



Annual diameter growth of *Pterocarpus angolensis* (Kiaat) and other woodland species in Namibia



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ABSTRACT

Pterocarpus angolensis DC. (Kiaat) is one of the most preferred timber species that occurs in most southern African countries, including Namibia. In Namibia, the species mainly occurs across the five regions in the north-eastern part of the country where commercial timber harvesting has taken place since the 1940s. Information about the growth rates of the species is currently lacking, yet this information is required to determine a sustainable harvesting regime in Namibia. Therefore, more data about diameter increment is needed. This study aims to (1) determine annual diameter increment of *P. angolensis* in order to assist in planning for sustainable harvesting levels in the northern regions of Namibia, (2) compare growth of *P. angolensis* with other woodland species (*Burkea africana*, *Baikiaea plurijuga*, *Terminalia sericea* and *Schinziophyton rautanenii*) and (3) compare *P. angolensis* growth rates found in northern Namibia with those found in other countries within its distribution range. A total of 111 increment cores and 73 stem discs were collected for tree-ring analysis. The results showed that the average diameter increment of *P. angolensis* was higher in the Kavango regions (0.71–0.80 cm yr⁻¹) than in neighbouring regions (0.35–0.41 cm yr⁻¹). The northern Namibian growth rate is estimated as 0.50 cm yr⁻¹ and lies within the growth range reported for southern Africa. Growth rates of *P. angolensis* were more than 0.10 cm yr⁻¹ lower than rates of *T. sericea* and *S. rautanenii*, but 0.10 cm yr⁻¹ higher than *B. africana* and *B. plurijuga*. Age–diameter relationships of *P. angolensis* may be a good indicator of tree age if a sufficient number of samples are obtained. Our results revealed a rotation cycle of 95–100 years to reach the minimum harvesting diameter of 45 cm in the Kavango regions. This rotation cycle should be a good guideline for sustainable management of this species. This study suggests that simple ring counting on increment cores and stem discs with additional diameter data can provide valuable information on growth rates and rotation cycles. Additional data and work on older trees (>100 years) is required to complete the age–diameter framework.

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1. Introduction

Pterocarpus angolensis DC. (Fabaceae) also known as Kiaat, Transvaal teak or bloodwood tree is one of the most integral African savannah trees used in timber production (Mendelsohn and Obeid, 2005). In Namibia, *P. angolensis* is situated in the

north-eastern regions of the country where woodland is the most dominant vegetation type (Mendelsohn and Obeid, 2005). The species has been harvested on a commercial scale since the 1940s (Mendelsohn and Obeid, 2005), and is not only favoured by wood importers but also by carvers for sculptures, which has resulted in increased illegal logging of existing populations (Barnes, 2010). This illegal logging mostly supports local sawmilling industries (Pröpper et al., 2010). From a forestry point of view, forests dominated by *P. angolensis*, *Baikiaea plurijuga* Harms (Fabaceae) and *Burkea africana* Hook (Fabaceae) are economically valuable wood stock (Chakanga, 2000).

In Namibia, land clearing for crop farming is largely responsible for the decline in forest area. Although recent values are unavailable,

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a total of 4% of the land was cleared between 1943 and 1996 (Mendelsohn and Obeid, 2005; Pröpper et al., 2010). Poor soil fertility means that soil nutrients are generally depleted after a few growth seasons and hence farmers must continue to clear new areas (Pröpper et al., 2010). Every year, 34% of the Kavango regions in the north-eastern corner of Namibia are burnt to encourage the growth of new grass for cattle or to clear fields (Mendelsohn and Obeid, 2005). Unfortunately, many fires burn out of control due to wind and some areas are burnt every three years on average (Mendelsohn and Obeid, 2005). Annual fire disturbance may cause eventual tree mortality, limited recruitment, decreasing growth, accelerated nutrient loss and finally reduced soil fertility (Geldenhuys, 1977; Mendelsohn and Obeid, 2005; Verlinden and Laamanen, 2006).

Regeneration of *P. angolensis* appears to be problematic in South Africa leading to a diminishing stock (van Daalen, 1991). For Tanzania, it has been found that *P. angolensis* regeneration was not sufficient for sustainability given present harvest intensities (Boaler and Sciwale, 1966; Schwartz et al., 2002; Caro et al., 2005). Both the low regeneration rate and the length of time it takes for seedlings to be recruited into populations mean that the species will not be able to supply the markets continuously in future years (Schwartz et al., 2002). Caro et al. (2005) concluded that *P. angolensis* has been driven to local extinction in Tanzania at a rapid rate due to wholesale removal, and very low recruitment has been observed in protected areas, suggesting that these populations might also be declining despite being protected (Schwartz et al., 2002; Caro et al., 2005).

Efforts to manage commercial plantations of *P. angolensis* in South Africa have been largely unsuccessful (van Daalen, 1991). Silvicultural problems occurred at all stages of the species' development (Boaler and Sciwale, 1966). There is a need for vigorous research programmes on sustainability of *P. angolensis* harvest and use. Scientific data on growth and fire behaviour are crucial and documentation must be distributed to support sustainable forest management (Geldenhuys, 1996).

Annual growth rings provide a strong basis for age determination of species and have important applications for forest ecology and sustainable management (Stahle et al., 1999). Stahle et al. (1999) indicated annual growth rings in indigenous *P. angolensis* forests of western Zimbabwe, and Trouet (2004) and Fichtler et al. (2004) have both described the annual nature of tree rings in *P. angolensis* and *B. africana* from the semi-arid regions of Namibia.

Currently, there is insufficient growth data available for *P. angolensis* to determine if logging is sustainable. In the past, several studies focused on the climate–growth relation of *P. angolensis* (Stahle et al., 1999; Shackleton, 2002; Fichtler et al., 2004; Therrell et al., 2007). Unfortunately, very few studies have been done with a silvicultural approach. Therrell et al. (2007) is an important exception and suggested that it would take more than 100 years for trees of this species to reach harvestable sizes of 35–40 cm in the distribution area (Therrell et al., 2007). This does not necessarily mean that rotation periods have to be this long. Our observations indicate difficulty in finding *P. angolensis* trees exceeding 100 years of age in Namibia, indicating that rotations of 100 years may not be possible. Within the Kavango regions of Namibia no studies on growth rate have yet been performed, except for measurements in permanent plots of a burning trial (Geldenhuys, 1977). In Namibia, the species is near its southern distributional limit and one could expect that annual growth would be lower than within more northern countries in the core distribution area, where growing conditions are more favourable. We aim to compare growth rates within different regions in north-eastern Namibia and determine suitable rotation cycles for application in sustainable management strategies.

The objectives of this study are (I) to estimate the annual growth of *P. angolensis* in Namibia, (II) to compare the growth of this species with other economically important species within the northern regions of Namibia, and (III) to compare the growth of *P. angolensis* in the northern regions of Namibia with other regions outside Namibia where *P. angolensis* occurs.

2. Material and methods

2.1. Study area descriptions

At three sites in the Kavango regions of northern Namibia, increment cores were taken from 109 trees of five different species during the dry season of 2014 (Fig. 1). For *P. angolensis* increment cores were collected in Hamoye (18°14'S, 19°43'E), Mashare (17°53'S, 20°12'E) and Divundu (18°7'S, 21°37'E) (SASSCAL, 2015). *Terminalia sericea* Burch. ex DC., *B. africana*, *B. plurijuga* and *Schinziophyton rautanenii* Hutch. ex Radcl.-Sm. were sampled only at Hamoye.

Stem discs from four additional study sites in four regions (Kavango West, Kavango East, Oshikoto and Zambezi) were also available (Fig. 1) (Fichtler et al., 2004; Moses, 2013). In Kavango West, three stem discs from individual *P. angolensis* trees were available from the Hamoye State Forest for the The Future Okavango (TFO) project. In Kavango East another 15 *P. angolensis* stem discs were available from two adjacent leasehold farms located about 205 km south of Rundu in the Karukuvisa District – Farm No. 1428 (19°08'54.36"S and 20°00'2.68"E) and Farm No. 1412 (19°16'36.36"S and 20°01'15.96"E) (Moses, 2013).

At two other sites in northern Namibia, Oshikoto region close to Ondangwa (17°56'S, 15°59'E) and Katima Mulilo, Zambezi region (17°30'S, 24°17'E), data regarding stem discs from four different species and 55 individual trees was released (Fichtler et al., 2004; Worbes, unpublished report).

Fig. 1 shows the complete sample collection and geographical location, and Table 1 lists the samples selected for further tree-ring analyses and includes a short description of differences between the sample sites.

All study areas are characterised by an annual dry season of 5–7 months with less than 50 mm precipitation, lasting from May to October.

The overall study design was based on random selection and accessibility. The influence of roads and the edge of the forest were minimised by establishing transects perpendicular to roads. Individual trees within these transects included trees in two different forest types, Community Forest and State Forest, if these forest types were present at the transect.

2.2. Tree species

All five species briefly described below are common in southern African woodlands and within the Kavango regions. *P. angolensis* is a medium sized to large tree growing up to 30 m in height under ideal conditions (von Breitenbach, 1973). In Namibia, height is reduced to 16 m due to the more arid conditions (Coates Palgrave, 2002). It is one of the best known, most widely used and most valuable timber species in southern Africa. Trees are deciduous and leaves are shed around June (Graz, 2004). The species is known to have a suffrutex or dieback stage where plants develop shoots that may reach heights of up to three metres each growing season (Graz, 2004). In the dry season, shoots die back to a depth of 2–36 cm below the surface protecting the meristem from fire damage. Shoots renew every year in order to prevent damage from the dry season fires. The suffrutex stage will last for a decade, although this may be extended to a length of 25 years by high

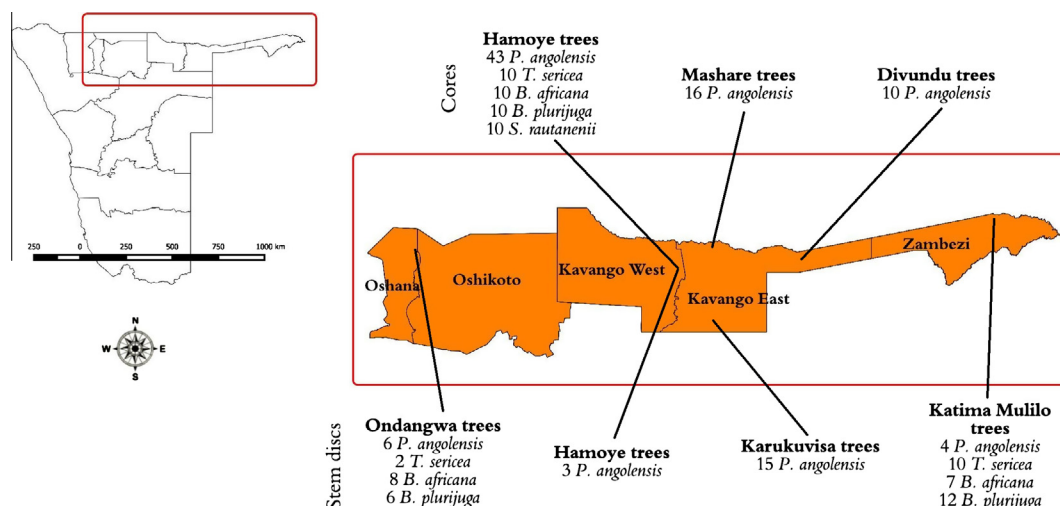


Fig. 1. Location of increment core and stem disc sampling sites within the northern regions of Namibia. The number of the sampled trees is listed per species.

Table 1

Overview of the number of analysed tree samples separated by the region, sample site with descriptions, species name and sample type. Sample site altitude (m) (SASSCAL, 2015), annual rainfall (mm), annual average temperature (°C) (<http://www.cgiar-csi.org/>) and the forest types are provided. 'NA': Not Available.

| Region | Sample sites | Altitude (m) | Annual rainfall (mm) | Annual average temp (°C) | Forest types | Sample species | Number of cores | Sample year | Number of stem discs | Sample year |
|--------------|---------------|--------------|----------------------|--------------------------|--|----------------------|-----------------|--------------------------------|----------------------|-------------------------------------|
| Kavango West | Hamoye | 1122 | 577 | 22 | Hamoye State Forest and Community Forest | <i>P. angolensis</i> | 43 | All cores were sampled in 2014 | 3 | 2012 |
| | | | | | | <i>T. sericea</i> | 10 | | NA | |
| | | | | | | <i>B. plurijuga</i> | 7 | | NA | |
| | | | | | | <i>B. africana</i> | 9 | | NA | |
| | | | | | | <i>S. rautanenii</i> | 16 | | NA | |
| Kavango East | Mashare | 1066 | 570 | 22 | Open Forest | <i>P. angolensis</i> | 16 | 2014 | NA | |
| Kavango East | Divundu | 1008 | 580 | 22 | Open Forest | <i>P. angolensis</i> | 10 | 2014 | NA | |
| Kavango East | Karukuvisa | 1153 | 468 | 22 | Open Forest | <i>P. angolensis</i> | NA | | 15 | 2012 |
| Oshikoto | Ondangwa | 1100 | 454 | 23 | Open Forest | <i>P. angolensis</i> | NA | | 6 | All stem discs were sampled in 2000 |
| | | | | | | <i>T. sericea</i> | NA | | 2 | |
| | | | | | | <i>B. plurijuga</i> | NA | | 6 | |
| | | | | | | <i>B. africana</i> | NA | | 8 | |
| | | | | | | <i>B. plurijuga</i> | NA | | 8 | |
| Zambezi | Katima Mulilo | 982 | 672 | 22 | Open Forest | <i>P. angolensis</i> | NA | | 4 | All stem discs were sampled in 1998 |
| | | | | | | <i>T. sericea</i> | NA | | 10 | |
| | | | | | | <i>B. plurijuga</i> | NA | | 12 | |
| | | | | | | <i>B. africana</i> | NA | | 7 | |
| | | | | | | <i>B. plurijuga</i> | NA | | 7 | |

frequencies of fires. During this stage, the root system develops to an extent where it may collect water and nutrients to support a permanent shoot through the dry season (von Breitenbach, 1973).

B. africana is a deciduous medium sized tree that reaches up to 20 m in height (Maroyi, 2010). Like *P. angolensis*, it is part of the Fabaceae family and a true multi-purpose tree. Leaves are shed around May and flush in August (Maroyi, 2010). *B. plurijuga*, also known as Zambezi teak (Fabaceae), is an evergreen medium-sized to large tree that grows up to 27 m in height (Childes,

1989; Coates Palgrave, 2002). *B. plurijuga* has a large, dense, spreading crown and is characteristic of areas of deep Kalahari sand, usually occurring in open deciduous woodlands. It is fire sensitive and one of most valuable timber trees in drier parts of tropical Africa (Lemmens, 2012). *T. sericea* is another multi-purpose pioneer species, especially important for fencing, furniture and other wood products (Shackleton, 2001; Coates Palgrave, 2002; Graz, 2006; Lemmens, 2009). This deciduous tree is usually small to medium-sized but can grow up to 15 m high. Leaf flush usually

takes place between September and November (Lemmens, 2009). *S. rautanenii* is a large, spreading tree (Coates Palgrave, 2002). This stem succulent is a member of the Euphorbiaceae family and known to be a deciduous tall tree that grows up to 24 m (Graz, 2002). Trees are leafless from March–May to October–November (Graz, 2002). The nuts are commonly harvested and are an important traditional source of food in the Namib Desert.

2.3. Sample collection and preparation

Two increment cores per individual tree were collected for each of the five species from the Hamoye State Forest. Trees sampled in the Hamoye Community Forest and trees in Mashare and Divundu were only sampled by one increment core per tree. Only living, straight and standing stems were suitable for sampling. If there were multi-stemmed trees, the thickest stem was chosen. Before coring, diameter at breast height (DBH) including the bark was measured for all trees.

Increment samples were collected with a 5 mm increment borer (Haglöf, Sweden). Coring depth was estimated on the basis of tree DBH and an additional extra 1–2 cm added to increase the chance of including the pith. Sampling was primarily performed at stump height since breast and stump heights were similar. Where two cores per tree were collected, the second sample was taken at DBH from a different angle relative to the stump height core. All samples were air-dried for several weeks. Increment cores were prepared for measurements by using the WSL core-microtome (Gärtner and Nievergelt, 2010). The transverse surface of each core was cut in steps of 10–20 μm . Position and angle of the blade varied depending on the density of the species, and even from core to core (Gärtner and Nievergelt, 2010). After sample preparation, samples were mounted on wooden supports.

The transverse surfaces of all 18 stem discs of Karukuvisa and Hamoye were sanded (grain 80–118) and polished per radius (grain 150–600). These stem discs were collected in 2012 based on their commercial volume and thus timber capacity. Only discs from large trees were collected (Moses, 2013).

Stem discs from Zambezi and Oshikoto were collected in 1998 and 2000 respectively. Collection of discs from these sites was predicated on covering all diameter classes available. These stem discs were previously used in a study by Fichtler et al. (2004). Central holes, double centres, missing parts or downgraded wood on stem discs are undesirable. All discs were air-dried, progressively sanded up to grit 600 and studied by Worbes (unpubl. data) and Fichtler et al. (2004).

2.4. Tree-ring analysis

P. angolensis stem discs from the Kavango regions were studied with a magnifying glass to mark tree-ring boundaries. Rings in *T. sericea*, *B. africana*, *B. plurijuga* and *P. angolensis* stem discs from the Oshikoto and Zambezi regions were counted using a stereomicroscope with low magnification. Radii selection on the discs was done with caution, avoiding areas with wedging rings. Ring boundaries were marked and counted from the centre to the edge on three or four different radii. Tree rings on increment cores were counted using a stereomicroscope and a LINTAB device with TSAP Win software (Rinn and Jäkel, 1997). Distinct tree-ring boundaries were marked and doubtful rings (wedging rings) noted. Tree rings were measured to the nearest 0.01 mm. Counting was performed from the innermost (pith) ring to the outermost complete ring. Eccentricity was minimal and not an issue for ring measurement or counting. Three *B. plurijuga*, one *B. africana* and four *S. rautanenii* cores were unsuitable for analysis due to incorrect orientation in the core mount or extreme fragmentation or destruction.

Mean annual diameter increments from cores and stem discs were determined for each tree on each site by dividing the tree DBH by the tree age. DBH measurements included bark. The age of each tree is the mean result of ring-count values per disc or core. If the age of two cores from one tree was different due to eccentricity or missing piths, only the representative samples with pith were included in mean annual diameter increment (MDI) calculations. To calculate average values of MDI per species and site, we weighed averages by age. This weighing was performed to counter differences in growth rates that are age-linked. If one site was much older than the other sites and growth rates were not weighed, this age-effect might blur the actual difference in growth rate. Age–diameter relations for *P. angolensis* were estimated by plotting mean age and DBH per tree and making the best-fitted regression line to obtain mean growth curves for each site.

There is currently no dendrochronological assessment of *S. rautanenii* in the literature. Samples were investigated macroscopically, as well as microscopically to investigate which anatomical features of wood are responsible for the visible coloured layers and to identify possible growth-ring boundaries. We used 30 μm slides from a polished increment core to investigate the nature of rings in this species. Microscopic slides were prepared using conventional methods (Jansen et al., 1998).

3. Results

3.1. Tree-ring structures

Distinct tree rings were observed on stem discs and increment cores for all five species investigated here.

The wood structure of *P. angolensis* is characterised by many larger and mainly solitary vessels that tend to concentrate at the beginning of the ring (Fig. 2a). Confluent parenchyma is present throughout the entire ring. Most rings are delimited by a thin marginal parenchyma band and a slight difference in fibre cell-wall thickness. *T. sericea* is characterised by a zone with higher vessel density at the beginning of the ring. Afterwards the vessel density decreases and the parenchyma become aliform to confluent (over several vessels) towards the end of the ring. At the ring boundary, a thin boundary of discontinuous marginal parenchyma can be found (Fig. 2b). Intercellular canals of traumatic origin appear in several samples (Fig. 2b marked by the left arrow) and wedging rings are very common, with most of the stems of this species having eccentric piths.

B. plurijuga is characterised by the occurrence of many minute vessels. Parenchyma and vessels are mostly absent at the start of the ring and parenchyma then goes from aliform to confluent. Tree-ring boundaries are often rather vague and characterised by a zone of flattened fibres (Fig. 2c).

The tree-ring boundary of *B. africana* is characterised by a marginal parenchyma band, often combined with a zone containing very few pores. In some rings, the wood rays distend at the ring boundary. Apart from the boundary, vessel densities appear to be uniform over the entire ring. Vasicentric parenchyma is present throughout the entire tree-ring (Fig. 2d).

The wood structure of *S. rautanenii* is characterised by few large solitary vessels; very thin-walled fibres and reticulate parenchyma (Figs. 2e and 3). No clear annual patterns in vessel density and vessel dimensions are observed although Fig. 3a might suggest a higher vessel density at the end and the start of a tree-ring. Tree rings are harder to distinguish at a macroscopic level (Fig. 2e) but microscopic slides enable the separation of true from false tree rings. True tree rings are delineated by an abrupt reduction of the radial fibre diameter (Fig. 3b) whilst this reduction is more gradual for false tree rings (Fig. 3c). In true tree rings, every cell can be

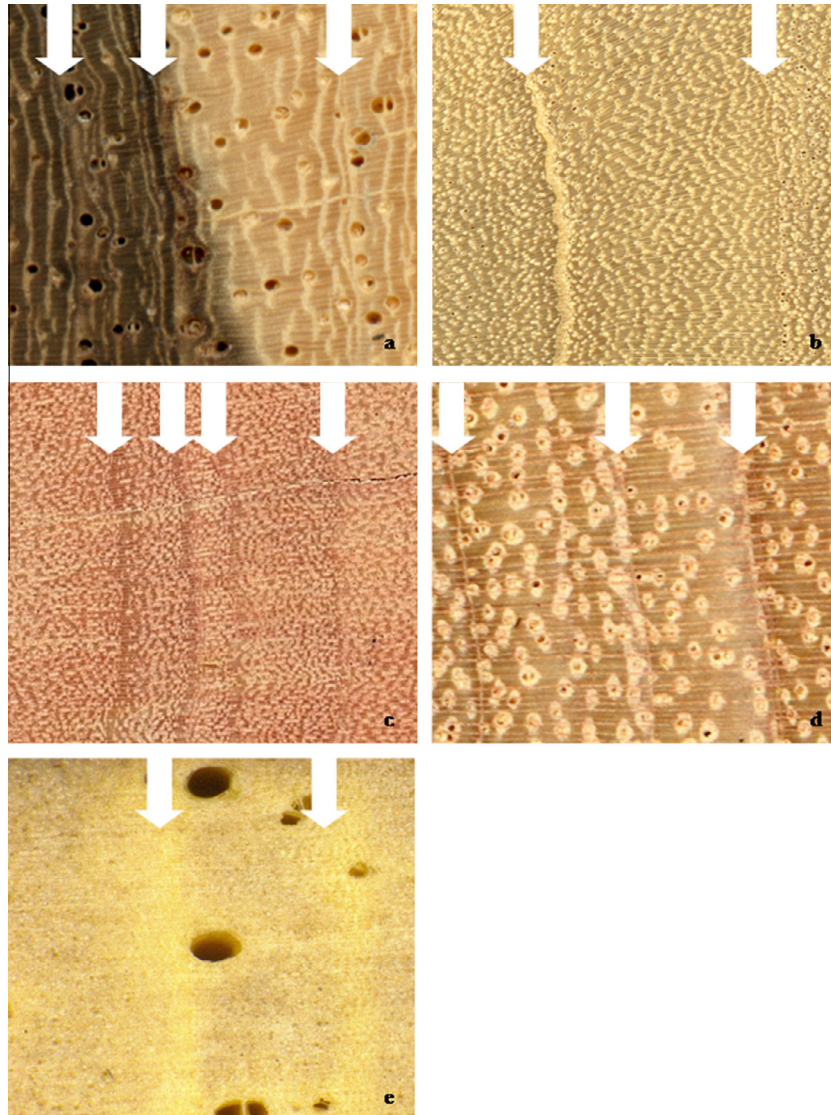


Fig. 2. High-resolution scan of polished stem surfaces of (a) *P. angolensis*, (b) *T. sericea* where the first ring (left) has a traumatic character, (c) *B. plurijuga*, (d) *B. africana* and (e) *S. rautanenii*. The pith is always situated on the left side. The white arrows indicate tree-ring boundaries.

allocated to one particular tree-ring whilst this is not possible for false tree rings. Tree-ring boundaries are difficult to characterise by parenchyma cells as the reticulate parenchyma network cannot be easily dissociated from marginal parenchyma.

3.2. Diameter growth

Overall, the mean number of tree rings (all stems) of *P. angolensis* is 64. Mean tree diameter ranges from 32.36 cm in Hamoye (Kavango) to 43.21 cm in Karukuvisa (Kavango). Mean tree diameter across all sites is 30.29 cm. MDI-values of *P. angolensis* range from 0.35 ± 0.12 cm in Zambezi to 0.80 ± 0.16 cm in Divundu (Kavango). Mean diameter increment of *P. angolensis* across all sites is 0.50 ± 0.21 cm (Table 2). It should be noted that tree ages are considered as minimum values due to the suffrutex stage. Presentation of cylindrical stems in this species means that the numbers of tree rings at stump height and breast height are equal. Although sampling at Karukuvisa differed from sampling in Kavango, no significant differences in MDI occurred (Table 2).

Overall mean number of tree rings (all stems) of *T. sericea* is 43. Mean tree diameter across all sites is 24.31 cm. MDI-values of

T. sericea are ranging from 0.42 ± 0.03 cm in Oshikoto to 0.89 ± 0.14 cm in Kavango (Fig. 4). MDI of *T. sericea* across all sites is 0.63 ± 0.24 cm. Within northern Namibia *T. sericea* has the highest growth rate.

B. plurijuga overall mean number of tree rings is 78. Mean tree diameter across all sites is 30.60 cm. MDI-values of *B. plurijuga* range from 0.31 ± 0.04 cm in Oshikoto to 0.48 ± 0.19 cm in Kavango (Fig. 4). MDI of *B. plurijuga* across all sites is 0.39 ± 0.08 cm. *B. plurijuga* and *B. africana* samples from Kavango and northern Namibia has the lowest growth rates.

The mean number of tree rings of all *B. africana* stems is 66. Mean tree diameter across all sites is 26.92 cm. MDI-values of *B. africana* range from 0.33 ± 0.04 cm in Oshikoto to 0.52 ± 0.22 cm in Kavango (Fig. 4). MDI of *B. africana* across all sites was 0.42 ± 0.09 cm.

Overall, the mean number of tree rings (all stems) of *S. rautanenii* was 44. Mean tree diameter across Hamoye (Kavango) is 33.15 cm. MDI of *S. rautanenii* across Hamoye (Kavango) is 0.76 ± 0.18 cm, and is the highest within the Kavango regions (Fig. 4).

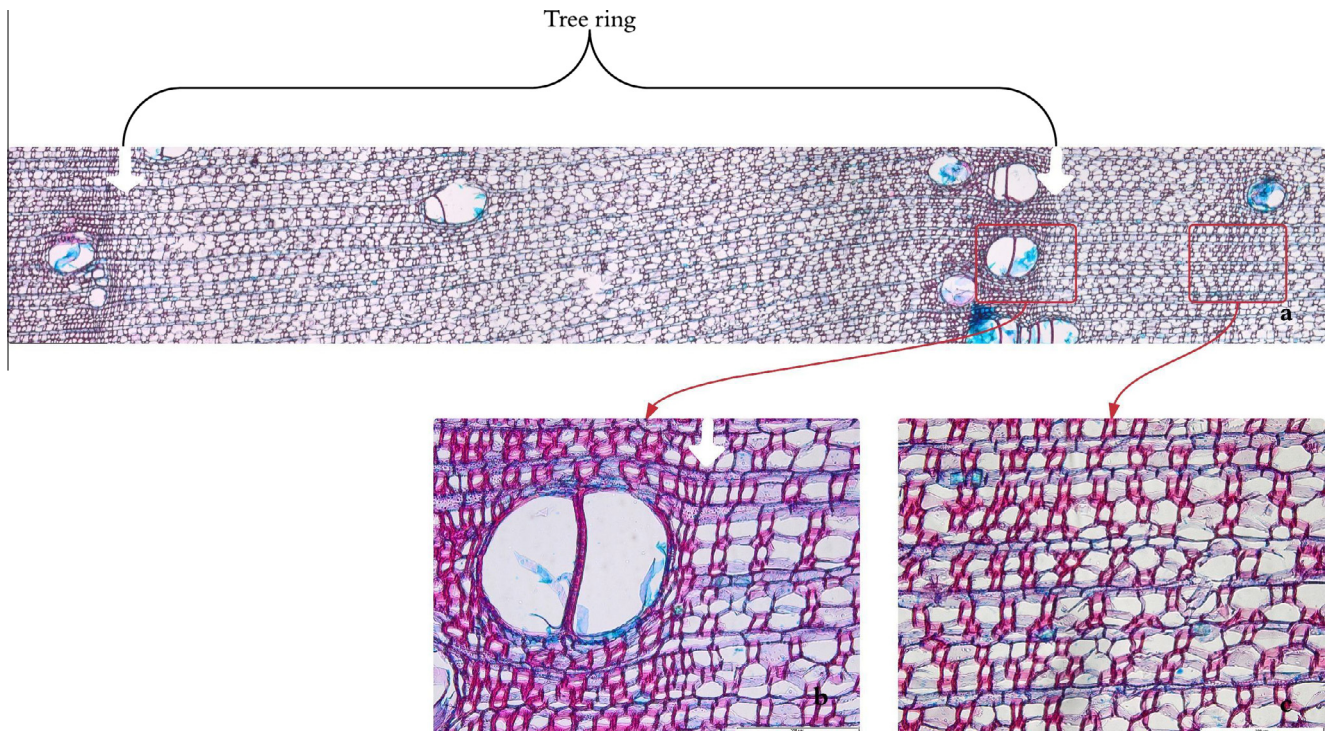


Fig. 3. Microscopic images of *S. rautanenii*. The pith is always situated on the left side. The white arrows indicate tree-ring boundaries. Picture (a) is a 25× magnification with clear indications of an entire ring, (b) is a 100× magnification of a ring boundary and (c) is a 100× magnification of a false ring.

Table 2

Mean DBH (cm), mean number of tree rings and mean annual diameter increment (MDI) (cm) for *P. angolensis* at its matching study sites. *N* is the total number of trees included in every calculation.

| Study site | Mean DBH (cm) | Mean number of tree rings | MDI (cm) | <i>N</i> |
|------------|---------------|---------------------------|-------------|----------|
| Kavango | 35.61 | 48 | 0.74 ± 0.30 | 87 |
| Hamoye | 32.36 | 46 | 0.71 ± 0.38 | 46 |
| Divundu | 35.10 | 44 | 0.80 ± 0.16 | 10 |
| Mashare | 38.34 | 50 | 0.77 ± 0.24 | 16 |
| Karukuvisa | 43.21 | 57 | 0.76 ± 0.12 | 15 |
| Zambezi | 25.40 | 72 | 0.35 ± 0.12 | 4 |
| Oshikoto | 29.85 | 73 | 0.41 ± 0.11 | 6 |

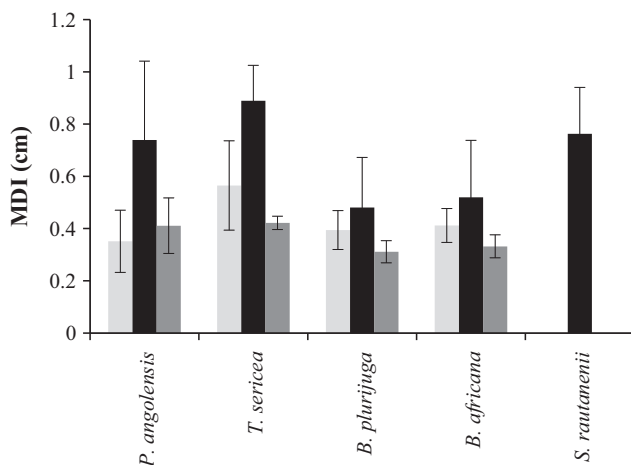


Fig. 4. Mean annual diameter increment per species defined by area/region. For every species MDI-values were calculated per tree, then averaged and weighted by age. For all species except *S. rautanenii*, MDI at three study areas were calculated: Zambezi (■), Kavango (■) and Oshikoto (■).

3.3. Age–diameter relationships

If the mean number of tree rings and DBH are plotted for all sampled *P. angolensis* trees in Kavango, Zambezi and Oshikoto, a predictive trend-line can be fitted. The Kavango trend-line shows a decreasing growth rate with increasing age. The other regions' trend-lines are more or less directly proportional but contain fewer data compared with Kavango (Fig. 5). The Pearson correlation value and significance slope levels of the trend-line can be used to assess the relationship between age and diameter. Best-fit power trend-lines are selected as a prediction of the growth curve. The trend-line indicates that it takes about 95–100 years for a Kavango *P. angolensis* seedling that has outgrown the suffrutex/dieback stage to reach a minimum harvest size of 45 cm DBH. For Zambezi and Oshikoto, harvestable sizes are reached after 130–135 years and 150–155 years respectively, estimated by the age–diameter curve. For Kavango, ages do not exceed 100 years in our study. In Zambezi and Oshikoto, ages exceed 100 years (Fig. 5).

4. Discussion

For all but one species, distinctness of tree rings was published (Maroyi, 2010; Fichtler et al., 2010; Wheeler, 2011). For *S. rautanenii*, indistinct rings were found in the literature (Wheeler, 2011), but the species has a wide distribution area hence seasonality and distinctness of tree rings could be site specific. Ring boundaries of *B. plurijuga* and *S. rautanenii* were relatively difficult to distinguish. Distinct tree-ring boundaries of *B. plurijuga* were clearly observable and distinct rings of *S. rautanenii* were present in the Kavango regions. Climatic data indicates a pronounced seasonality of rainfall and temperature in Namibia and all species except *B. plurijuga* react to this seasonality by shedding their leaves. Simply because a species is evergreen does not necessarily mean tree rings are indistinct, as in the case of *B. plurijuga*. Climatic seasonality can induce a period of slow growth and lead to an

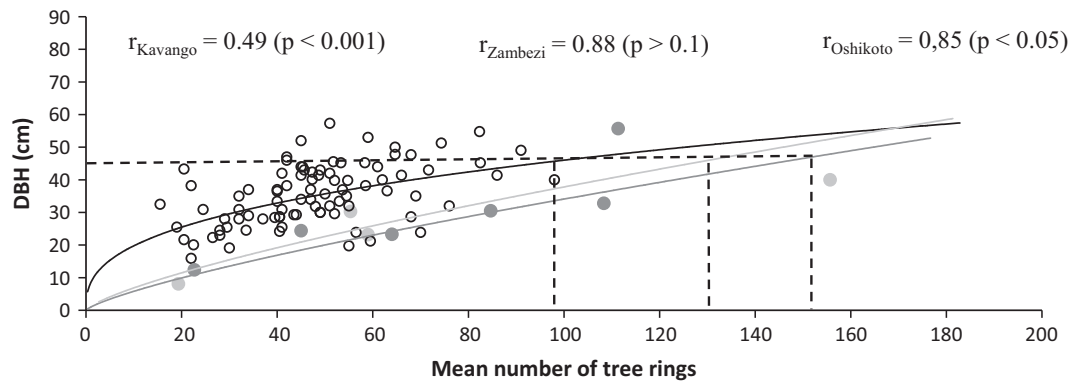


Fig. 5. Age-diameter curve for *P. angolensis* at all three study areas: Kavango (○), Zambezi (●) and Oshikoto (●), where every dot represents a tree by number of tree rings and DBH (cm). The dotted lines give an estimation of the number of formed tree rings at minimum harvestable size of 45 cm DBH.

annual cycle that still allows for formation of annual rings (Worbes, 1995, 2002). We can thus assume that tree rings in all species of this study are of an annual nature. When a comparison is made between all species within northern Namibia, *S. rautanenii* has the highest growth rate (0.76 cm yr^{-1}), however this is very local data and cannot be considered as the mean value of northern Namibia. Instead, *T. sericea*, with a growth rate of 0.63 cm yr^{-1} , is by far the fastest grower compared with *P. angolensis*, *B. africana* and *B. plurijuga* indicated from this study. *T. sericea* is the only pioneer species in this study and is characterised by a fast offset growth. It can thereby establish easily in previously unwooded areas. *B. africana* and *B. plurijuga* both have the lowest growth rate ($\pm 0.40 \text{ cm yr}^{-1}$) in northern Namibia. They are the slowest growers of the five species in this study.

The average MDI across all sites from northern Namibia in this study is 0.50 cm yr^{-1} . This is comparable with the MDI of 0.54 cm yr^{-1} previously reported by Lückhoff (1969; unpublished report cited in van Daalen et al., 1992). Their value included trees from northern Namibia (Lückhoff, 1969; unpublished report cited in van Daalen et al., 1992). The overall growth rate of *P. angolensis* in northern Namibia is high compared to reported MDI-values in the literature for South Africa ($0.15\text{--}0.37 \text{ cm}$) and Tanzania ($0.15\text{--}0.49 \text{ cm}$) but within ranges reported for Zambia and Zimbabwe ($0.29\text{--}1.07$) (Groome et al., 1957; Lückhoff, 1969, unpublished report cited in van Daalen et al., 1992; Stahle et al., 1999; von Maltitz and Rathogwa, 1999; Shackleton, 2002; Schwartz et al., 2002; Trouet, 2004). Therrell et al. (2007) reported that MDI for *P. angolensis* varied across its distributional range: from 0.2 cm in Sikumi, Zimbabwe up to 0.4 cm in Mzola, Zimbabwe and Mozambique (Therrell et al., 2007).

Our results indicate that there are distinct differences in MDI between sites and that different regions have specific growth rates. Growth rates in Kavango are higher compared to other regions. MDI-values reported ranged from 0.35 cm yr^{-1} in Zambezi region to 0.80 cm yr^{-1} in Divundu (Kavango regions). This suggests that it would take over 130 years after the suffrutex stage for trees in Zambezi to reach harvestable sizes of 45 cm. Even in Kavango where overall growth is estimated as 0.74 cm yr^{-1} , it would take more than 95 years after a suffrutex stage of ten years or more (Graz, 2004), to reach the required harvest diameter. Therrell et al. (2007) reported that it would take 85–100 years or more to reach harvestable sizes of 35–40 cm in the distribution area of *P. angolensis*. Results from the Oshikoto and Zambezi regions are comparable with each other, although the number of samples might not be sufficient to draw definitive conclusions (<10 trees, non-significant age–diameter relation). More sampling for both regions will allow better comparisons. Age–diameter relations reveal a fast offset of growth in the first decades of *P. angolensis*

in Kavango regions, which is then followed by a decreasing growth rate according to our prediction. Additional sampling of trees exceeding the 100-year age limit will provide valuable input to further development of the growth curve.

A rotation period of 95–100 years is very long compared with the rotations of 40–75 years currently in use (Takawira-Nyenywa, 2005). For both industry and individual loggers, longer rotations may not be feasible, depending on *P. angolensis* stock. Therefore, the volume of *P. angolensis* available and growth rates at specific locations both need to be determined prior to estimation of the rotation length, although this is more easily said than done. It should be noted that calculation of suitable rotation lengths is simply a first indication and may not provide feasible guidelines for the local forest industry. Since the average life span of *P. angolensis* in Namibia is 90–100 years, this would mean trees in Namibia are harvested at the end of their lifetimes (own observations). Whilst this is desirable from a sustainability point of view, it is not commercially feasible. Percentages of heartwood compared to stem diameter and age allows the estimation of more feasible rotation lengths according to Therrell et al. (2007).

Since there are distinct differences in growth rates within and between regions and sites, we suggest that even at the stand level, trees of similar diameter could have significantly different ages. Climate, soil, depth of the ground water table and others parameters of major influence may differ from stand to stand (Burke, 2006; Holdo, 2006). In Kavango, all sampling took place within $\sim 20 \text{ km}$ of rivers or dry river beds which we suggest provide a good basis for germination and initial tree-growth after suffrutex (Graz, 2004). These circumstances could explain the higher growth rates in the first decades of tree-growth, especially for *P. angolensis*. Fire frequencies are also higher in the Zambezi, which could explain the lower growth rates within this area (Burke, 2006; Holdo, 2006).

Future research on the growth dynamics of *P. angolensis* and other woodland species across southern Africa should include more sampling over a specified area and include a wide range of tree ages and diameters in order to obtain the best estimations of age–diameter relation and MDI. Another direct way to determine growth is to use the width of each growth ring measured on samples from larger trees and thereby provide good coverage of different diameters and ages on fewer samples (Therrell et al., 2007). Research on factors influencing growth should be extended to determine which additional factors play an important role at the local scale. It should be noted that coring is a useful way to retrieve more data, although this should never be the only sampling method to estimate age and diameter relations for tropical trees (Stahle et al., 1999). For the five species described here, high quality increment cores were obtained for *P. angolensis*, *T. sericea* and *S.*

rautaneii, but quality varied for *B. africana* and *B. plurijuga*. For these two last species, extreme fragmentation during coring is frequent, although some intact increment cores can still be obtained. We therefore recommend that increment cores be collected with extreme caution and used to supplement stem disc collections or plot inventory data.

5. Conclusion

Growth rates suggest that it takes about 95–100 years after sprouting for the average *P. angolensis* tree in Kavango to reach a minimum harvestable size of 45 cm DBH. Other regions in northern Namibia revealed lower growth rates and hence longer rotations may be required. The overall growth rate for *P. angolensis* in Namibia can be considered fast compared with neighbouring countries. Site-specific parameters, such as inventory data or climate data, provide important additional information about tree growth and also provide a valuable comparison of data obtained through coring or from stem discs. This study suggests that simple ring counting on increment cores and stem discs can provide valuable information about MDI and age–diameter relationships for all species in this study. Samples from older trees (>100 years) would help complete the age–diameter framework and validate the extrapolations made in this study.

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