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Research Article

Improving *Jatropha curcas* L. photosynthesis-related parameters using poultry litter and its biochar

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Abstract

Poultry litter and biochar contribute to improved plant growth due to their high nutrient content. However, to the best of our knowledge, how incorporating poultry litter and its biochar in soil affects photosynthesis-related parameters of *Jatropha curcas* L. has not been reported. Therefore, a greenhouse pot experiment was conducted using a complete randomised design with three replicates per treatment to determine the effects of poultry litter, biochar pyrolysed at 350 °C and 750 °C at different application rates (0, 0.5, 1, 2, 3 gkg^{-1}) on *Jatropha curcas* L. photosynthesis parameters. The control plants recorded the lowest values of photosynthesis-related parameters compared to the treated plants except for water use efficiency. The study observed a significant ($P < 0.05$) increase in leaf surface area (1807 m^2, PL), dark-adapted F_v/F_m ratio, carbon dioxide uptake, and transpiration rate for PL and BC350 with increased application rates, compared to BC750 treatments. BC350 treated plants exhibited higher values (0.79) of Light-adapted Fv'/Fm'. The quantum yield of PSII electron transport displayed an increase with an application rate of 3 gkg^{-1}in PL (0.75) treated soils. Comparing organic amendments used, BC350 exhibited a significantly higher value of carbon dioxide uptake rate (2.67 $\mu mol\ m^{-2}\ s^{-1}$) and transpiration rate (2.20 $mmol\ m^{-2}\ s^{-1}$); however, WUE increased at an application rate of 3 gkg^{-1} in BC750 (3.8 $\mu mol\ (CO_2)\ mol^{-1}(H_2O)$) treated plants. The study results indicate that poultry litter and biochar produced at a lower temperature significantly improved photosynthesis parameters than biochar produced at a higher temperature.

Keywords: biochar; chlorophyll fluorescence; *Jatropha curcas* L.; photosynthesis parameters; poultry litter

Introduction

Poultry litter is one among the organic fertilisers used as an alternate source of plant nutrients and it has been deliberated for the past years to improve soil properties and enhancing crop quality and yields (Khan *et al.*, 2007; Bolan *et al.*, 2010; Revell *et al.*, 2012; Li *et al.*, 2018; van Zwieten, 2018; Bohara *et al.*, 2019). Moreover, organic fertilizers are an essential contribution of organic matter that improves soil's physical and chemical characteristics (Onwu *et al.*, 2018) and has a beneficial effect on increasing the soil's organic matter content (Scotti *et al.*, 2015). Furthermore, poultry litter has high NPK and microelements (Steiner *et al.*, 2010) essential for plant growth. Nonetheless, the study on the photosynthesis-related parameters concerning soil

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nutrient provision by poultry litter and its biochar has received less attention even though photosynthesis parameters are among the key factors contributing to plant growth and determining crop health. Additionally, the photosynthesis rate is a critical trait for assessing plant fitness and its general performance (Xu *et al.*, 2015).

Although poultry litter has been useful as a soil amendment, some studies (Chan *et al.*, 2008; Laghari *et al.*, 2016; Bohara *et al.*, 2019) have shown that organic waste conversion into biochar makes them even more effective than the feedstock. Biochar refers to the carbon-rich material produced from the slow pyrolysis (heating in the absence of oxygen) of biomass (Chan *et al.*, 2008). Biochar production provides a beneficial alternative method of improving poultry litter quality, ultimately improving plant growth (Xu *et al.*, 2015) and soil fertility (Roberts *et al.*, 2009). Comparative to feedstock, biochar resists decomposition, effectively sequestering carbon (Biederman and Harpole, 2013). It also acts as an absorber of ammonia (NH_3) and water-soluble ammonium (NH_4^+) and might reduce nitrogen losses through NH_3 volatilization (Steiner *et al.*, 2010). Additionally, it can also stimulate mineralization, supply Nitrogen (N) embodied in the biochar to biomass, reduce nitrous oxide (N_2O) emissions (Clough *et al.*, 2013) and modify soil N dynamics (Clough and Condron, 2010; Clough *et al.*, 2013). Though nutrients supply from either raw feedstock or biochar may determine crop quality and yields, a physiological process like photosynthesis contributes to plant health but relies on plant nutrients.

Plant nutrients supply maintains the synthesis of critical photosynthetic components (Kalaji *et al.*, 2018) that avoids photosynthetic apparatus disruption. Hence, it is mandatory to retain the required optimum soil nutrient content level to improve photosynthetic efficiency, including apparatus structure and functions and PSII photochemistry (Kalaji *et al.*, 2014). Besides, nutrient availability directly contributes to protein and chlorophyll synthesis (Chapin III, 1980), and the lower the nutrient supply, the lower the protein and chlorophyll synthesis rate, and the decline of light-saturated photosynthesis rates (Chapin III, 1980). For instance, leaf nitrogen concentration needs to be optimal as it is a component of photosynthetic enzymes and chlorophyll (Jongschaap *et al.*, 2007a). Nitrogen is one of the most biologically essential elements. It can regulate leaf steady-state photosynthesis through several strategies, such as a considerable investment of leaf N to Rubisco and its involvement in the stomatal opening (Xu *et al.*, 2015; Sun *et al.*, 2016). As a result, organic amendments are an alternate option to maintain plant nutrients where they are limited and improve photosynthesis-related parameters.

Jatropha curcas L. commonly called Jatropha (Leela *et al.*, 2011) or physic nut (Tatikonda *et al.*, 2009) is a multipurpose, low nutrient requiring perennial shrub that can survive in marginal areas (Laird, 2008; Blesgraaf, 2009; Agbogidi *et al.*, 2013) and semi-arid condition (Kumar and Sharma, 2008; Jongh and van der Putten, 2010; Geply *et al.*, 2011; Rajaona *et al.*, 2012). Hence, it is considered as a low nutrient requiring plant (Blesgraaf, 2009; Agbogidi *et al.*, 2013). Moreover, Jatropha has been documented as one of the emerging and potential renewable biofuel plant (Mahajan *et al.*, 2009; Dias *et al.*, 2012) with high potential for socio-economic development (Matsumoto *et al.*, 2014) where there is high price of inputs. *Jatropha* provides a viable alternative in semi-arid areas, contributing to increased resource use efficiency, erosion control (Dias *et al.*, 2012), local energy supply and rural development (Jongschaap *et al.*, 2007b). Furthermore, *Jatropha curcas* L. can be used to reclaim land, as a hedge, provide employment, improve the environment and enhance the quality of rural life (Openshaw, 2000). Under semi-arid conditions Jatropha curcas root system has a possibility for reclaiming marginal soils by recycling nutrients from deeper soil layers, providing shadow to the soil and thereby reducing risks of erosion and desertification (Jongschaap *et al.*, 2007b). Despite all the possible potentialities of growing Jatropha as a biofuel plant for either home consumption or commercial purpose it has not been economically viable mainly due to low seed yield, high cost of production, delayed production and uncompetitive, feedstock prices (Kgathi *et al.*, 2017).

The photosynthesis process is a significant target to increase crop biomass production (Evans, 2013) and yield potential (Qu *et al.*, 2017). The process is sensitive to environmental stresses (Kuhlgert *et al.*, 2016), mostly extreme temperatures and low water content that can be detrimental to the photosynthesis apparatus. It has been observed that studies regarding photosynthesis are mainly focused on factors like water stress

(Moseki and Dintwe, 2011); drought, and flooding stress (Osei-Bonsu *et al.*, 2016); atmospheric environment (Fukuzawa *et al.*, 2012) rather than organic amendments as a source of available soil nutrients. However, understanding poultry litter's influence and its biochar as a soil amendment on plant physiological properties will provide insights into the functional mechanisms responsible for the reported agronomic benefits of soil organic amendments.

The main objective of this study was to evaluate the effect of incorporating organic amendments on photosynthetic-related parameters of Jatropha *curcas* L. plant under greenhouse. Even though there are limited findings on this topic of research, the study hypothesizes that poultry litter and its biochar will significantly improve *Jatropha curcas* L.'s photosynthesis-related parameters due to their beneficial properties that improve soil properties, as previously mentioned in the above paragraphs.

Materials and Methods

Experimental design and treatments

A greenhouse experiment was conducted at the Department of Biology, University of Botswana, Gaborone, Botswana. Jatropha (*Jatropha curcas* L.) seeds were soaked in tap water for 2 hours to break dormancy before sowing them in moist growing media filled in seedling trays. After germination six weeks old seedlings were transplanted in pots. A randomised complete design was employed with three replication per treatment at different application rates of 0, 0.5, 1, 2, 3 gkg^{-1}. The experimental pots were previously filled with 6 kg of a homogenous mix of soil with three different organic soil amendments: (i) poultry litter (PL), (ii) poultry litter biochar pyrolyzed at temperatures of 350 °C (BC350) and (iii) poultry litter biochar 750 °C (BC750). Henceforth, poultry litter, biochar pyrolyzed at 350 °C, and 750 °C are referred to as PL, BC350, and BC750, respectively, in this study. The environmental conditions recorded were an average ambient temperature of 33.1 °C, 25% humidity, and plants were watered with 600 ml water on alternate days. The analytical results for soil properties classified the soil as sandy by using a Multisizer analyzer, a soil pH_{H2O} value of 7.77, and electrical conductivity of 169.6 dS/m were recorded from a soil solution (Ibitoye, 2006). The moisture content of 0.94 % was recorded after oven-dry analysis, and organic matter content of 0.37% with an oxidized organic carbon of 0.22% (Walkley and Black, 1934) was observed.


(A) (B) (C)

Figure 1. Biochar production equipment set-p (A), Poultry litter biochar produced at pyrolysis temperature of 350 °C (B) and Poultry litter biochar produced at 750 °C (C) pyrolysis temperature

Assessment of physiological parameters

Vegetative traits: Leaf surface area (m^2)

At physiological maturity, leaf area (m^2) was estimated based on a non-destructive method using leaf length and width dimensions (Montero *et al.*, 2000) measured with a simple ruler and recorded to the nearest 0.1 cm. Three leaves of each plant were selected and the length and width (widest part) were measured (length X width) and their average were multiplied with the total number of leaves of each plant as an estimated leaf surface area.

Chlorophyll fluorescence: Light-adapted Fv'/Fm' ratio, Quantum yield of PSII electron transport (ΦPSII) and maximum photochemical efficiency of PSII (Estimated from dark-adapted Fv/Fm ratio)

For chlorophyll fluorescence properties a Fluorometer Monitoring System (FMS) (Hansatech Instruments Ltd. Narborough Road, Pentney, King's Lynn, Norfolk, PE32 1JL, England) for measurements at physiological maturity. The PAR / Temperature Leaf-Clip was used for light saturation measurements under ambient light conditions, whereas, for dark adaptation, adaptation leaf clips were put in the middle part of the adaxial leaf blade of each Jatropha plant simultaneously for about 15-20 minutes before taking measurements.

Physiological properties: Carbon dioxide uptake ($\mu molm^{-2}s^{-1}$), transpiration rate ($mmolm^{-2}s^{-1}$), and water use efficiency ($\mu mol\ (CO_2)\ mol^{-1}(H_2O)$) were determined.

Infrared gas analyser (LCi Photosynthetic System; ADC BioScientific Ltd) was used. An 'Open System' configuration in which fresh gas (air) passes through the PLC (Plant Leaf Chamber) continuously took measurements. The obtained results for Carbon dioxide uptake and transpiration rate were used to express water use efficiency on a leaf basis, as follows:

Leaf water use efficiency ($\mu mol\ (CO_2)\ mol^{-1}\ (H_2O)$ = photosynthesis rate ($\mu mol^{-2}\ s^{-1}$)/transpiration rate ($mmolm^{-2}s^{-1}$) (1)

Statistical analysis

A completely randomized design was used with three replicates for each treatment. The reported data of photosynthetic parameters represent the mean +/− standard error. Mean variations were compared at P = 5%, with ANOVA test followed using the Tukey HSD test ($p< 0.05$) to test the significance of the difference between the treatments. IBM SPSS Statistic 22 software (IBM Corporation, Armonk, NY, USA) was used for performing the statistical analysis of the data.

Results

Leaf surface area

The response of leaf surface area (m^2) of *Jatropha curcas* L. to different application rates of poultry litter and biochar is shown in Figure 2. Generally, a significant increase of leaf surface area with application rates in response to organic amendments has been observed (Figure 2). The amendment of PL had a greater effect on leaf surface growth (1807 m^2) in comparison to BC350 (1099 m^2); however, BC750 (262 m^2) has shown less effect on leaf surface area. Furthermore, the application rate of 3 gkg^{-1} (PL) exhibited an increase in leaf surface area. A statistically significant difference was observed among PL (F (4, 10) = 13.60, $p < 0.001$) and BC350 F (4, 10) = 34.66, $p < 0.001$) whereas BC750 treated plants exhibit no statistical means difference ($p > 0.05$).

Chlorophyll fluorescence

Light-adapted Fv'/Fm' ratio:

The efficiency of excitation energy transfer to *open* PSII centers was estimated (Moseki and Dintwe, 2011). Table 1 generally indicates the highest light-adapted Fv'/Fm' ratio (0.79 ± 0.01) among the BC350 treated plants, significantly impacting BC750 treated plants contributing to the lowest ratio (0.65 ± 0.05). Among the organic amendments, only PL treated plants have a statistically significant difference (F (4, 10) =

4.43, $p < 0.05$). Based on the application rate, control plants recorded the lowest light-adapted Fv'/Fm' ratio than the treated plants. However, there was a slight decrease in the ratio for BC350 and BC750 treated plants at an application rate of 3 gkg^{-1}.

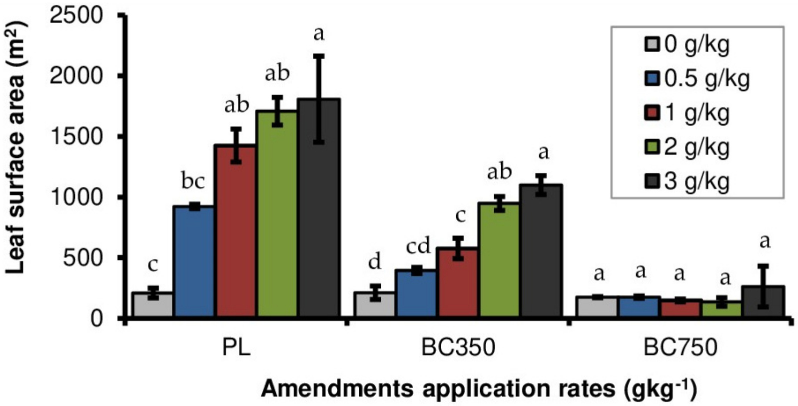

Figure 2. Leaf surface area (M ± SE) of genus *Jatropha* plants in soils treated with different organic amendments (PL, BC350 & BC750)

The trends reflect the variations in leaf surface area of *Jatropha* plants exposed to five different application rates (0, 0.5, 1, 2, and 3 gkg^{-1}). Means with the same letter are not significantly different (Tukey HSD test, $p < 0.05$).

Quantum yield of PSII electron transport (ΦPSII)

ΦPSII represents electron flow beyond PSII (Moseki and Dintwe, 2011), and it contains valuable information on the status of the photosynthetic apparatus. The findings of ΦPSII (Table 1) were generally lower for BC750 ranging from 0.58 ± 0.02 to 0.68 ± 0.01 compared to BC350 and PL treated plants. However, PL significantly shows the highest (0.75 ± 0.01) ΦPSII at an application rate of 3 gkg^{-1}. Moreover, the ΦPSII for BC750 at different application rates were statistically insignificant ($p > 0.05$).

Maximum photochemical efficiency of PSII

Estimates the efficiency of excitation energy capture by *open* PSII reaction centers and provides a rapid method for determining changes in the maximum quantum efficiency of PSII photochemistry (Moseki and Dintwe, 2011). As observed in the study results (Table 1), dark-adapted Fv/Fm ration for BC350 was higher (0.78 ± 0.01), with BC750 showing a lower ratio (0.62 ± 0.01) for treated plants. Although other treated plants recorded the lowest dark adaptation Fv/Fm ratio, increasing the application rate of organic amendments increased the dark adaptation Fv/Fm ratio in *Jatroph*a plants.

Carbon dioxide uptake, transpiration rate, and water use efficiency

Generally, the carbon dioxide uptake (Table 2) increased with increased application rates, and increased plant nutrient levels may have contributed to that. A significant decrease in carbon dioxide (CO_2) uptake of BC750 compared to PL and BC350 treated plants was observed in Table 2. Moreover, there was a slight decrease of CO_2 uptake with increasing application rate exhibited by PL (1 gkg^{-1}) and BC350 (3 gkg^{-1}). As for BC750 treated plants, CO_2 uptake significantly decreased with increasing application rates compared to the control. There was no statistical difference ($P > 0.05$) observed in plants grown in PL and BC750 treated soils.

The study results on transpiration rate displayed a significantly lower transpiration rate of BC750 treated plants with an increased application rate (Table 2). However, control plants have shown a higher transpiration rate than treated plants. The transpiration rate ranged from 0.44 ± 0.08 (No organic amendment) to 2.20 ± 0.13 (BC350 treated soils).

Table 1. Effect of poultry derived biochar on chlorophyll fluorescence parameters of *Jatropha* plant at different application rates

Application rate (gkg^{-1})	PL	BC350	BC750
Light-adapted Fv'/Fm' ratio			
0	0.66 ± 0.02^{b}	0.66 ± 0.06^{a}	0.56 ± 0.03^{a}
0.5	0.77 ± 0.01^{a}	0.79 ± 0.01^{a}	0.66 ± 0.04^{a}
1	0.72 ± 0.03^{ab}	0.76 ± 0.03^{a}	0.69 ± 0.01^{a}
2	0.72 ± 0.01^{ab}	0.79 ± 0.01^{a}	0.65 ± 0.05^{a}
3	0.74 ± 0.02^{ab}	0.73 ± 0.04^{a}	0.72 ± 0.03^{a}
p-value	**0.03**	**0.10**	**0.07**
Quantum yield of PSII electron transport (ΦPSII)			
0	0.62 ± 0.02^{b}	0.67 ± 0.03^{a}	0.58 ± 0.02^{a}
0.5	0.71 ± 0.01^{a}	0.70 ± 0.03^{a}	0.57 ± 0.06^{a}
1	0.72 ± 0.00^{a}	0.74 ± 0.02^{a}	0.56 ± 0.03^{a}
2	0.75 ± 0.02^{a}	0.74 ± 0.01^{a}	0.59 ± 0.03^{a}
3	0.75 ± 0.01^{a}	0.71 ± 0.04^{a}	0.68 ± 0.01^{a}
p-value	**0.001**	**0.45**	**0.23**
Maximum photochemical efficiency of PSII (Estimated-dark adapted ratio)			
0	0.69 ± 0.03^{a}	0.69 ± 0.01^{d}	0.61 ± 0.01^{b}
0.5	0.74 ± 0.01^{a}	0.75 ± 0.01^{c}	0.62 ± 0.01^{ab}
1	0.74 ± 0.01^{a}	0.73 ± 0.01^{bcd}	0.65 ± 0.02^{ab}
2	0.75 ± 0.02^{a}	0.78 ± 0.01^{ac}	0.67 ± 0.01^{a}
3	0.75 ± 0.01^{a}	0.76 ± 0.01^{abc}	0.68 ± 0.01^{a}
p-value	**0.14**	**0.001**	**0.02**

Table 2. The effect of poultry derived biochar on carbon dioxide uptake (µmol m^{-2} s^{-1}) and transpiration rate (mol m^{-2} s^{-1}) at different application rates of *Jatropha curcas* L.

Application rate (gkg^{-1})	PL	BC350	BC750
Carbon dioxide uptake (µmol m^{-2} s^{-1})			
0	1.66 ± 0.44^{a}	1.62 ± 0.14^{b}	1.84 ± 0.73 ^{a}
0.5	2.18 ± 0.50 ^{a}	2.17 ± 0.25 ^{ab}	1.62 ± 0.37 ^{a}
1	2.10 ± 0.27 ^{a}	2.56 ± 0.27^{ab}	1.83 ± 0.26^{a}
2	2.48 ± 0.15^{a}	2.51 ± 0.25^{ab}	1.28 ± 0.03^{a}
3	2.52 ± 0.16^{a}	2.67 ± 0.04^{a}	1.40 ± 0.37^{a}
p-value	**0.42**	**0.03**	**0.83**
Transpiration rate (mmol m^{-2} s^{-1})			
0	0.44 ± 0.08^{b}	0.88 ± 0.21^{b}	0.66 ± 0.23^{a}
0.5	1.02 ± 0.10^{ab}	1.41 ± 0.16^{b}	0.98 ± 0.02^{a}
1	1.30 ± 0.14^{ab}	1.48 ± 0.11^{b}	1.31 ± 0.18^{a}
2	1.35 ± 0.31^{ab}	1.31 ± 0.08^{b}	0.84 ± 0.14^{a}
3	2.06 ± 0.40^{a}	2.20 ± 0.13^{a}	0.64 ± 0.11^{a}
p-value	**0.01**	**0.001**	**0.62**

Carbon dioxide uptake means photosynthetic rate. Means denoted by a different letter indicate statistical differences between treatments (Tukey HSD, $p < 0.05$ test).

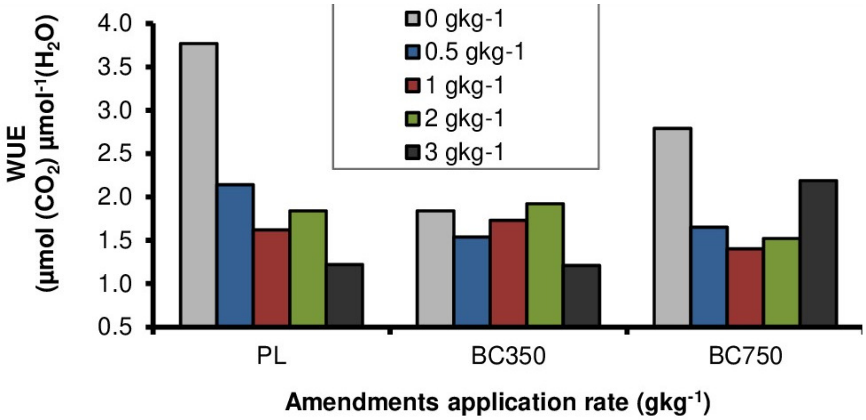

Figure 3. Water use efficiency (WUE) in µmol (CO_2) mol^{-1} (H_2O) of *Jatropha* plants treated with different soil organic amendment (PL, BC350, and BC750) considering three replications at five different application rates (0, 0.5, 1, 2, and 3 gkg^{-1})

Moreover, Figure 3 indicates high water use efficiency (WUE) for the control plants with a slight decrease in the application rate of organic amendments except for BC750 at an application rate of 3 gkg^{-1}. WUE decreased with the application rate for PL treated plants and for BC350 treated plants; however, there was a slight increase at an application rate of 1 to 2 gkg^{-1}. Further, plants grown in BC750 treated soil have higher water use efficiency values 2.2 µmol (CO_2) $µmol^{-1}$(H_2O) compared to PL and BC350 treatments and BC750 treated plants WUE ranges from 1.7 to 2.2 µmol (CO_2) $µmol^{-1}$(H_2O).

Discussion

Plant stress, either biotic or abiotic, is one of the main factors that may effectively trigger physiological disturbances in plants (Aucique-Perez *et al.*, 2020) due to its effect on chlorophyll parameters. For instance, the greater the plant stress, the fewer the open reaction centers available and the lower Fv/Fm (Murchie and Lawson, 2013) due to photoinhibition, which is brought about by a drop in maximum light absorption efficiency. Furthermore, deficiency of plant-available nutrients like manganese (Mn), potassium (K), molybdenum (Mo), nitrogen (N), magnesium (Mg), and calcium (Ca) are amongst the factors that influence the production of chlorophyll (Morgan and Connolly, 2013). Moreover, the lower plant available nutrients below the optimum requirement may cause stunted growth, death of plant tissues, and yellowing of plant leaves (Bottrill *et al.*, 1970) that will eventually depress the photosynthesis rate. For instance, leaf senescence is also influenced by N and is related to a decline in photosynthetic capacity. According to (Bottrill *et al.*, 1970), the resupply of nutrients in algae may result in the rapid recovery of photosynthesis, resulting from new chlorophyll. Hence available plant nutrients are required for increased plant productivity by improving the photosynthesis process that produces food (glucose) for the plants.

Leaf surface area

It is evident from the results of this study that organic amendments improved the leaf surface area of plants grown in treated soil compared to control plants (Figure 2). High nutrient content in PL (Bolan *et al.*, 2010) may have increased plant-available nutrients in the soil, thus improving soil fertility and promoting plant growth (Yu *et al.*, 2018). For instance, nitrogen strongly influences photosynthesis performance and biomass production (Zivcak *et al.*, 2014), the larger the leaf surface area absorbs maximal light (Moseki and Dintwe, 2011) that may contribute to a higher photosynthetic rate, ultimately improving plant growth. Additionally, other parameters that may be enhanced by the increase of poultry litter application rate are total chlorophyll content, carbon content, water holding capacity, and decreased bulk density of soil, all of which interplay to increase leaf area and total chlorophyll content of the plant (Enujeke, 2013). This is consistent with the findings of (Onwu *et al.*, 2018), who reported that increased poultry manure application significantly increases leaf area of physic nut because of sufficient nitrogen availability, which improves the vegetative growth of the crop.

Chlorophyll fluorescence

Plant stress because of limited available plant nutrients may have affected photosynthetic apparatus; hence lower light-adapted Fv'/Fm' ratio, ΦPSII levels, and dark adaptation Fv/Fm ration (Table 1) were observed on plants in soils treated with an organic amendment that has lower nutrient content (BC750). The Quantum yield of PSII represents electron flow beyond PSII (Dintwe and Moseki, 2011). In corroboration (Zivcak *et al.*, 2014), organic amendments contributed to the lower quantum yield of PSII (ΦPSII <0.8) value, and the decrease of ΦPSII may show that the proportion of energy harnessed by chlorophyll to stimulate the photochemical process is not efficiently used (Aucique-Perez *et al.*, 2020). Photosynthesis increases linearly with the increase in leaf N content (Bassi *et al.*, 2018). The lower the nitrogen content contributes to the lower the pigment-protein complexes in PSII, PSI, and light-harvesting complexes (Murchie and Lawson, 2013), later on, values may have contributed to the decreased ΦPSII levels in BC750 treated plants because of failure to transfer required excitation energy to PSII centers.

Furthermore, Table 1 displays the trend for light adaptation Fv'/Fm' ratio correlates with ΦPSII; explaining that the lower the light-adapted Fv'/Fm' ratio, the lesser the ΦPSII expected or vice versa. As for dark-adapted Fv/Fm ratio, lower values are linked with the results of light-adapted Fv'/Fm' and ΦPSII, including leaf nitrogen content. Based on Table 1, the lower dark-adapted Fv'/Fm' in plants treated with BC750 compared to BC350 and PL may be due to the effects of changing ΦPSII levels as they significantly affect dark-adapted Fv'/Fm'. The lower the ΦPSII levels, the lower the levels of dark-adapted Fv/Fm ratio, as the energy captured efficiency depends on the electron flow beyond PSII reaction centers. Lower chlorophyll molecules may have resulted in lowering energy molecules (ATP and NADPH), necessary for the dark reaction process.

Carbon dioxide uptake, transpiration rate, and water use efficiency (WUE)

As observed in Table 2 a lower carbon dioxide (CO_2) uptake rate in BC750 compared to BC350 and PL may be due to the inadequate energy absorbed by the chlorophyll molecules for photochemistry. Additionally, a decrease in the CO_2 conductance (Longstreth and Nobel, 1980) may have reduced the CO_2 uptake rate at low nutrient levels. Increased photosynthesis rate may have been significant due to the increased leaf surface area at the highest application rate for plants grown in soils treated with organic amendments (PL) with the highest nutrient content (Bolan *et al.*, 2010) necessary for biomass growth (Longstreth and Nobel, 1980).

Furthermore, increasing pyrolysis temperatures (Gai *et al.*, 2014) during biochar production from manure and biosolids results in biochars with decreasing hydrolysable organic N because aromatic and heterocyclic structures increase (Clough *et al.*, 2013; Sun *et al.*, 2016) and nutrients susceptible to volatilization, violate after pyrolysis (Gaskin *et al.*, 2008). The deficiency of nitrogen strongly influences crop photosynthetic performance and biomass production (Zivcak *et al.*, 2014) as it is a significant component of photosynthetic apparatus (Bassi *et al.*, 2018). Therefore, limited soil and leaf nitrogen composition (Alvino and Sorrentino, 1996) may lower photosynthesis rate due to lower chlorophyll parameters as shown by plants grown in BC750 treated soils (Table 2). For this reason, the photosynthesis rate significantly increased in plants grown in PL and BC350 treated soils (Table 2), probably due to high nitrogen content (Bolan *et al.*, 2010). Besides nitrogen, potassium (K) content may have influenced CO_2 uptake because it is necessary for stomatal opening or closing and cellular growth, and its deficiency leads to chlorosis (Morgan and Connolly, 2013). The lower K concentrations lead to the lesser stomatal opening that results in lesser CO_2 concentration, consequently lowering the carbon rate incorporated into carbohydrates.

Moreover, the higher photosynthetic rate in PL and BC350 (Table 2) may be due to the increased number of leaves (Figure 2**Error! Reference source not found.**) that may as well have increased the capacity chlorophyll content (Halim *et al.*, 2018) required for the process of photosynthesis. Also, the study results of photosynthesis rate were lower than the recommended range of 10-25 μmolm^{-2}s^{-1} (Fukuzawa *et al.*, 2012) or 9-18 μmol(CO_2)m^{-2}s^{-1} (Yong *et al.*, 2010) despite the increase of organic amendments application rate; therefore higher application rate than 3 gkg^{-1} may increase photosynthesis rate to the optimum level. Furthermore, Murchie and Lawson (2013) and Zivcak *et al.* (2014), stated that the more profound photosynthesis rate increase below 0.80-0.83 indicates the organic amendment's negative influence on photosynthetic apparatus. However, BC350 has a slightly lower CO_2 uptake compared to recommended maximum photosynthetic rate (Murchie and Lawson, 2013; Zivcak *et al.*, 2014), indicating that a slight increase of nitrogen content may increase the photosynthesis rate to its optimum level. According to Zoghi *et al.* (2019), the increase of biochar application rates results in higher photosynthesis rates, which agrees with the study results as shown in Table 2. Additionally, WUE (Figure 3) may have a significant contribution to the lower photosynthetic rate output (Table 2) as WUE lowers the stomatal conductance (Zoghi *et al.*, 2019), eventually reducing plant growth (Ruggiero *et al.*, 2017) as observed in this study.

As for transpiration rate, the increased leaf surface area (Figure 2) may have affected the transpiration rate effectively as reflected in Table 2. The plants that have shown larger leaf surface area (Figure 2) exhibit an increased transpiration rate (Table 2) and vice versa. Nonetheless, the highest transpiration rate recorded was within the maximum range of 2-6 mmolm^{-2}s^{-1} (Fukuzawa *et al.*, 2012). Also, there was a slight variation of transpiration rate; this may be due to the dropping of leaves by Jatropha plants as a water conservation management technique. For WUE, it is the ratio of water used by the plant metabolism to water lost by the plant through transpiration (Ruggiero *et al.*, 2017). The study results show that WUE increased in BC750 treated plants compared to PL and BC350 (Figure 3). Moreover, the PL and BC350 WUE generally decreased with the increase of application rate compared to the control. The increase of WUE in BC750 and control may be due to the smaller leaf surface area (Figure 2), thus less transpiration rate (Table 2); hence more water use efficiency. As for BC750 treated plants, the larger surface area of biochar (BC750) can increase soil water holding capacity (Hui *et al.*, 2018); therefore, the small pores of biochar (Revell, 2011) and high porosity with a larger surface area (Brantley *et al.*, 2015) help with the water holding capacity of sandy soils, eventually improving water use efficiency (Basso and Ritchie, 2012). The leaf surface area also affects the transpiration rate and water use efficiency as these physiological processes occur in the leaves (Nakanwagi *et al.*, 2018). For instance, the larger leaf surface area for BC350 was linked with a higher transpiration rate and reduced WUE as the application rate increased; however, the opposite occurred in BC750 treated plants.

Furthermore, underwater deficit biochar significantly ($P < 0.01$) improves photosynthesis, stomatal conductance, transpiration, and xylem water potential (Zoghi *et al.*, 2019), and that was not the case in this study. According to Halim *et al.* (2018) study, photosynthesis rate increased under conditions of lower transpiration rate and high WUE when plants treated with compost that is not the case in this study, probably due to the organic amendment used that has a lower content of nitrogen, which is essential for the process of photosynthesis.

Conclusions

The incorporation of organic amendments in soil has significantly influenced *Jatropha* photosynthesis-related parameters. Among the organic amendments used, biochar pyrolyzed at 350°c improved Jatropha photosynthetic-related parameters. Therefore, the study considers BC350 suitable for Jatropha growth as it has the potential to improve *Jatropha* photosynthesis-related parameters that will eventually enhance plant growth.

Authors' Contributions

Conceptualization: BLM and OD; Methodology: BLM and OD; Formal analysis: BLM; Investigation: BLM; Resources: BM; Writing-original draft preparation: BLM; Writing-review and editing: BLM and BM; Supervision: OD and BM; Funding acquisition: BM.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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