	4.67 ± 1.2	7 ± 0.87
Width of the primary wall zone (µm)	135.67 ± 33.74	152.67 ± 11.41
Rate of tracheid production (tracheids d^{-1})	0.98 ± 0.2	1.69 ± 0.18
Cell cycle duration (d)	4.68 ± 0.32	4.27 ± 0.71
Rate of tracheid radial enlargement (µm d^{-1})	4.9 ± 1.14	8.14 ± 0.86
Duration of tracheid enlargement (d)	4.89 ± 1.25	2.79 ± 0.36
Diameter of most recently formed tracheids (µm)	31.97 ± 1.57	33.45 ± 0.79

Figures

Figure 1: Short-term (hourly) stem size variation in a single tree over 9 days late in the wet season in 2011, showing daily shrinkage, subsequent expansion and increment. Note that over a period of several days, when there was no rain (March 30 to April 3), there was no measurable increment, but rather a net stem shrinkage. Following a rainfall event, large increment, followed by increment in subsequent days, resulted. Dark shading indicates daily shrinkage; lighter shading indicates recovery and/or increment.

Figure 2: Cumulative change in stem radius in isolated (a) and grove (b) trees, shown with standard error (grey), and estimated soil matric potential (dashed lines indicate data derived from SWC model). Micrographs of the 2009 - 2010 and 2010 – 2011 growth rings from a typical isolated and grove tree are shown at right. In (c) is total daily rainfall (bars) and average daily VPD (line). The durations of the 2009 – 2010 and 2010 growing seasons are indicated with vertical dashed lines.

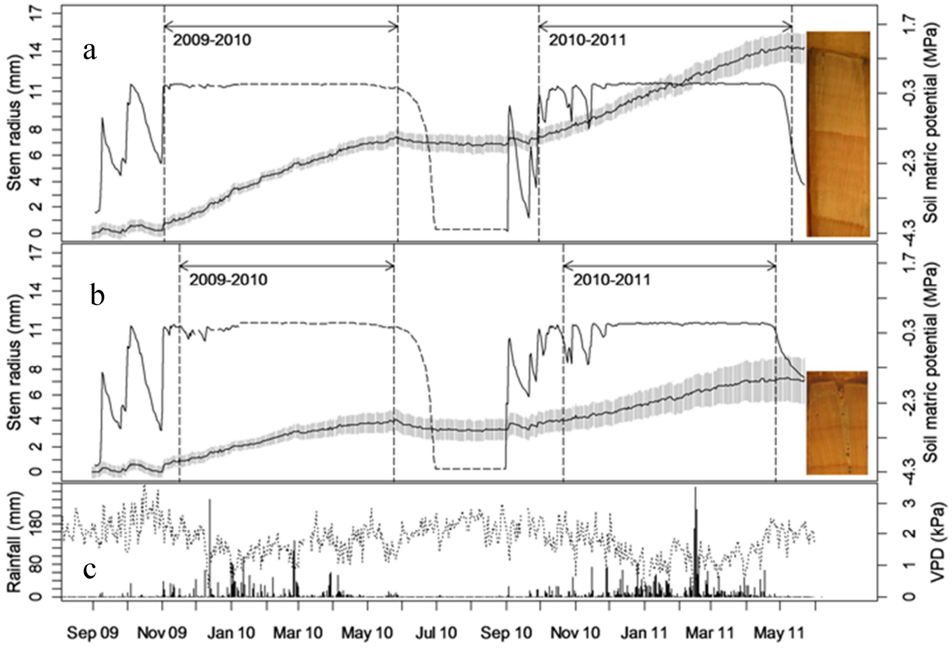
Figure 3: Average cumulative stem radius change in isolated (thick line) and grove (thin line) trees, with cambial characteristics at various points during the 2010 wet and dry seasons shown in micrographs. Arrows indicate the occasions on which cambial samples were taken. In the micrographs, xylem is at the top of the image, phloem at the bottom. The width of the cambial zone and zone of enlarging cells is indicated with an arrow in each image. The scale bar in the first image is 0.5 mm.

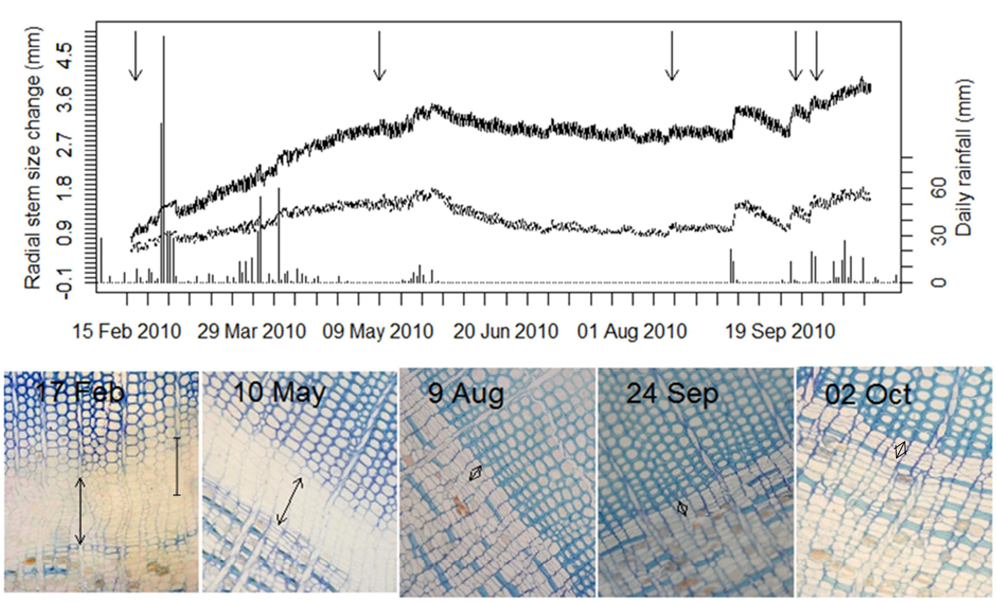


Shrinkage begins at sunrise

Some expansion begins later in the day, but no increment

Rainfall causes the tree to respond rapidly: **increment occurs**




Radial stem size change (mm)
-0.1
0.9
1.8
2.7
3.6
4.5
Daily rainfall (mm)
0
30
60
15 Feb 2010
29 Mar 2010
09 May 2010
20 Jun 2010
01 Aug 2010
19 Sep 2010
17 Feb
10 May
9 Aug
24 Sep
02 Oct