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Variation in baobab (*Adansonia digitata* L.) root tuber development and leaf number among different growth conditions for five provenances in Malawi

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Abstract

The baobab tree is an underutilised indigenous fruit tree in sub-Saharan Africa which, at the same time is vulnerable to overexploitation in areas close to centres of demand, as currently baobab use is limited to wild, baobab trees. Baobab seedlings are known to form root tubers, but little is known about their growth characteristics and its yield potential. This study aims to investigate the root tuber and leaf development of baobab seedlings grown from seeds of five provenances, sown at three different planting distances in two nursery trials at climatically distinct locations in Malawi, namely Mzuzu and Mangochi. The observed yield data was fed into preliminary farm-gate profitability analyses for three different scenarios that differed by planting distance. Results indicate increased growth rates for root dry mass and number of developed leaves with increasing planting distance. However, we did not find a significant effect of seedling provenance on any of the measured plant growth parameters. Seedlings invested mainly into root development during the growth period, with root tubers reaching an average fresh weight of 41 ± 39 g and an average length of 24 ± 11.9 cm at 138 days after sowing. Profitability analyses showed a potential total net benefit of 12.78 USD per harvest cycle of 16 weeks and per 100 m^2 of land cultivated with baobab root tubers, which was better than an alternative scenario of maize cropping on the same area that showed a negative total net benefit when cost of family labour was included. However, the heterogeneity of root tuber development as affected by abiotic and biotic factors like soil fertility and water availability, as well as genetic origin warrant further investigation.

Keywords: Baobab, indigenous fruit tree, Malawi, root tubers, underutilised plants

1 Introduction

The baobab tree (*Adansonia digitata* L.) is one of around 1,200 wild edible fruit species in Africa (Gebauer *et al.*, 2016) and belongs to the wooden 'Big Five' of fruit trees in Africa (Jama *et al.*, 2008) together with tamarind (*Tamarindus indica* L.), jujube (*Zizyphus mauritiana* L.), marula (*Sclerocarya birrea* L.) and mango (*Mangifera indica* L.). Baobab usually inhabits the driest parts of tropical dry forests (De Smedt *et al.*, 2012) and is considered a key species of the African savannah and an iconic visual landmark (Jenya *et al.*, 2016).

Indigenous fruit trees (IFTs) like baobab help fulfil subsistence and commercial objectives such as improving nutrition, food security, fostering rural development and supporting sustainable landscape management (Gebauer *et al.*, 2016; Jäckering *et al.*, 2019) but are increasingly threatened by habitat loss and ecosystem degradation as a result of climate change and population growth-related land-use changes (De Smedt *et al.*, 2012; Sanchez *et al.*, 2011a; Venter *et al.*, 2013). Baobab is especially vulnerable due to its low cultivation status and low natural regeneration as well as the 'scattered' dispersal of the species (Gebauer *et al.*, 2002; Sanchez 2011b) resulting in many baobab populations consisting of old individuals and/or decreasing in number (Sanchez 2011b; Venter *et al.*, 2013). Overexploitation

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of natural stands is a pressing issue for conservation of the species' genetic resources, as human baobab propagation is uncommon and conservation strategies have not been widely implemented so far (Sanchez, 2011b; Gebauer & Luedeling, 2013; Gebauer *et al*., 2016).

As anthropogenic pressure on the tree is expected to increase with the international approval of baobab fruit pulp as a food ingredient (Buchmann *et al*., 2010; Sanchez 2011a), the tree has become a priority species for domestication (Gebauer *et al*., 2016; Jenya *et al*., 2016; Munthali *et al*., 2016; Sanchez 2011b; Venter *et al*., 2013). Widespread decline of baobab populations would have negative effects on African societies with locals losing nutritional, pharmaceutical and income-generating resources (Sanchez *et al*., 2011a). While baobab and its products have the potential to become a 1bn USD industry that could generate significant foreign exchange reserves for African countries (Sanchez 2011b), exploitation of the species might not be sustainable in the long run (Sanchez 2011a) in absence of sustainable harvesting and propagation practices as well as of targeted breeding operations to maintain baobab populations. Solving these problems would secure a continued supply of baobab products to foreign and domestic markets (Jenya *et al*., 2016; Munthali *et al*., 2016).

Malawi has emerged as a prime target country with baobab populations exhibiting the highest densities found in sub-Saharan Africa (Sanchez 2011b) and a high genetic diversity across populations available for setting breeding targets (Munthali *et al*., 2016). The country is also a forerunner with regard to the development of the baobab fruit pulp processing sector (Meinhold *et al*., 2018) but the nascent industry is held back by poor raw material (fruits and fruit pulp) quality, unsustainable fruit harvesting and collection on open access lands by mostly informal actors such as local villagers as well as little to no utilisation of waste and side stream products of baobab processing (Dohse, 2013; Meinhold *et al*., 2018). During the last decade, commercial baobab demand in Malawi has substantially increased (Sanchez, 2011a), increasing the risk of overexploitation of available natural stands: land-use types and ecosystems conducive to baobab regeneration are not common and existing populations are not healthy, with a considerable share of trees being weakened by excessive debarking or diseased (Sanchez, 2011b) and the absence of propagation efforts by local people (Sanchez, 2011a).

The current low level of baobab cultivation, the time-lag for planted trees to grow to fruit-harvestable size at 8-23 years (Jenya *et al*., 2016) as well as the limited focus of processing and valorisation efforts on fruit pulp are major obstacles for efficient commercialisation of this underutilised resource (Meinhold *et al*., 2018). Other baobab products such as leaves and root tubers which are consumed in parts of Africa either regularly or in times of food scarcity (Gebauer *et al*., 2016) showcase the potential of value addition for baobab seedlings that do not bear fruits yet. People are more likely to appreciate and preserve baobab trees if it has various uses (Sanchez *et al*., 2011a), which will reduce the pressure and may lead to regeneration of baobab stands in the long run. While the seeds, their oil and the leaves of the tree are widely consumed and their properties have been intensively studied (DiLucchio *et al*., 2018; Kaboré *et al*., 2011; Komane *et al*., 2017; Zahra'u *et al*., 2018) little is known about the root tubers, their development or their phenology (Gebauer *et al*., 2016).

Based on the observation that baobab seedlings develop a tuber-like taproot which can be consumed as a vegetable (Kaboré *et al*., 2011), our study aimed at investigating the yield potential of baobab root tubers from five different Malawian provenances and the influence of planting distance on root development in a field trial at two locations. Additionally, leaf number and shoot weight/length were investigated to assess baobab's potential as a dual-use crop; the leaves yield suitable animal fodder. Shoot and leaf development have been found to vary with seedling provenance and growth conditions (Sanchez, 2011a; De Smedt *et al*., 2011). Findings may help inform selection of provenances or morphotypes suitable for domestication and widen public perception of the species through a potential entrepreneurial and nutritional use that does not rely on adult trees, but instead on planting of new seedlings, which thereby might indirectly promote baobab conservation. To this end, we investigated the financial potential of the cultivated baobab tuber and leaves as a marketable vegetable for subsistence farm households.

2 Materials and methods

2.1 Study site description

Malawi is a sub-Saharan African country with subtropical climate with a warm-wet season from November to April that receives 95 % of annual precipitation and a dry season that is divided into a cool and a hot segment. Climate differences in the country are not related to latitude but to altitude, with heavily forested, sub-humid highlands, as opposed to the dry or semi-arid lowland savannahs (Sanchez, 2011a).

The northern study site was located in Mzuzu, Malawi (Supplement: Fig. S1) on the grounds of Mzuzu University's Forestry Department nursery (11°25'14.9" S and 33°59'33.6" E) at an altitude of 1,270 m a.s.l. in the centre of an agricultural region focusing on tea, coffee and rubber cultivation and which is dominated by wooded, hilly terrain and a cold climate in the dry season (Briggs, 2016). Mean annual temperatures range from 13.5 °C in the cool dry season to 24 °C in the wet season and the area receives a mean annual rainfall of 1250 mm. The forest department nursery is a clearing surrounded by indigenous woodland and shaded during morning and afternoon hours. Soils in the area are highly weathered sandy ferrisols or ferralitic soils which are common in humid regions in Malawi (Lowole *et al*., 1983).

The southern study site was located in the dry lowland at the southern lake shore and belongs to the village Nkope Chiwalo (14°12'57.92" S and 35°1'49.78" E). Average altitude in this area is between 200 and 700 m asl with a mean annual temperature of between 22 °C and 25 °C and an annual mean precipitation of 760 mm. The predominant soil types are alluvial calcimorphics, vertisols and hydromorphic soils (Sanchez, 2011b). The plot was previously cultivated with cowpeas (*Vigna unguiculata* L.) and had to be cleared from perennial weeds before use.

Soils at both study sites were analysed for soil pH, soil organic matter (SOM) content, total nitrogen, extractable potassium and phosphorus contents and soil texture at Luyangwa Agricultural Research Station in Mzuzu (see Table 1).

Table 1: *Soil properties as measured at Luyangwa Agricultural Research Station in Mzuzu, Malawi.*

Plot site	*pH (H_2O)*	*SOM (%)*	*N_t (%)*	*P (µg/g)*	*K (mg/L)*	*Sand %*
Mangochi	5.56	0.7	0.04	21.3	29	66
Mzuzu	5.30	0.3	0.03	32.1	58	67

Data are means but no standard deviation was given. SOM = soil organic matter; N_t = total nitrogen

Over the course of the experiment, minimum and maximum temperature, rainfall and humidity were recorded daily in Mzuzu by an automatic weather station operated by the Mzuzu University Geography Department (see Figure 1). Measurements were taken every day at 8 am and 2 pm and averaged. The same data were obtained from the District Agricultural Development Office (DADO) in Mangochi for the Mangochi site (see Figure 2).

2.2 Trial design

2.2.1 Selection of plant material

In 2016, seeds were collected from trees in Karonga (KA), Chikwawa (CK), Mangochi (MH), Neno (NN) and Salima (SA, Supplement Fig. S1) and were subsequently stored in labelled plastic bags, mentioning the tree's fruit shape and

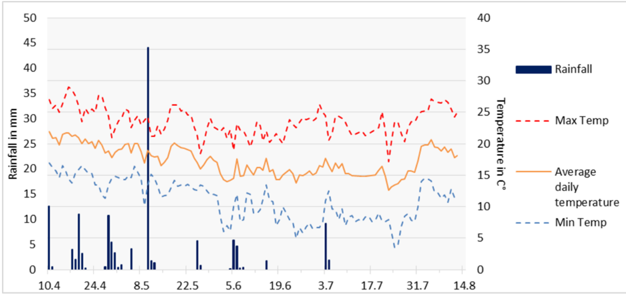

Fig. 1: *Meteorological data from the Mzuzu University weather station from 10th of April 2019 to the 14th of August 2019, the time course of the field trial.*

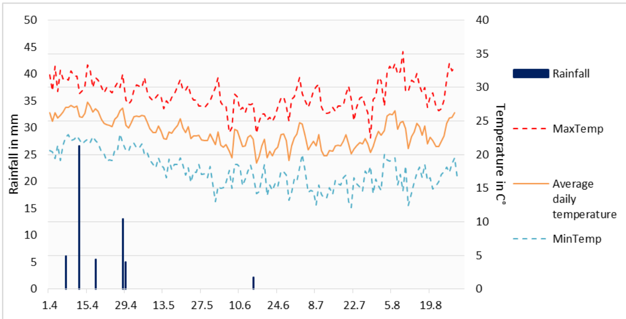

Fig. 2: *Meteorological data from the Mangochi District Agricultural Development Office from 1st of April 2019 to the 31st of August 2019. The trial lasted until 8 September, but no current weather data could be obtained for the additional 8 days until the last harvest.*

tree provenance, in dark and dry conditions. For the experiments, from 15 bags per provenance, 20 seeds were randomly selected, yielding 300 seeds per provenance. Selected seeds were then nicked with garden secateurs in order to enhance germination by enabling water imbibition. All viable nicked seeds from a single provenance were then pooled in a bag from which seeds were randomly picked for planting. This process was repeated for all five provenances.

2.2.2 Experimental setup

We used a field trial in which seeds were planted on 28 ridges with three replicates per provenance and planting distance and 18 seeds per replicate to allow for weekly harvests from May 2019 until September 2019. At each study site, an area of roughly 14 m by 7 m was cleared and ploughed with hack shovels to a depth of 20 cm. The loosly upturned soil was then used to form 28 ridges with a height of 20 cm, a width of 40 cm and with 20 cm wide furrows between them. In Mzuzu, a drainage ditch was dug around the perimeter with shape of a vertically inverted ridge. In Mangochi no drainage ditch was dug. Due to the higher temperatures in

Mangochi, straw was used as mulching material to reduce evapotranspiration after irrigation.

Treatments consisted of sowing seeds of the five provenances at three different planting distances: 10 cm, 20 cm and 30 cm (see supplementary material for experimental design). The three replicates per provenance and planting distance were always planted in adjacent ridges, with seeds with 10 cm and 20 cm distance between them, planted in a single ridge in order to effectively make use of the available space and labour force. Seeds were sown by manually digging a small hole roughly 3 cm deep and placing the nicked seed inside on its flat side, then covering the seed with soil. Seedlings were irrigated using watering cans with tap water until germination. From then on, watering was done in the furrows in order to promote root development. Irrigation was performed when soil felt dry at a depth of 5 cm, using 3 watering cans at a rate of 15 L per ridge. In Mzuzu, this meant watering every 4-5 days, whereas in Mangochi a more frequent irrigation regime had to be performed, with the seedlings being initially watered twice a day in the morning and in the evening. Subsequently, when seedlings were one month old, irrigation frequency was reduced to one time per day with a leap day every two days, when no irrigation at all was performed.

2.2.3 *Cultivation*

Seedlings in Mzuzu were fertilised with a granular N:P:K fertiliser (8:18:15) on 15^{th} of May because they were deemed nutritionally deficient, judging by their stunted growth and pale leaf colour. Fertiliser granules were applied by pushing four granules at 4 cm distance at 90° angles around each seedling into the soil to a depth of 0.5 cm. The Mzuzu seedlings were also sprayed with a combination of an insecticide (Fipronil, Farmers Africa) and a fungicide (Dithane M45, Southern Ag) against leaf damage by caterpillars and sudden fungal infection by an unknown species, respectively, on May 23^{rd} and again on June 12^{th}, using a hand sprayer. Caterpillars were further removed manually when encountered during daily and weekly check-ups throughout the experiment. Seedlings in Mangochi were sprayed with an infusion of Neem leaves using a hand sprayer following an aphid infestation on the 23^{rd} and 26^{th} of May.

2.2.4 *Data collection*

Seedlings in Mzuzu were planted on the 11^{th} of April. Total germination was monitored every day until 30 days after planting. Seedlings were considered germinated once the hypocotyl hook had breached the soil surface. A first harvest was done 6 weeks after planting on the 24^{th} of May and every three weeks thereafter until the 14^{th} of August resulting in five harvests in total. Three seedlings were sampled with every harvesting round for each provenance and planting distance combination. Seedlings in Mangochi were planted on the 23^{rd} of April. There, the first harvest was performed on the 15^{th} of June. Germination was monitored every week. Plants were harvested biweekly the $8^{th}$of September, resulting in seven harvests in total. The provenance Salima at 20 and 30 cm planting distance failed to germinate in sufficient numbers and was excluded from all measurements.

With every harvest, the forward-most seedlings were harvested first. When, for a single provenance x plant distance treatment combination, two seedlings were at the same forward-most position on two adjacent ridges or replications, the one on the ridge with the lower replication number (one to three) was harvested first. This system was followed until three seedlings from each provenance *X* treatment combination were harvested. Seedling characteristics recorded were root and shoot fresh and dry mass (air-dried in labelled paper bags in a greenhouse propagator on a wire mesh for a minimum of two weeks). Furthermore, root and shoot length and developed leaf number were recorded. At harvest, roots were cut at the stem base and root length was measured from the cut to the extent of the longest fibrous root still attached to the main root. Shoot length was measured from the cut to the extent of the top-most leaf. Shoot mass (fresh and dried) included the stem with the leaves attached. Abscised leaves were included in the count of number of developed leaves but not in the shoot weight measurement. For the last three harvests in Mzuzu and all harvests in Mangochi, root tuber diameter was also measured at the thickest section of the tuber. Length and diameter measurements were taken with a digital calliper or a folding ruler. Weight measurements were taken with an HRB series precision balance (d = 0.1 g). Throughout the whole experiment, material, labour and financial inputs were recorded: man hours of required work for the field preparation, maintenance and treatment as well as chemical inputs, amounts of irrigation water and all associated costs of materials necessary for cultivation of the experimental plots based on local prices.

2.2.5 *Statistical analyses and methods*

Data were analysed with R Studio 3.5.3 (R Core Team, 2019) using the tidyverse (Wickham *et al.*, 2019), effsize (Torchiano, 2019) and car (Fox & Weisberg, 2019) packages. Graphs were generated using the Cairo Graphics Library for R (Urbanek & Horner, 2019). In order to obtain a single growth variable that could be subjected to factorial analysis, an estimate of the Mean Relative Growth Rate (mean RGR) was computed using the slope of the first-order regressions of the ln-transformed plant size data as described in Hoffmann & Poorter (2002). Mean RGR was computed for every measured plant characteristic (e.g. root length) individually. No between-site comparisons of plant growth data were performed due to abnormally weak development of the Mzuzu seedlings. Within-site comparisons between provenances and planting densities were carried out using one-way ANOVA for each plot separately. The assumptions for normal distribution were tested graphically using a Q-Q plot as well as the Shapiro-Wilke test using the pastecs package (Grosjean & Ibanez, 2018) in R. Homogeneity of variances was tested graphically with residuals vs. fitted plots as well as Levene's test. +/- Significance of differences between means was investigated with Tukey's HSD test using the multcompview package (Graves *et al.*, 2015) in R. Effect sizes were calculated as Cohen's d. Statistical significance was established at p-values < 0.05. All analyses were performed with a confidence interval of 95 %.

Profitability analyses were performed on Mangochi data using the assumption of a cultivation area of 100 m^2 and an imputed cost of family labour of 160 Malawian Kwacha (MWK) or 0.20 USD per hour based on the estimated opportunity cost of labour. Material input costs and depreciation for equipment were included in the profitability model. Local yam tuber and sweet potato leaf prices at the time of study in September 2019 were used to derive a price estimate for baobab root tubers and leaves, yielding 1,000 MWK or 1.25 USD and 600 MWK or 0.75 USD per kg tubers or leaves, respectively. Average baobab tuber and leaf yields after a 4–month growth period were calculated individually for three cultivation scenarios using the mean RGRs of root DM and leaf number of the respective treatments: planting at 10 cm, at 20 cm and at 30 cm planting distance. Profitability of all three scenarios was compared to the alternative of cultivating maize on the same area of land. Average maize yields for Malawi were obtained from Komarek *et al.* (2017) and a maize price was determined at 350 MWK/kg using IFPRI Malawi's Monthly Maize Market Report from December 2019 (IFPRI, 2019).

3 Results

3.1 Germination percentages

Final germination rates were determined at 30 days after sowing and were, on average, not found to be significantly different between sites. As planting density was regarded as having no effect on germination, germination percentages were only compared between provenances. All provenances had low germination rates (12-41 %) with Neno (NN), Mangochi (MH) and Chikwawa (CK) germinating at similar rates at both sites (Table 2). Karonga (KA) performed lowest in Mzuzu with only 16 % of planted seeds germinating but achieved the second-best germination percentage in Mangochi at 35 % while Salima (SA) performed lower in Mangochi than in Mzuzu with only 12 % of germinating seeds compared to 21 %, respectively. Average germination rates per plot were similar at 30 %.

Table 2: *Baobab seed germination percentages by provenance and trial site.*

	germination %	
Provenance	*Mzuzu trial site*	*Mangochi trial site*
Karonga (KA)	16^{a}	35^{a}
Salima (SA)	21^{ab}	12^{b}
Neno (NN)	36^{ab}	27^{ab}
Mangochi (MH)	34^{ab}	38^{a}
Chikwawa (CK)	41^{b}	33^{a}
Plot average	30	29

Superscript letters indicate significant ($p < 0.05$) differences between provenances.

Fig. 3: *Harvested baobab root tubers (125 days after sowing) with shoots still attached at Mzuzu, exhibiting different morphologies. Plants are horizontally aligned at shoot-root junction. Provenances from left to right: Karonga (KA), Salima (SA), Neno (NN), Mangochi (MH), and Chikwawa (CK).*

3.2 Root tuber development

Root tuber development in Mzuzu was minimal, with negative mean RGRs for root length in the 20 and 30 cm treatments and for root dry mass in the 10 cm treatment (Table 3). Root tubers were often thin, with a tuberous top

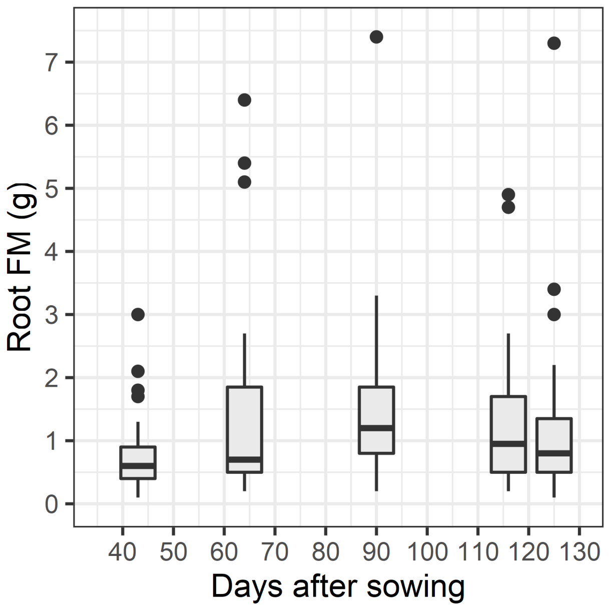

Fig. 4: *Boxplots of baobab root fresh mass (FM) measured at Mzuzu per harvest date. Data includes all provenances and planting distances.*

part and the rest of the tuber tapering off until fibrous, giving the roots a carrot-like appearance (Figure 3). Root fresh mass (FM) was only 1.1 ± 1.2 g on average at the final harvest (125 days after sowing/DAS), though individual plants could reach weights of > 5 g (Figure 4). Maximum and minimum root FM measured at the final harvest were 7.3 g and 0.1 g, respectively.

Root dry mass (DM) showed a similar development with an average of 0.27 g on the third harvest declining to 0.23 g at the final harvest. Average tuber diameter reached a maximum of 8 mm and declined to 7 mm on the final harvest, with the absolute maxima declining from 15 mm to 10 mm. While the root length growth was less affected, means stagnated around 110 mm with no developmental trend visible from the data after the third harvest. The average root length measured at the final harvest was 109 mm, with a minimum of 24 mm and a maximum of 223 mm. The regressive nature of the root development became apparent from the mean RGRs, which turned out negative for tuber diameter and root length parameters in the majority of treatments, even though the standard deviations point to a lack of a clear trend in the data (Table 3).

The seedlings in Mangochi developed better and thus gave higher root tuber yields, with the root FM reaching a maximum of 223 g at the final harvest for one root tuber (data not shown) and a clear, positive growth trend visible that started to level off at the 5th harvest (Figure 5) with the average root

Table 3: *Mean relative growth rate (RGR) ± standard deviations of baobab plant parameters in ‰ averaged by planting distance (Dist. in cm) and grouped by plot site.*

Variable	*Dist.*	*Mzuzu*	*Mangochi*
Root length	10	2.30 ± 2.97	4.88^{b} ± 2.21
	20	-0.96 ± 2.86	8.58^{ab} ± 3.04
	30	-3.08 ± 3.68	11.36^{a} ± 2.63
Shoot length	10	-6.20 ± 3.43	1.24 ± 1.27
	20	-3.58 ± 3.46	0.93 ± 1.72
	30	-5.11 ± 0.81	2.53 ± 1.40
Tuber diam.	10	0.09 ± 5.41	3.98 ± 4.27
	20	-1.93 ± 25.01	3.72 ± 2.54
	30	-1.43 ± 19.14	2.42 ± 2.12
Number of dev. leaves	10	1.98 ± 4.26	-2.21^{b} ± 2.31
	20	4.32 ± 3.88	0.11^{ab} ± 4.20
	30	0.65 ± 0.89	4.07^{a} ± 3.01
Root DM	10	-0.93 ± 8.19	18.19^{b} ± 6.27
	20	3.47 ± 8.79	26.14^{ab} ± 7.55
	30	3.39 ± 9.95	29.67^{a} ± 2.28
Shoot DM	10	-7.95 ± 4.56	7.08 ± 4.40
	20	-2.52 ± 3.17	7.89 ± 5.63
	30	-7.54 ± 4.53	12.59 ± 3.06

Superscript letters indicate significant differences ($p < 0.05$) between means of planting distances. DM = dry matter

FM increasing from 40 g at the 5th harvest (118 DAS) to 42 g at the last harvest (138 DAS).

Tuber diameter and root length data reflected the positive root tuber development as well, with tuber diameter reaching an average of 20 mm and the average root length reaching 242 mm at the last harvest. (Figure 6).

All plant root-related mean RGRs for Mangochi were positive, with the root DM increasing most steeply of all measured plant parameters (Table 3). Seedling size varied from a minimum length of 30 mm while the maxima fan out to 583 mm at the final harvest. The tuber diameter, while on average larger than in Mzuzu, showed a positive growth trend with the average increasing from 9 mm at the 1st (53 DAS) to 19 mm at the 5th harvest after which it no longer increased. The tuber diameter mean RGR is the lowest of all plant root-related growth parameters at Mangochi.

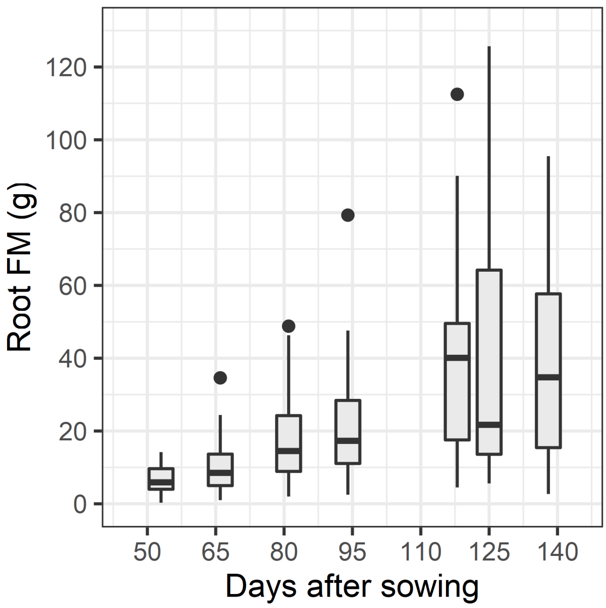

Fig. 5: *Root fresh mass (FM) of baobab seedlings measured at Mangochi displayed using boxplots grouped on a per-harvest basis. One data point (outlier) not shown (223 g at 138 DAS) for better readability of figure. Data shown includes all provenances and planting distances.*

Fig. 6: *Harvested baobab root tubers (125 DAS) with shoots removed at Mangochi showing different morphologies. Plants are horizontally aligned at shoot-root junction. Provenances from left to right: Karonga (KA), Salima (SA), Neno (NN), Mangochi (MH), and Chikwawa (CK).*

3.3 Shoot and leaf development

Seedlings in Mzuzu were infected with a leaf fungus of unknown origin and exhibited negative mean RGRs for the shoot FM and DM, but not for the number of developed leaves. Average shoot FM declined from 1.4 g at the 1st harvest to 0.5 g at the final harvest. The minimum shoot DM was 0.1 g and was 0.2 g on average at the final harvest. The number of developed leaves per seedling was 6 for almost all seedlings except for one seedling with 7 leaves. Average leaf number was 5.5 per seedling at the last harvest. The shoot length average decreased for all harvests after the 2^{nd}, starting at 92 mm at the first harvest with a slight increase to 96 mm on the 2^{nd} harvest but then declining to 63 mm on the 5^{th} harvest.

The Mangochi seedlings did not exhibit negative mean RGRs for all shoot-related growth parameters except for leaf number, which varied from -2.21 ‰ day^{-1} for the 10 cm treatment to 4.07 ‰ day^{-1} for the 30 cm treatment. We did not observe compound leaves during the experiment. Mean number of developed leaves per seedling was 7.1 and 8.1 at the first and final harvests, respectively. Mean shoot length was 155 mm at the first harvest and 166 mm at the last harvest. The maximum shoot length of 316 mm was measured at the last harvest. Average shoot FM grew to 8.1 g at the last harvest. While small individuals with shoot FM $\leq$ 2 g were still present at the last harvest, shoots with FM $\geq$ 10 g were more frequent. Average shoot FM decreased after the 5^{th} harvest, when it was 8.3 g. Mean shoot DM was 2.1 g at both the fifth and final harvests.

3.4 Effect of planting density and provenance on plant relative growth rates

No significant influence of seedling provenance was found for all measured plant parameters. Provenance had no significant influence on the mean relative growth rates of any plant parameters of seedlings in Mangochi either. No significant interactions between provenance and planting distance was found for both sites. While no significant effects on RGRs were found for planting density in Mzuzu, there was a trend for the mean RGRs of the root length and root FM where the seedlings planted at 30 cm distance performed better than the ones planted at 10 and 20 cm distance (Supplement Table S1). Mean relative growth rates of Mangochi seedlings' root length, number of developed leaves and root DM, showed significant differences between planting densities (Table 3). Mean RGR of root length of seedlings planted at 30 cm distance performed significantly better than seedlings planted at 10 cm distance with a positive trend with increasing planting density treatments (Figure 7a). Effect size (Cohen's d) was -2.63, meaning the 30 cm treatment had a positive effect on the root length mean RGR. Mean RGR of the root DM showed a similar pattern with the 30 cm treatment significantly outperforming the 10 cm treatment (Figure 7b). Root and shoot FMs were not significantly different between planting distances. Also the mean RGR of the number of developed leaves in the 30 cm treatment significantly outperformed that of the 10 cm treatment (Table 3). Both 10 and 20 cm treatments exhibited negative mean RGRs for leaf number and shoot length in the dataset of KA and CK provenances (data not shown), meaning that shoot development was decreasing on average over the cultivation period, which was not observed in the 30 cm plant distance treatment for any plant parameter measured.

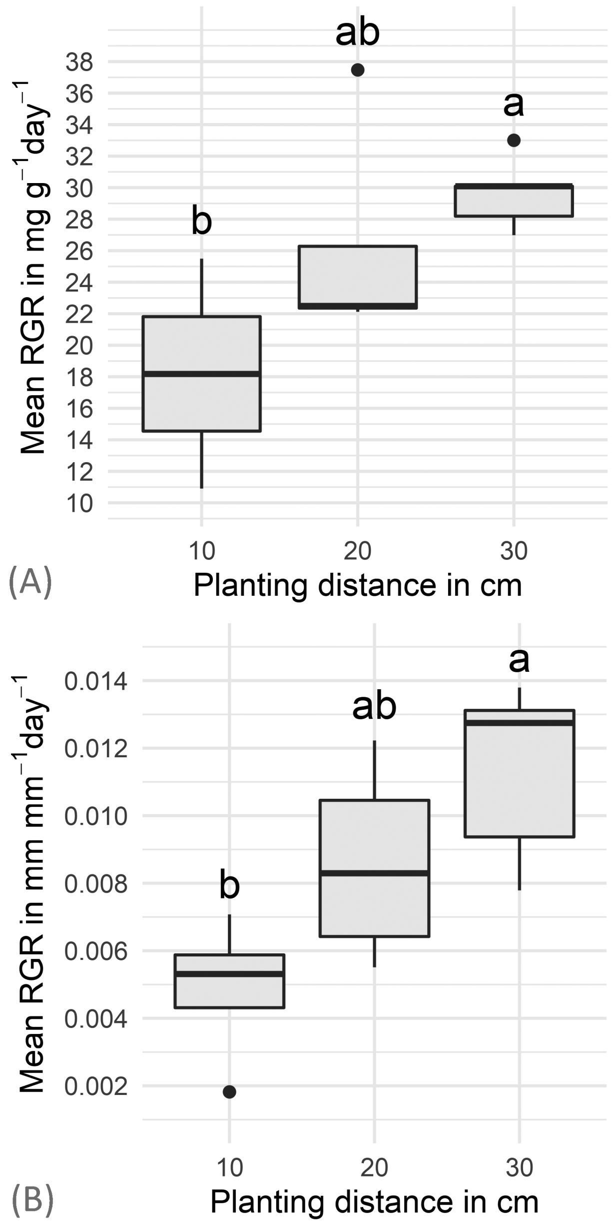

Fig. 7: *(A) Mean relative growth rates (RGRs) of root dry mass (DM) of baobab seedlings in Mangochi by planting distance. Letters above boxplots indicate significant ($p < 0.05$) differences. (B) Mean RGRs of the root length of seedlings in Mangochi by planting distance. Letters above boxplot indicate significant differences.*

3.5 *Profitability analysis*

Even though a 30 cm planting density seemed to indicate stronger growth in Mangochi, the profitability analysis resulted in a narrow win for the 10 cm planting density scenario, as it allowed three times the amount of plants to be cultivated in the same area. Cultivating triple the amount of plants increased the total input costs by 12 % and 24 % compared to the 20 cm and 30 cm planting densities respectively, especially the cost of manual labour due to the increased time needed to pre-treat and plant the seeds. The projected yield potential for the 30 cm scenario was 4.5 t root tubers per hectare and 240 kg leaves per hectare, and the resulting net benefit per 100 m² of land amounted to 9,725 MWK or 12 USD per harvest cycle of 16 weeks. The 10 cm scenario yielded 5.9 t root tubers and 560 kg leaves per hectare, with a larger net benefit per 100 m² land unit of 10,358 MWK or 12.78 USD, resulting in a 6 % increase in profits compared to a planting distance of 30 cm. Assuming 3 rotations per annum, this could accumulate to an annual income per 100 m² of 31,074 MWK or 38.36 USD. Net incomes in all scenarios were better than in the alternative scenario of maize cultivation: the low price of maize in Malawi and the average yield of 1.8 t per hectare employed in that scenario only generated 7,200 MWK in revenue and its total net benefit per 100 m² of land amounted to -29,000 MWK or -35.80 USD when the imputed cost of family labour was included.

4 Discussion

Germination rates observed in Mzuzu confirm earlier results from Munthali *et al.* (2012a), where seedlings from CK significantly outperformed seedlings from KA. Previous studies on baobab germination found that baobab seed source was more important than seed age in explaining viability (Venter & Witkowski, 2011). In an earlier experiment conducted at Mzuzu University, much higher baobab germination rates were found after using the same pre-treatment method and baobab seed stock from the same Malawian provenances (Munthali *et al.*, 2012b). However, in the latter experiment, seeds were planted in a greenhouse during the rainy season and experienced more favourable growth conditions. This suggests that the phenology of individual baobab trees is highly specialised, with the same tree possibly behaving differently under different ecological conditions. This is compounded by the fact that germination rates of provenances varied with the site they were planted in. A way to circumvent this inherent variability in germination and phenology could be vegetative propagation, which proved to be successful in two thirds of both top-cleft and side-veneer grafted baobab seedlings (Jenya *et al.*, 2016).

Mzuzu seedlings failed to reach their genetic potential, with leaf abscission and disease leading to an early growth stop for many seedlings. Orwa *et al.* (2009) described baobab as highly sensitive to waterlogging and frost. Stunted growth and early onset of fungal diseases can be caused by a combination of adverse weather conditions and improper seed pre-treatment. In our experiment, seed coats may have been excessively removed and may have led to sudden water imbibition, thereby shocking the seed embryo. Seed coat removal might also have damaged the cotyledons, providing a gateway for early pathogen infection. Gebauer *et al.* (2016) identified pests and diseases of baobab as one of the current knowledge gaps in the research of this species. While the negative mean RGRs of shoot length, FM and DM can be explained by leaf loss and necrosis, losses in average root FM and DM starting from the 4^{th} harvest on, indicate that the seedling had used resources stored in the taproot in order to survive and possibly to flush new leaves. The role of the taproot as a survival organ for first-year droughts has been suggested by Van den Bilcke *et al.* (2013) as well as Venter & Witkowski (2013).

DiLucchio *et al.* (2012) found that the baobab leaf phenology is not only influenced by water availability, but also by day length. This means that shade of the trees surrounding the experimental plot as well as reduced sun hours due to the winter season could have further stunted leaf development and precluded regeneration, as leaf area in baobab is regulated to be maximal during the rainy season, maximizing sunlight exposure (DiLucchio *et al.*, 2012; Van den Bilcke *et al.*, 2013). These findings illustrate the importance of seedling phenology and the planting time in baobab cultivation, as water stress (excessive as well as insufficient moisture) and temperature or day length strongly influence seedling development, especially when it has been initially weakened or damaged through improper seed pre-treatment.

The Mangochi seedlings grew faster and had root and shoot FM averages measured at the final harvest that were respectively 47 times and 15 times higher than in Mzuzu. While we did not find significant effects of provenance on seedling development, Munthali *et al.* (2012a) found significant influences of seedling provenance on multiple growth parameters like seedling height, tuber weight and diameter. Sanchez *et al.* (2011b) did not find significant influence of provenance on RGRs of total plant biomass, even though biomass allocation to different plant parts was influenced by seedling origin. Seedlings with provenances from wetter areas invested significantly less in their taproot than those with drier provenances. Seedlings from drier provenances invested less in shoot development. Munthali *et al.* (2012a; 2012b) obtained similar results, showing genetic adaptation of the root tuber to drought and showcasing domestication potential as a large variety of heritable growth traits enables an efficient selection of suitable or outstanding cultivars for propagation. The magnitude and phenology of these effects differ between baobabs with Eastern and Western African provenances as well, with East African origins being more susceptible to drought stress and early leaf shedding (DiLucchio *et al.*, 2012), which is indicated by some provenance $\times$ treatment combinations exhibiting negative mean RGRs for shoot length and leaf number in Mangochi over the growth period, namely KA 10 and KA 20 as well as CK 20. Some authors report that morphological variations between baobab seedlings of different provenances do not become significant until a seedling age of 18 weeks (Sanchez *et al.*, 2011b), which indicates that the experiment in the present study might have been too short to yield reliable results on provenance-individual morphologies or significant interaction effects between provenance and planting distance. Still, our results confirm that baobab seedlings are root-succulent and mainly invest in taproot development in their first year of life, which is indicated by the larger mean RGR of the root DM than that of the shoot DM and by the finding that most seedlings develop a taproot.

The effect of planting distance on the mean RGRs of root DM and root length leads to significant differences in harvestable tuber mass over the same timeframe: extrapolating from a starting root DM of 0.6 g 70 days into the future results in a final root DM of 2.3 g versus 5.0 g for the 10 cm and 30 cm planting density treatments, respectively. Using the average water content of baobab root tubers of 90 % calculated by Van den Bilcke *et al.* (2013) for seedlings of similar age, this would imply a possible net gain of roughly 30 g root FM per plant. Planting density therefore is a significant agronomic factor of baobab cultivation. A larger planting distances might decrease competition for water between the seedlings, and promote root as well as shoot development. The number of leaves was significantly affected by the planting distance as well, even though the effect translates into ± 1 leaf over the 80 day measurement period only and can be considered of no relevance to baobab cultivation. Additionally, the number of leaves does not represent the number of leaves present at harvest, only the number of leaves developed until that time.

Profitability analysis revealed the possibility of generating financial returns while decreasing labour and material inputs and requiring fewer plants to be cultivated through increased planting distance. While planting at 10 cm was financially the best scenario, total net benefit was only 0.78 USD higher per land unit and cropping season compared to the 30 cm scenario while requiring triple the amount of plants and 1.5

times the amount of man hours to cultivate. Thus, particularly during the agricultural peak season, when baobab seedling cultivation competes with other farming activities for scarce labour, the higher planting distance is recommended. Planting at a higher planting distance may also yield indirect benefits to plant growth such as lower risk of pest and disease incidence, and slower exhaustion of soil resources. These benefits may also lead to lower costs and time investment for pest control and soil management, further cushioning the loss in absolute yield compared to a smaller planting distance-scenario. No markets for baobab root tubers exist yet, so prices were based on a similar produce by look and weight and may be overestimated, given that yam is an energy-rich starchy tuber with nutritional significance as staple food while the baobab root tuber is not. On the other hand, given their vegetable-like appearance and nutritional qualities, these tubers may have some potential as fitness food for health-conscious consumers in urban upmarkets. Kamanula *et al*. (2018) found high levels of magnesium in root tubers, but other nutritional information on the root tuber is still scarce. The results presented in this study give reason to be hopeful for economically feasible baobab cultivation being attractive to smallholder farmers, potentially contributing to improving the livelihoods and nutritional status of participating communities.

5 Conclusions

It could be confirmed that root succulence in baobab seedlings is a common phenological stage that can be influenced by agronomic variables such as planting distance, even though seedling development varied highly between the two experimental sites. The latter highlights the importance of choosing seedling provenances best adapted to the local ecology before considering cultivation conditions, such as planting density, fertilisation regime or harvest time. Our economic analysis employing the measured growth parameters indicates that despite a trade-off between increased yield and planting distance, baobab cultivation can be profitable. As the growth parameters were recorded in a dry-season growth period, planting in the rainy season may further increase yields and economic benefits of baobab cultivation. Considering the stagnant or even declining trend in baobab population numbers available for selection of suitable ecotypes and domestication, there is need for sustainable and efficient cultivation methods in order to facilitate baobab's potential use as a food crop and reduce overexploitation. Choosing a higher planting distance could contribute to both objectives by optimizing management and inputs while concurrently using fewer seeds and offering increased yield per plant. Further research is recommended to i) quantify the effect of planting distance and other factors such as watering regime, soil salinity and soil nutrition in combination with different rooting media on root tuber development on baobab tuber yield and nutritional composition in a baobab-appropriate nursery as well as to facilitate the development of best practice guidelines for on-farm baobab cultivation of baobab; ii) develop efficient and effective seed pre-treatment that does not harm the seed embryo while providing proper germination conditions; iii) identify and establish pest control strategies in baobab cultivation; and iv) further assess the economic potential of baobab root tubers in the food market.

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Conflict of interest

The authors declare that they have no conflict of interest.

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