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Seasonal effect on *Moringa oleifera* gaseous exchange and water use efficiency under diverse planting densities

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Summary

The study on *Moringa oleifera* was conducted over twelve months during 2014-2015 to evaluate the impact of the growing season and varying planting densities on biomass yield and physiological attributes under dryland conditions. Trial was established at densities of 5000, 2500, 1667 and 1250 plants ha^{-1}, with eight replicates. The increase in planting density led to an increase in biomass production. The monthly and seasonal data collected showed significant differences in net photosynthetic rate, transpiration, sub-stomatal CO_2 and stomatal conductance. However, planting densities of *M. oleifera* had no significant effect on all the gaseous exchange parameters measured. The results further revealed that the amount of carbon dioxide assimilated by the tree is not attributable to photosynthetic and transpiration rates as well as stomatal conductance. Under water shortage condition and high temperature, *M. oleifera* used an adaptation strategy by reducing stomatal conductance and transpiration and hence increasing water use efficiency. *Moringa oleifera* thus has the ability to sequester carbon even under water stress conditions. The tree can therefore be recommended for planting at a relatively high density of 5000 plants ha^{-1} in many parts of Limpopo province where temperatures are favorable for improved farmers' livelihoods as well as for climate change mitigation.

Keywords: Biomass; climate change; monthly; *Moringa oleifera*; physiological response; planting density

Introduction

Moringa oleifera is a highly valued tree that is widely distributed in many countries of the tropics and subtropics. It is considered as one of the most useful trees, since almost every part of the tree is a valuable source of food, medication and industrial purposes (Morton, 1991; Foidl et al., 2001). *Moringa oleifera* is a fast growing plant tolerant to harsh climatic and environmental conditions where many agricultural plants would not survive, requiring only 400 mm of annual rainfall (Morton, 1991; Reyes-Sánchez, 2006; Pandey et al., 2011). *Moringa oleifera* trees can play a significant role in mitigating adverse effects of climate change, due to its ability to capture carbon (DABA, 2016). It also has the potential to improve the income and livelihood of smallholder farmers as well as nutritional needs of rural communities (Mabapa et al., 2017; Babu, 2000; Moyo et al., 2011).

Through observations, South Africa and other countries globally are already affected by severe negative consequences of climate change. This is particularly evident in the smallholder farming sector that relies on natural resources for production. Best practices of agriculture can contribute towards climate change mitigation and adaptation by adopting various agricultural management practices that could minimize adverse effects of unpredictable rainfall patterns as well as other extreme weather conditions (Hulme, 2005; Pareek, 2017). Pareek (2017) reported that various agricultural adaptation management practices are available to attenuate the effects of climate change on crop production. This include broader agronomic management strategies such as altering planting densities, row spacing, planting time as well as introducing new germplasms that are resistant to heat and drought stress. There is no information on literature regarding carbon sequestration through *M. oleifera* trees as influenced by varying plant densities in the South African context. It is known from the literature that *M. oleifera* has been described as a tree that can be grown in the drier ecological zones (Asante et al., 2014; Seresinhe and Marapana, 2011). However, no quantitative information is available in South Africa about the *M. oleifera*'s gaseous exchange response such as stomatal conductance, stomatal CO_2, transpiration and photosynthetic rate to planting density over the different seasons. This study was therefore established to evaluate the seasonal response of *M. oleifera* in terms of biomass yield and gaseous exchange under varying planting densities as a contribution towards climate change mitigation.

Materials and methods

Study location

The study was conducted over twelve months to cater for four seasons, summer (December - February), autumn (March - May), winter (June - August) and spring (September - November) during 2014 – 2015, at NTL Baraka Eco-Farming Organic Farm (23°57.691'S and 30°35.205'E), situated in Eiland. The farm is situated about 50 km on the eastern side of Tzaneen in the Limpopo province. The area is a tropical region and receives about 429 mm of rain per annum, with most rainfall occurring during mid-summer. The annual rainfall data were derived from the total monthly values for Eiland averaged in the past 7 years. The area received the lowest average rainfall (<0.5mm) in June and July; the highest in December and January of more than 120 mm in the past 7 years. The monthly temperature distribution shows that, the average maximum monthly temperatures for Eiland could rise above 31 °C, while minimum temperatures could range between 7 to 25 °C, during winter and summer seasons, respectively.

Experimental design, planting and management

A 60 m length and 40 m breadth demarcated area was prepared by conventional tillage using disk ploughing, followed by two disk harrowing and manual digging of shallow holes for planting.

The experiment was laid out in a two factor (months and plant spacing) factorial Randomized Complete Block Design (RCBD) with eight replicates. The blocks were divided into four plots where treatments were placed. The treatments consisted of 12 months: May'14, June'14, July'14, August'14, September'14, October'14, November'14, December'14, January'15, February'15, March'15 and April'15 as well as four levels of intra-row spacing: D1= 1 m, D2= 2 m, D3= 3 m and D4= 4 m, with a uniform inter-row spacing of 2 m, giving total populations of 5000, 2500, 1667 and 1250 plants ha^{-1}, respectively.

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Untreated seeds of *M. oleifera* were used for planting by placing 2 seeds per hole at a depth of 2 cm during December 2013.

Each plot measured 4 m × 12 m and plots were separated from each other by 2 meters walkways. Irrigation was applied for four hours twice a week using a micro jet irrigation system until the tenth week to encourage good tree establishment, after which the study was allowed to run under rainfed conditions. Eight weeks after trial establishment, plants were thinned out to the right densities, retaining only the healthier plants during the thinning process. Prior to data collection, the whole experiment was uniformly cut at a height of 50 cm aboveground and all foliage was removed but not weighed.

Leaf gaseous exchange and water use efficiency measurements

Leaf gaseous exchange measurements were measured monthly on a fully-expanded leaf on the abaxial side of three selected leaves per experimental unit, using a portable photosynthesis system (ADC Bio Scientific, UK). Monthly measurements were averaged for each season to come up with seasonal data. The photosynthetic rate (A), stomatal conductance (gs), transpiration rate (E) and sub-stomatal CO_2 (Ci) were simultaneously determined for each species using a non-destructive method. All the measurements were carried out under steady-state conditions in full sun between 10:00 am and 14:00 pm (Clifford et al., 1997). The instantaneous water use efficiency (WUE) which is defined as the ratio of photosynthetic capacity to the rate of transpiration was calculated for each density as A/E (Field et al., 1983; Rivas et al., 2013).

Plant Biomass determination

Leaf biomass was collected once from a net plot of 12 m^2 during harvesting in April 2015. The leaf yield (kg) was determined by separating the leaves from the petiole. The fresh leaf biomass was shade-dried at room temperature for 72 hours and later weighed using a battery-operated top loading weighing balance (RADWAG, W/C6/12/C1/R Model).

Statistical analysis

Data were subjected to analysis of variance using Statistix 10.0 to compare the response of *M. oleifera* planting density on measured variables. A significance level of $p<0.05$ was used for determining differences among the interaction of months and plant spacing on leaf gaseous exchange and water use efficiency. The differences among the obtained mean values of measured parameters were compared and computed by using Tukey's HSD test considering 5% probability level (Gomez and Gomez, 1996). Where significant F-values from density treatment effects were observed on biomass yield, means were separated by Least Significant Difference (LSD) at probability level of 0.05 (Gomez and Gomez, 1996). Correlation and regression analyses were performed using both Statistix 10.0 and Microsoft Excel, to determine the relationship between gaseous exchanges.

Results

Weather parameters of the study area

Data on weather parameters measured during the study and anomaly in rainfall distribution are presented in Tab. 1 and Fig. 1. Rainfall dropped during summer season (November - February) of 2014/15, whereby the rainfall was below 100 mm as compared to the past two years during which the amount exceeded 200 mm. The temperatures

Tab. 1: Total monthly rainfall (mm), mean minimum and maximum temperatures recorded between May 2014 and April 2015 at the study site.

Month/Year	Total monthly rainfall (mm)	Min Temp (°C)	Max Temp
May'14	0.00	10.29	28.06
June'14	0.00	6.29	26.23
July'14	0.51	6.19	24.79
August'14	8.38	8.31	26.41
September'14	0.51	12.37	30.15
October'14	25.91	15.26	29.48
November'14	13.97	18.99	30.39
December'14	95.49	20.40	30.94
January'15	17.26	21.39	31.91
February'15	99.31	21.06	32.41
March'15	12.18	19.37	32.47
April'15	41.15	16.65	29.42

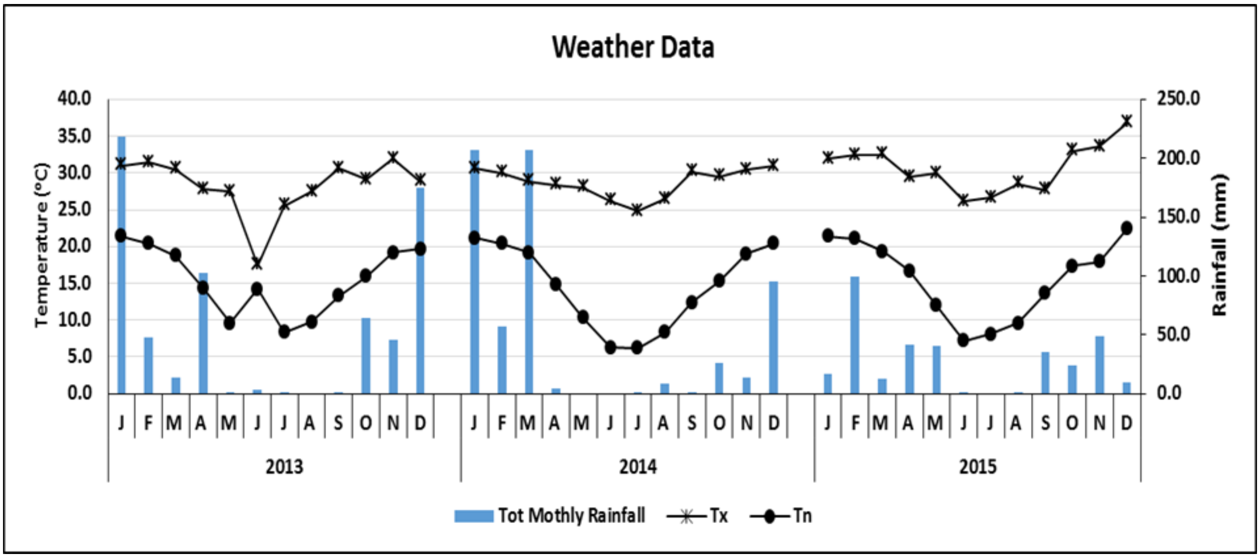

Fig. 1: Total monthly rainfall (mm), average maximum (Tx) and minimum (Tn) temperatures collected at Eiland from during the production seasons.

increased during summer season with the maximum temperature exceeding 32 °C (Fig. 1). The drought that was experienced during 2015 had a significant influence on rainfall anomaly. The accelerated heat accompanied by moisture deficit led to below average rainfall anomaly mainly during the year 2015 as compared with the years 2013 and 2014, in which the rainfall anomaly was above average in many instances, mainly during the rainy season (Fig. 2).

Monthly gaseous exchange and water use efficiency of *M. oleifera* as influenced by planting density

The monthly data collected showed highly significant differences in all gaseous exchange parameters and water use efficiency (Tab. 2). However, planting density of *M. oleifera* had no effect on photosynthetic rate, transpiration rate, sub-stomatal CO_2 and stomatal conductance as well as water use efficiency (Tab. 2).

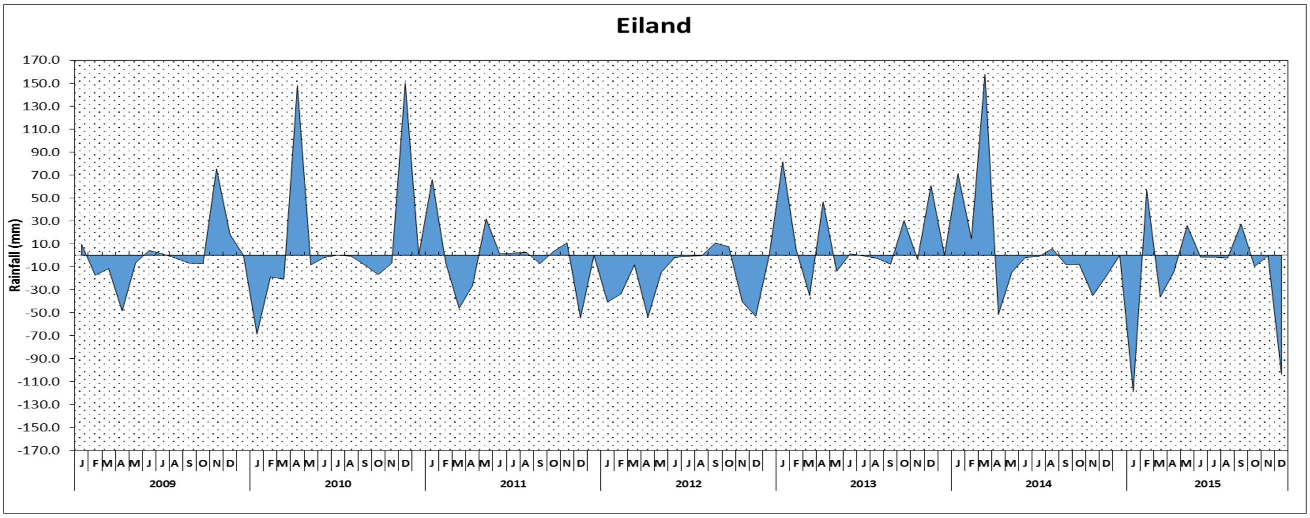

Fig. 2: Rainfall (mm) anomaly at Eiland as compared to long term average rainfall from 2009 to 2015.

Tab. 2: Leaf gaseous exchange parameters and instantaneous water use efficiency of *M. oleifera* as influenced by month and planting density.

Treatments/Factor	Transpiration rate (E) mmol m^{-2} s^{-1}	Stomatal conductance (gs) mol m^{-2} s^{-1}	Photosynthetic rate (A) µmol m^{-2} s^{-1}	Sub-stomatal CO_2 (Ci) vpm	WUE inst µmol mol^{-1}
Month/Year					
May'14	2.88^{abc}	0.15^{b}	6.73^{bc}	276.91^{ab}	2.33^{cde}
June'14	3.49^{a}	0.09^{d}	6.73^{bc}	220.75^{bcd}	1.91^{de}
July'14	2.53^{bc}	0.07^{de}	10.65^{a}	133.38^{f}	4.37^{a}
August'14	2.46^{bc}	0.07^{de}	9.04^{ab}	152.12^{ef}	3.72^{ab}
September'14	3.14^{ab}	0.05^{fg}	4.31^{cde}	246.22^{abcd}	1.29^{e}
October'14	2.10^{cd}	0.19^{a}	8.96^{ab}	270.41^{abc}	4.29^{a}
November'14	2.19^{cd}	0.05^{ef}	5.54^{cd}	190.81^{def}	2.68^{bcd}
December'14	2.65^{abc}	0.07^{de}	5.85^{cd}	207.31^{cde}	2.38^{bcde}
January'15	1.47^{de}	0.03^{g}	3.46^{de}	195.53^{def}	3.40^{abc}
February'15	1.06^{e}	0.04^{fg}	1.76^{e}	297.03^{a}	2.16^{cde}
March'15	3.28^{ab}	0.13^{c}	8.98^{ab}	229.03^{bcd}	2.55^{bcde}
April'15	1.39^{de}	0.06^{ef}	4.667^{cde}	215.50^{bcde}	4.2659^{a}
Significance	***	***	***	***	***
Density (Plants ha^{-1})					
5000	2.29	0.08	6.57	221.75	3.24
2500	2.51	0.09	6.30	224.69	2.71
1667	2.30	0.08	6.09	213.10	2.83
1250	2.46	0.09	6.60	218.79	3.00
Significance	ns	ns	ns	ns	ns
Interaction (Month × Density)	ns	ns	ns	ns	ns

Significance levels: *P<0.05, ** P<0.01, *** P<0.05, ns: not significant. Means with different letters are statistically significant.

Seasonal effect on *M. oleifera* gaseous exchange

The seasonal effect significantly influenced all the measured gaseous exchange parameters (Fig. 3). Photosynthetic rate, stomatal conductance and transpiration rate were reduced during summer season, whilst the sub-stomatal CO_2 concentration increased during the same season. Furthermore, the photosynthetic rate and stomatal conductance were higher during winter season when temperatures were low. No significant differences in transpiration were found during winter, autumn and spring seasons, while sub-stomatal CO_2 was found not to change during the three seasons except in the winter season.

Correlations and regression of *M. oleifera* gaseous exchange parameters

Seasonal relationships between gaseous exchange are presented in Fig. 4. Transpiration rate and photosynthetic rate showed a strong positive relationship. A similar relationship was observed between stomatal conductance and photosynthetic rate as well as between stomatal conductance and transpiration rate (Fig. 4). However, sub-stomatal CO_2 had a negative relationship with photosynthetic rate, transpiration rate and stomatal conductance.

Biomass production of *M. oleifera* as influenced by planting density

Tab. 3 shows the effect of planting density on biomass production at harvest in April 2015. The planting density had a significant influence on both total and leaf biomass yields, where increasing planting density led to an increase in biomass yield. Leaf and total biomass yields had no significant difference at the densities of 1667 and 1250 plants ha^{-1}. Leaf biomass yield increased by 118.1 and 63.0 kg ha^{-1} at densities 5 000 and 2500 plants ha^{-1}, respectively, relative to a population of 1250 plants ha^{-1}. On the other hand, total biomass yield increased by 93.2 and 55.5 kg ha^{-1} at densities 5000 and 2500 plants ha^{-1}, respectively relative to a population of 1250 plants ha^{-1}.

Discussion

Weather parameters of the study area

During data collection between 2014 and 2015, the study area experienced extreme drought and high temperatures. A total rainfall of 432 mm was received during this period. It was observed from the 2014 and 2015 summer season, that Eiland received below average rainfall with the situation worsening during 2015 where the rainfall anomaly was greater than 100 mm below average. These data show the magnitude of abiotic stress experienced in the study area. Study by ANJUM et al. (2011), reported that environmental abiotic stresses, mainly drought, salinity and extreme temperatures could impair plant growth and development and as such limit the productivity of many agricultural crops.

Monthly gaseous exchange and water use efficiency of *M. oleifera* as influenced by planting density

The effect of planting density on gaseous exchange was not significant during the study period. However, there was noticeable significant effect on monthly gaseous exchange parameters. This might be due to variable monthly temperatures and rainfall which influenced

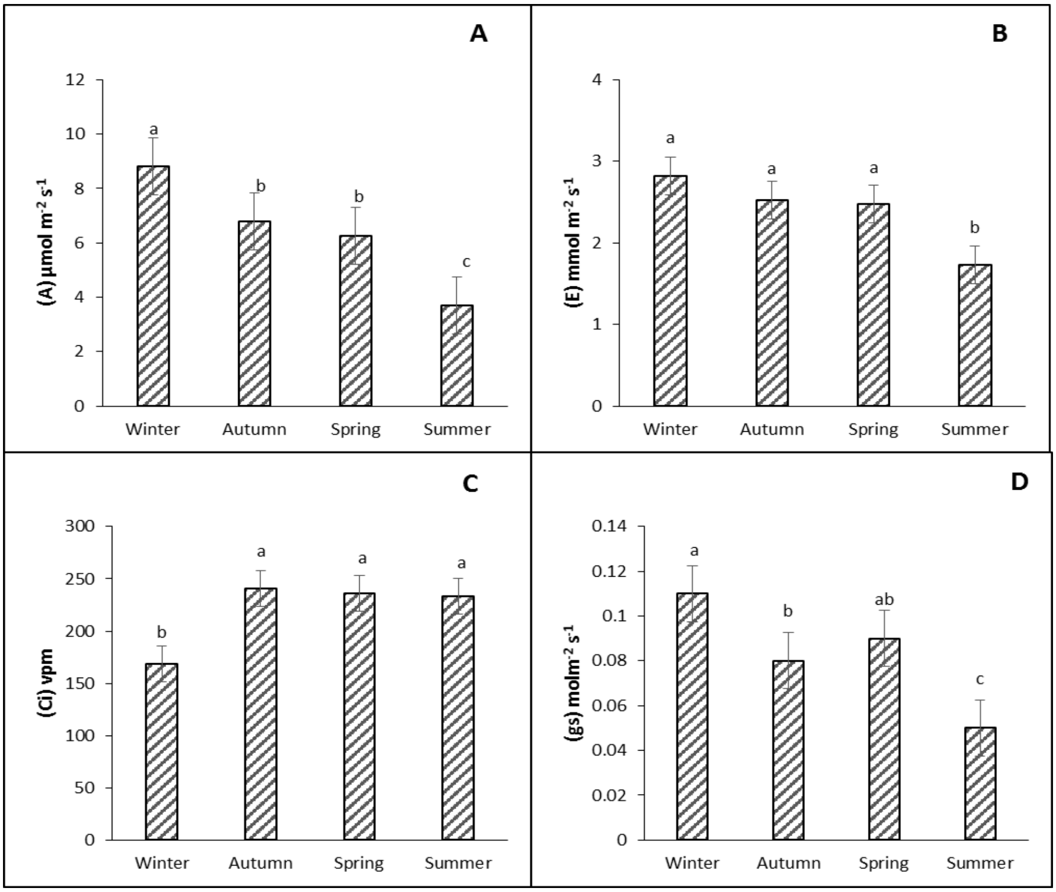

Fig. 3: (A) Photosynthetic rate (A), (B) Transpiration rate (E), (C) Sub-stomatal CO_2 (Ci) and (D) Stomatal conductance (gs) as affected by season irrespective of planting density. Means with different letters are statistically significant.

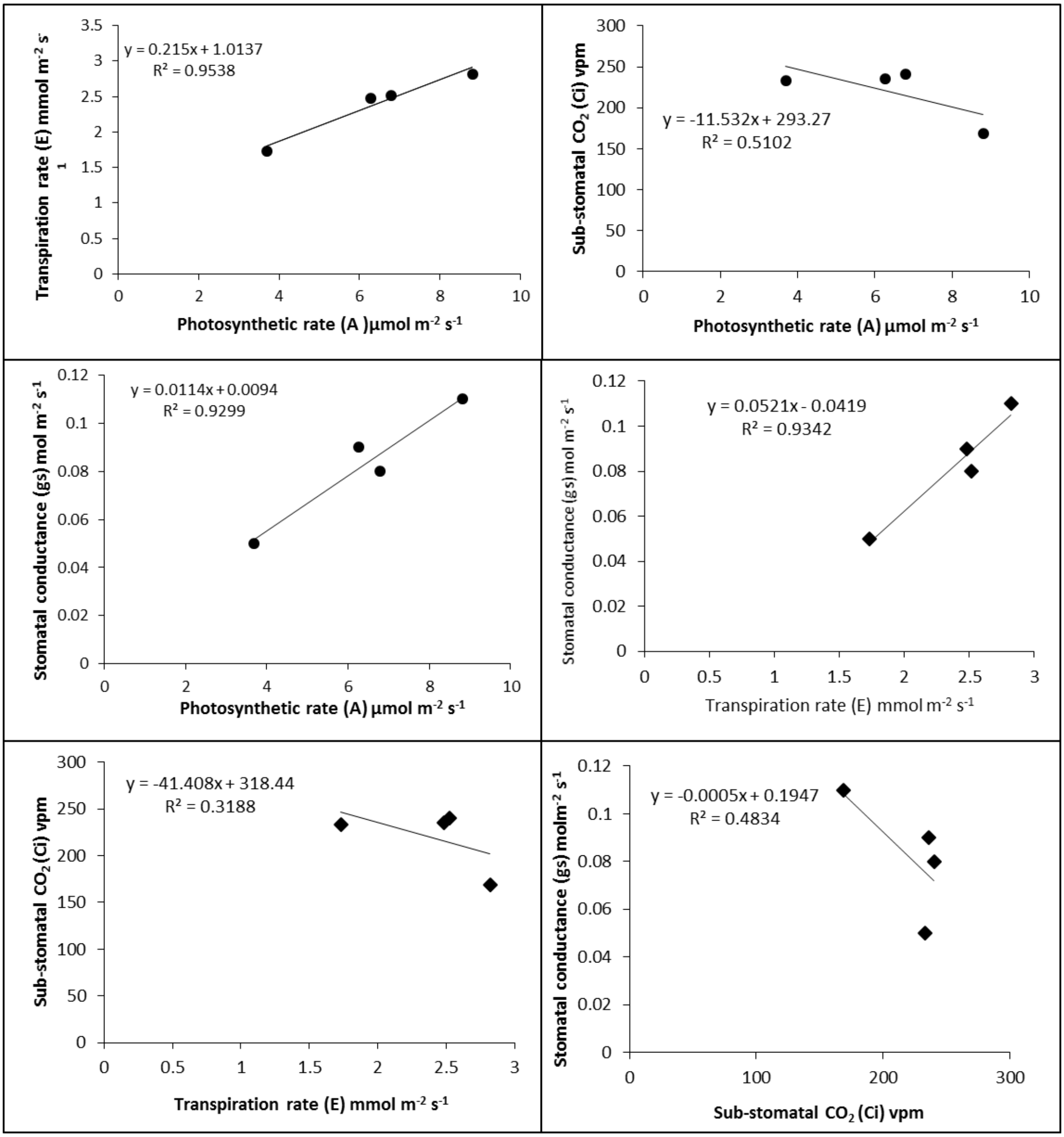

Fig. 4: Seasonal linear regression for *M. oleifera* gaseous exchanges.

Tab. 3: Biomass yield (kg. ha $^{-1}$) production of *M. oleifera* under different densities at Eiland during the harvest in April 2015.

Density (Plants ha^{-1})	Dry leaf yield (kg ha^{-1})	Total dry biomass yield (kg ha^{-1})
5000	447.91^{a}	1250.6^{a}
2500	338.80^{b}	1006.6^{ab}
1667	263.13b^{c}	805.2^{bc}
1250	205.33^{c}	647.3^{c}
P value	0.000	0.001
CV%	23.79	28.18
Significance (0.05)	**	**

Significance levels: *$P<0.05$, ** $P<0.01$, *** $P<0.05$, ns: not significant. Means with different letters are statistically significant.

the response of *M. oleifera* trees. Findings from this study revealed the survival mechanism utilized by *M. oleifera* to tolerate harsh environmental and climatic conditions. It was observed that *M. oleifera* does not rely on moisture from immediate rainfall; instead, the tree absorbs and stores water within the roots and other succulent tissues to utilize it when there is water deficit in the soil. This was evident because when rainfall was low or in deficit, *M. oleifera* still exhibited high transpiration rate which was influenced by high temperature. However, when temperature continues to rise under moisture shortage, *M. oleifera* showed adaptation strategy by also reducing the transpiration rate. These results concur with findings by RIVAS et al. (2013) who reported that *M. oleifera* can maintain a high leaf relative water content (RWC) under low soil moisture which helps to maintain cellular physiological processes and growth. Another study conducted on drought resistant bread wheat cultivars showed that, under drought stress conditions, the cultivars had more RWC (KEYVAN, 2010).

Plants use several physiological mechanisms that contribute to their drought tolerance. The first mechanism utilized by most plants, is through decreased stomatal conductance. When the resistance to H_2O is greater than that to CO_2, there is an increase in the water use efficiency (RIVAS et al., 2013; GALLE et al., 2011). Photosynthetic rate was reduced when there was water deficit in the soil and the plant itself and these response negatively affected water use efficiency (Tab. 1). Low moisture experienced until November 2014 and in January 2015 with increased temperature decreased stomatal conductance, photosynthetic rate and the extent of sub-stomatal CO_2.

Gaseous exchange activities, mainly photosynthetic rate, are among the primary processes to be negatively affected by drought and higher temperatures (CHAVES, 1991). Similar findings were reported by FROSI et al. (2017) on the response of two tropical evergreen species to drought stress. They found that gaseous exchange under severe drought stress showed a significant decrease with the average values of 0.01 (mol $m^{-2}s^{-1}$), 0.66 (mmol $m^{-2}s^{-1}$) and 0.4 (mmol $m^{-2}s^{-1}$) for stomatal conductance, photosynthetic rate and transpiration rate, respectively. RIVAS et al. (2013) also reported a drop in gaseous exchange due to water stress as compared to irrigated *M. oleifera* plants. When plants encounter water deficit, they respond by lowering stomatal conductance in order to reduce water loss which eventually results in decreased photosynthetic rate (MUNJONJI et al., 2016).

Seasonal effect on *M. oleifera* as influenced by gaseous exchange

This study revealed a significant influence of season on gaseous exchange of *M. oleifera*. The higher temperatures that were experienced during summer led to a decrease in photosynthetic rate, stomatal conductance, transpiration rate, while lower temperatures decreased the concentration of sub-stomatal CO_2. Under mild water stress, plants showed small decline in stomatal conductance which is a protective mechanism against stress, by allowing water saving and improving plant water use efficiency (CHAVES et al., 2009). Water use efficiency increased in stressed plants compared to irrigated *M. oleifera* plants. However, overtime, a rapid recovery from stress was observed on rehydrated plants through increased stomatal conductance (gs), net CO_2 assimilation (Pn), transpiration (E) and decreased water use efficiency (RIVAS et al., 2013).

A nursery study on irrigation interval revealed that irrigating *M. oleifera* seedlings at 8 days interval had a negative effect on gaseous exchange; however, the internal CO_2 concentration displayed significantly higher values as compared to shorter intervals (WAFA, 2015). The long taproot of *M. oleifera* and its succulent tubers enhances the drought resistance properties of the tree (JAGADHEESAN et al., 2011). Succulent plants often resist moderate water stress by storing water in their succulent tissues and utilizes it during the drought stress period (JAGADHEESAN et al., 2011).

Findings from this study showed that higher temperature favored assimilation of carbon dioxide by *M. oleifera* tree (Tab. 1). Results from current study concur with findings by NDUBUAKU et al. (2014) who reported that the higher rate of sub-stomatal CO_2 concentration is an indication that *M. oleifera* is able to partition carbon into different parts of the plants.

No literature is available on seasonal effect of *M. oleifera* on gaseous exchange. However, results from this study showed that higher temperatures, which prevail mainly in summer months, had a negative effect on transpiration, photosynthetic rate and stomatal conductance, but favored the accumulation of carbon dioxide in three out of four seasons of the year. During winter season, there was an excessive leaf fall and less soil moisture and this significantly affected carbon assimilation and plant growth. Under water stress conditions, plants generally produce a lower number of leaves, with general reduction in their size (JAGADHEESAN et al., 2011). MUHL et al. (2011) concluded that higher temperatures favor growth of *M. oleifera*, while low temperature leads to thickening of leaves which is symptomatic of an adaptation against temperature stress, resulting in reduced growth. Furthermore, JAGADHEESAN et al. (2011), reported that *M. oleifera* is sensitive to prolonged water stress which may result in a prominent decrease in cellular growth. Nevertheless, the tree is still able to produce satisfactory yields and high nutritional content from the leaves under such condition.

Correlation of *M. oleifera* gaseous exchange parameters

The findings from this study showed a strong positive relationship between photosynthetic rate and transpiration rate as well as stomatal conductance. Sub-stomatal CO_2 showed a moderate to weak negative relationship with photosynthetic and transpiration rates as well as stomatal conductance. Therefore, the amount of carbon dioxide assimilated by the tree cannot be determined by photosynthetic rate and transpiration rate as well as its stomatal conductance. The results from this study are in line with findings by ARAÚJO et al. (2016), who reported that the impairment of net CO_2 assimilation rate cannot be attributed to stomatal effects, since stresses did not reduce the intercellular CO_2 availability.

This study further showed a positive relationship between measured stomatal conductance and photosynthetic rate, whereby, the increase in stomatal conductance led to an increase in photosynthetic rate. This relation was mainly influenced by higher temperature and stored moisture in the plant. Similar results were reported by MUHL et al. (2011) who found out that the reduction in leaf stomatal conductance leads to a decrease in net photosynthetic rate. A study by RIVAS et al. (2013), further reported that *M. oleifera* can maintain high leaf relative water content even under drought stress and this helps the plant to maintain physiological processes and growth.

Leaf biomass production of *M. oleifera* as influenced by planting density

The effect of planting density on biomass was evident whereby the highest planting density of 5000 plants ha^{-1} produced the highest total leaf dry biomass yield of 1251kg ha^{-1}, with the leaf biomass yield of 448kg ha^{-1}, relative to lower planting densities of 2500, 1667 and 1250 plants ha^{-1}. Several authors have reported similar findings, where increase in planting density led to an increase in dry matter yield (FOIDL et al., 2001; SÁNCHEZ et al., 2006; BASRA et al., 2015). Planting density of 250 000 and 500 000 plants ha^{-1} established under dryland conditions had a total dry matter yield of 7.6 and 8.1 tons ha^{-1}, with leaf yield of 4.6 and 4.9 tons ha^{-1} (SÁNCHEZ et al., 2006).

Conclusions

In conclusion, this study showed that *M. oleifera* can survive harsh climatic and environmental conditions such as high temperatures and moisture deficit which commonly occur under the tropical climates. The study further revealed that planting density has no influence on various gaseous exchange parameters of *M. oleifera* tree. Under soil water deficit and high temperature, *M. oleifera* uses an adaptation strategy by reducing stomatal conductance and transpiration, thereby increasing the water use efficiency. The results also revealed that *M. oleifera* plant has the ability to sequester more carbon in its succulent parts throughout the growing seasons. Therefore, *M. oleifera* can be recommended for planting at a higher density of 5000 plants ha^{-1} in many parts of Limpopo province that experiences high temperatures, as the potential crop to contribute to climate change mitigation and nutritional security given its many nutritional attributes.

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