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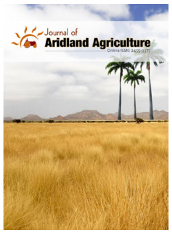

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Thermotolerance of various *Jatropha curcas* accessions to seasonal variations in the South East Botswana - A semi-arid country

Hilary Shoniwa*, Baleseng Moseki

Department of Biological Sciences, University of Botswana, Private Bag UB00704, Gaborone, Botswana

ABSTRACT

Thermotolerance is the ability of an organism to survive high temperatures. An organism's natural tolerance of heat is their basal thermotolerance. High temperatures are a common phenomenon in arid and semi -arid regions. Botswana is a semi-arid region where *Jatropha curcas* a plant well known for its medicinal and seed rich in oil for biodiesel uses. The study aimed to compare various *J. curcas* accessions' thermotolerance in this semi-arid region with a wide range of diurnal leaf temperatures throughout the year. Four accessions located in a field in the Department of Agricultural Research, Sebele, Botswana were studied. Measurements of photosynthetic rates, stomatal conduction, leaf temperatures, internal carbon dioxide, and vapour pressure deficit were performed diurnally in spring summer and autumn from 2015 to 2017 on various *J. curcas* accessions. Despite the interplay of the various parameters that influenced the photosynthetic performance of the accessions the impact of temperature was greatest. As a result of their higher photosynthetic activity the Ghana and Tlokweng accessions surfaced as more thermotolerant than the Tsamaya and Thabala accessions. In conclusion, as the Ghana and Tlokweng accessions appeared more thermotolerant than the Tsamaya and Thabala accessions the study recommends them to be incorporated into breeding programmes alongside other accessions with the ultimate objective of continuing to improve their photosynthetic activity.

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***Corresponding author:**
Hilary Shoniwa
E-mail: hilaryshoniwa@gmail.com

KEYWORDS: Thermotolerance, Photosynthetic rates, Stomatal conductance, Leaf temperatures, Internal carbon dioxide

INTRODUCTION

A plant that can survive high temperatures is described as thermotolerant. High temperatures are a common phenomenon in arid and semi -arid regions. Botswana is a semi-arid region where *Jatropha curcas* is widespread. Photosynthesis is one of the most important biological processes on earth as it is the source of energy for almost all living organisms. Photosynthesis takes place in the chloroplasts. It is a complex process taking place in two phases. The light phase absorbs energy from the sun and the dark phase uses the energy to assimilate CO_2 into the system for the production of sugars.

Temperature is an important limiting factor in photosynthesis. As one of the most important limiting factors of photosynthesis temperature is responsible for the geographical distribution of plants. Plants are therefore naturally subject to both spatial and temporal variation in temperature and light. The thermal optimum for C3 plants has been reported as ranging from 20-35 °C (Sage *et al.*, 2020).

Carbon metabolism and the photochemical processes in the thylakoid membranes are thought to be sites most sensitive to damage due to high temperature in chloroplasts (Hasanuzzaman *et al.*, 2013). High temperatures alter the structural organisation of the thylakoid membranes in the chloroplasts (Ashraf & Hafeez, 2004; Rodríguez *et al.*, 2005). In addition, high temperatures significantly decrease the activity of PSII (Hasanuzzaman *et al.*, 2013). Heat has a significant impact on the intercellular CO_2 concentration, leaf stomatal conductance, and leaf water status (Greer & Weedon, 2012). Another factor contributing to reduced photosynthesis that influences intercellular CO_2 is stomata closure under high temperatures (Ashraf & Hafeez, 2004). The decrease in the chlorophyll pigment is a consequence of lipid peroxidation of thylakoid and chloroplast membranes, as seen in sorghum under heat stress (40/30 °C, day/night) (Mohammed & Tarpley, 2010).

Most of the gas exchange between the atmosphere and the inside of the leaf is regulated by stomata. In order to meet photosynthetic demand and regulate leaf water loss, which affects evaporative cooling, nutrient uptake, and plant water status, stomatal behaviour is therefore crucial (Lawson *et al.*, 2010; Matthews & Lawson, 2019; Lawson & Matthews, 2020). Both internal leaf conditions and external cues cause stomata to open and close. According to Matthews and Lawson (2019), stomata typically open in response to high or increasing light intensity, low (internal) [CO_2], and low VPD, while closure is seen in response to the opposite conditions. Saibo *et al.* (2009) associate depressed photosynthetic rates with declining transpiration rates.

The study aimed to compare the basal thermotolerance of various *J. curcas* accessions growing under field conditions in the South East of Botswana, a semi-arid country, as the seasons varied over a period of three years.

MATERIALS AND METHODS

Study Site

The study was carried out at an agricultural field located in the Department of Agricultural Research, Sebele, Botswana (Tominaga *et al.*, 2014). It is a semi-arid area with a wide range of diurnal temperatures throughout the year. The average precipitation in this area is below 490 mm annually (Tominaga *et al.*, 2014). Precipitation occurring from October to March accounts for almost 100% of the annual rainfall (Tominaga *et al.*, 2014). Summer temperatures range from 15 °C in the morning to over 40 °C at midday and winter temperatures range from 3 °C early morning to 25 °C in the afternoons (Tominaga *et al.*, 2014). The soils are reddish brown are of the Rendzic Leptosol type. They are poor soils with high aluminium and iron content consisting of silt and clay (Tominaga *et al.*, 2014).

The field was established in 2011 from seedlings planted from the seed of various *J. curcas* accessions collected from different areas of Botswana (Tsamaya from the north, Thabala from the central region and Tlokweng from the South East region). One of the accessions was obtained from Ghana. The experiment was conducted in April 2015 to May 2016. The plants were grown in an area of 0.5 ha with a spacing of 2m x 2m between the plants.

Experimental Design and Treatments

The field experiment was laid out in a randomized block design with five replications. The treatments were four *J. curcas* accessions namely; Tsamaya, Thabala, Tlokweng, and Ghana. These accessions were randomly selected from several parts of the country and the accession from Ghana was regarded as the control, since it has been widely studied.

Gas Exchange Measurements

Gas exchange rate (μmol CO_2 $m^{-2}s^{-1}$), measurements were determined using a portable photosynthesis system (LICOR 6400XT equipped with a LED 2x3 cm leaf chamber, LICOR USA). The following variables were evaluated: photosynthesis (A), stomatal conductance (gs), transpiration (E), leaf temperature intracellular carbon dioxide (Ci). The CO_2 concentration inside the chamber, air and temperature varied depending on the environmental conditions. The ratio of instantaneous water use efficiency (A/E) was calculated using the measured values of A and E. Measurements were taken once a month seasonally on fully expanded tagged at the 5th or 6th node as follows: 2015 or year one (2015-2016 spring [October and November] summer [December January and February] and autumn [March and April]; 2016 or year two (2016-2017 spring [October and November] summer [December January and February] and autumn [March and April]; and 2017 or year three (2017-2018 spring [October and November] summer [December January and February] and autumn [March and April]. Measurements were determined diurnally three times 0600 h-0700 h recorded as 0700h, 1200-1300 h recorded as 1300 h also referred to as midday and 1700 h-1800 h recorded as 1800 h also referred to as late afternoon. Each day measurements were taken on the same leaf.

Data Analysis

The above experiments were carried out seasonally over three (2015, 2016 and 2017) years as stated repeatedly as specified for each separate experiment. The pooled data were presented and then assessed by ANOVA using Sigma Plot 11.0. Treatment means were compared using LSD at a probability level of 0.05.

RESULTS

The photosynthetic responses of the accessions in the three years covered in the study exhibit a dome shape, peaking in the season of 2016 (Figure 1). The spring of 2015 displays the lowest photosynthetic response followed by the autumn of 2017. The Thabala accession exhibits a conspicuously low photosynthetic performance compared to the other accessions while the Ghana and Tlokweng accessions display higher photosynthetic responses more frequently than the Tsamaya and Thabala accessions (Figure 1).

The seasons of 2016 display significantly lower leaf temperatures (Figure 2) in comparison to those of 2015 and 2017. In each year, the summers exhibited significantly higher ($P \leq 0.05$) leaf higher leaf temperatures than the spring and autumn seasons. The Tsamaya and Thabala accessions surface as having higher leaf temperatures more frequently than the Ghana and Tlokweng accessions (Figure 2).

Generally, air temperatures were lowest in 2016 and highest in 2017 and intermediate in 2015. Though in the autumn 2015 air tempratures were lower than those 2016 (Figure 3).

The diurnal leaf temperatures for the various *J. curcas* accessions peaked at midday and declined towards late afternoon. The Thabala and Tsamaya accessions displayed the higher leaf temperatures throughout the day compared to the Ghana and Tlokweng accessions (Figure 4).

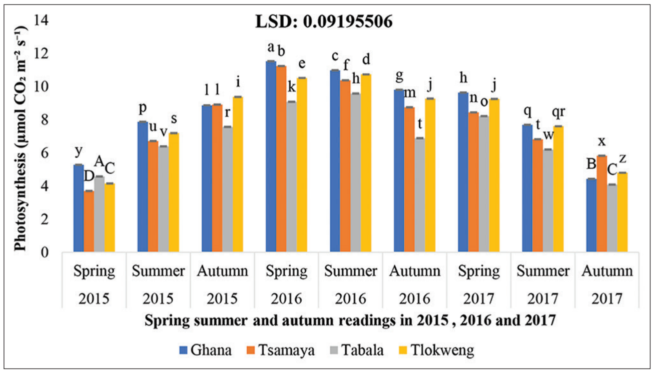

Figure 1: Seasonal (Spring Summer and Autumn) variations in the photosynthetic rates of *J. curcas* accession in 2015, 2016 and 2017 cultivated under field conditions in the South East District of Botswana, a semi-arid country. Means followed by different letters or numbers are significant at P ≤ 0.05 according to Fisher LSD. Bars represent SEM (n=5)

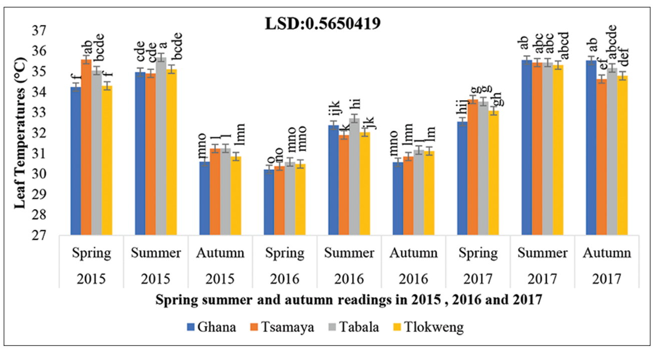

Figure 2: Seasonal (Spring Summer and Autumn) variations in the leaf temperatures of *J. curcas* accession in 2015, 2016 and 2017 cultivated under field conditions in the South East District of Botswana, a semi-arid country. Means followed by different letters or numbers are significant at P ≤ 0.05 according to Fisher LSD. Bars represent SEM (n=5)

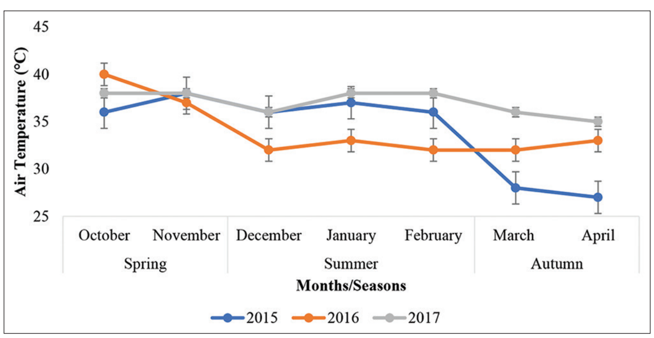

Figure 3: Air temperatures in the seasons of 2015, 2016 and 2017 (Data from Weather station in the Field at Sebele Department of Agricultural Research)

The internal carbon dioxide levels in the accessions were highest in the morning and declined throughout the day being lowest in the late afternoon (Figure 5). The Tsamaya accession exhibited higher internal carbon dioxide levels throughout the day and the Tlokweng accession exhibited the lowest. The Ghana and Thabala accessions were intermediate.

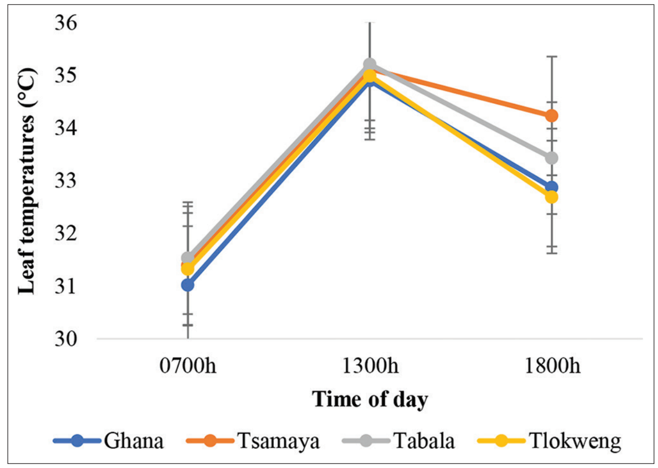

Figure 4: Diurnal leaf temperatures of the various *J. curcas* accession in 2015, 2016 and 2017 cultivated under field conditions in the South East District of Botswana, a semi-arid country. Bars represent SEM (n=5)

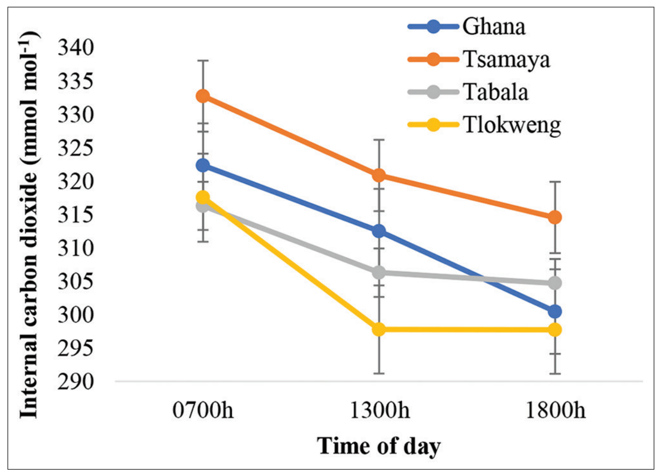

Figure 5: Diurnal internal carbon dioxide of the various *J. curcas* accession in 2015, 2016 and 2017 cultivated under field conditions in the South East District of Botswana, a semi-arid country. Means followed by different letters are significant at P ≤ 0.05 according to Fisher LSD. Bars represent SEM (n=5)

The photosynthetic rates and stomatal conductance of the various *J. curcas* accessions followed similar trends- midday depression and varying degrees of recovery by the late afternoon in each of the three years of the study (Figures 6a & b). The highest readings were recorded in 2016 for both photosynthesis and stomatal conductance. The year 2017 recorded the lowest midday readings for both photosynthesis and stomatal conductance but differed in the morning and later afternoon readings. The Ghana and Tlokweng accessions for both parameters performed better compared to the Tsamaya and Thabala accessions (Figures 6a & b).

The diurnal PPFD over the years peaked at midday and declined towards late afternoon (Figure 7). At each time of the day, the lowest PPFD was in the year 2016, and the highest varied between 2015 and 2017.

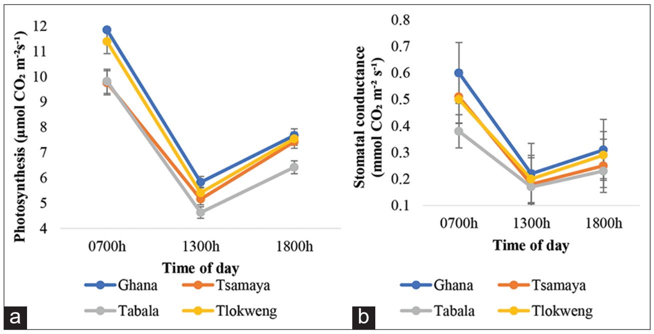

Figure 6: a) The average diurnal photosynthesis and b) the average stomatal conductance of the various *J. curcas* accession in 2015, 2016 and 2017 cultivated under field conditions in the South East District of Botswana, a semi-arid country. Bars represent SEM (n=5)

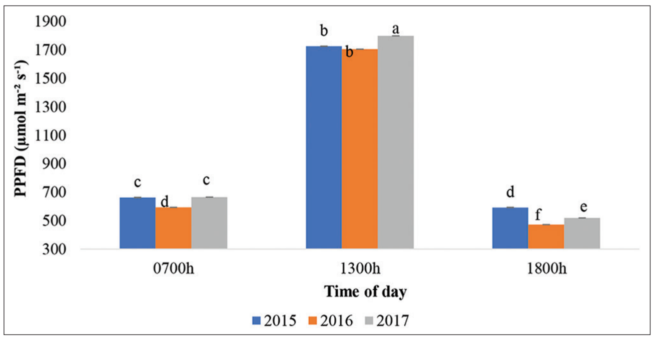

Figure 7: The diurnal variation of the photosynthetic photon flux density (PPFD) over three years, 2015, 2016 and 2017. Means followed by different letters are significant at P ≤ 0.05 according to Fisher LSD. Bars represent SEM (n=3)

DISCUSSION

The results show that both the diurnal and seasonal photosynthetic performance of the various *J. curcas* accessions over the three years of the study were higher in 2016 when leaf temperatures were lower (Figures 1 & 2). These 2016 results are in agreement with Carmo-Silva *et al.* (2012) who observed high photosynthesis on *J. curcas* plants free from heat stress. However, photosynthetic performance in 2015 and 2017 was lower, simultaneously with higher leaf temperatures (Figures 1, 2 & 3). Camejo *et al.* (2005) report that photosynthesis is a heat sensitive process that can be completely inhibited by heat. Camejo *et al.* (2005), Bagley *et al.* (2015) and Hatfield and Prueger (2015), report that extremely high temperatures negatively impact photosynthesis which is agreement with the results of this study. In addition to decreased photosynthetic performance research states that many physio-biochemical and molecular plant processes are dysfunctional at high temperatures. For instance, Cornic (2021) reports that plants' thermal optima are between 10 °C and 34 °C. Temperatures above the optimum are consequently associated with declining crop development and production (Ashraf, 2021). However, as the plants adapt to higher temperatures, net assimilation per unit leaf area decreases due to reduced CO_2 net absorption rate (Wang *et al.*, 2025). This adaptation may vary widely due to genetic differences across *J. carcus* accessions.

Plants are thought to be permanently damaged by high temperatures (Hasanuzzaman *et al.*, 2013; Nievola *et al.*, 2017), although they can undergo reversible alterations in growth and development when temperatures are moderate (Sharkey & Zhang, 2010). Though the general trend of the photosynthetic performance of the accessions is that the accessions exhibit a midday depression and recovery towards late afternoon (Figure 4a). In the autumn of 2017, the overall photosynthetic performance of the accessions declined in comparison to their summer performance showing no recovery in agreement with Hasanuzzaman *et al.* (2013).

The results show high PPFD (Figure 7) at midday which is consistent with Yu *et al.* (2009) who have pointed out that high midday PPFD inhibits photosynthesis. High temperatures and high light leading to increased vapour pressure deficit and stomatal closure ultimately depressing photosynthesis (Eamus & Jarvis, 2004; Oliver *et al.*, 2009; Fernandes-Silva *et al.*, 2016; Slot *et al.*, 2024). High temperature and an increase in vapour pressure deficit are among other causes that researchers say probably also contribute to depressed midday photosynthesis (Eamus & Jarvis, 2004; Oliver *et al.*, 2009). In the preceding discussions on the effects of heat on photosynthetic process the Ghana and Tlokweng accession surfaces as better performers than the Tsamaya and Thabala accessions.

Saibo *et al.* (2009) report that high temperatures caused stomatal closure leading to a decrease in internal carbon dioxide thus inhibiting photosynthesis. In the present study, the stomata did not close but conductance decreased significantly ($P \leq 0.05$) simultaneously reducing photosynthesis significantly ($P \leq 0.05$). The declines in photosynthetic responses can be linked to stomatal limitation (Figures 6a & b) precipitated by high leaf temperatures (Figure 2). These results are consistent with Eamus *et al.* (2008) and Oliver *et al.* (2009). There have however been conflicting results concerning this which suggest that as temperature increases so too does stomatal conductance (Schulze *et al.*, 1975; Urban *et al.*, 2017) others (Cerasoli *et al.*, 2014) found that temperature had no effect at all on stomata. Saibo *et al.* (2009) point out that stomata close in response to increase in temperature. In this study however stomatal conduction decreased but no stomatal closures were recorded. The results show that increasing leaf temperatures negatively influenced stomatal conduction photosynthetic rates and also transpiration. The results are consistent with Pompelli *et al.* (2019) who recorded a positive correlation of stomatal conduction with transpiration under high temperatures linked to water deficit. Over the years and in the seasons the Ghana and Tlokweng accessions are prominent in displaying higher stomatal conductance than the Tsamaya and Thabala accessions.

In the present study, at midday leaf temperatures reached their peak (Figure 4) leading to a reduction in stomatal conduction (Figure 6b) which caused a reduction in the internal carbon dioxide (Figure 5) that affected the photosynthetic rate (Figure 6a). However, as the day progressed though leaf temperatures decreased concomitant with increases in stomatal conduction and photosynthesis the internal carbon dioxide levels continued to decline. The implication is that at lower

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temperatures internal carbon dioxide is not limiting. Dos Santos *et al*. (2013) report that the negative correlation they recorded in their studies between internal carbon dioxide and photosynthetic performance suggests that the internal carbon dioxide was not limiting.

A look at air temperatures (Figure 3), leaf temperatures (Figure 2) and photosynthetic responses of the accessions (Figure 1) the Ghana and Tlokweng accessions appear more thermotolerant compared to the Tsamaya and Thabala accessions. In each summer, throughout the three years of the study, the Ghana and Tlokweng accessions generally exhibited lower leaf temperatures than the Tsamaya and Thabala accessions (Figure 2) yet performed better under the higher air temperatures. These results are consistent with Balfagón *et al.* (2022) who recorded in their work on citrus varieties that the variety Carrizo under high light and high temperature conditions exhibited low leaf temperatures which resulted in the variety performing better photosynthetically and producing more and healthier leaves than the variety Cleopatra. Carizzo was more thermotolerant than the variety Cleopatra as were the Ghana and Tlokweng accessions compared to the Tsamaya and Thabala accessions.

CONCLUSION

In conclusion, the photosynthetic responses of the accessions differed from season to season significantly influenced by air and leaf temperatures. The Ghana and Tlokweng accessions appeared to be more thermotolerant than the Tsamaya and Thabala accessions. These two accessions performed better at high air and leaf temperatures. Higher leaf temperatures influenced lower stomatal conductance which resulted in lower photosynthetic responses. The Ghana and Tlokweng accession can be recommended for growing in the Botswana semi-arid conditions, as valuable feedstock for the production of biodiesel, which is environmentally friendly, for soap production and shade around the village homesteads.

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