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Original Paper

Photosynthetic gas exchange characteristics in *Jatropha curcas* L.

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Abstract The use of Jatropha (*Jatropha curcas* L.) as a source of biofuel has been well-documented. However, the physiological characteristic and growth analysis studies of Jatropha have received considerably lesser attention. In the present study, to confirm the physiological characteristics of Jatropha, we measured the leaf gas exchange characteristics in response to various environmental conditions. Seedlings were grown in 1/5,000 a pots for 2–3 months under greenhouse conditions. Leaf gas exchange rates were measured in a handmade assimilation chamber (26×30×9 cm), in which a fully expanded whole leaf could be set. Based on the leaf gas exchange characteristics, Jatropha was considered to be a C_3 photosynthesis plant. The photosynthetic rate ranged between 10 and 25 $\mu mol\,m^{-2}\,s^{-1}$ and light saturation generally occurred at 500–1,000 $\mu mol\,m^{-2}\,s^{-1}$ photon flux densities (PFD), depending on the growth conditions and leaf positions. Leaf conductance and transpiration rates were saturated at 400–1,000 $\mu mol\,m^{-2}\,s^{-1}$ PFD, also depending on the growth conditions and leaf positions. Maximum rates of transpiration and leaf conductance were 2–6 $mmol\,m^{-2}\,s^{-1}$ and 200–1,200 $mmol\,m^{-2}\,s^{-1}$, respectively, which are very similar to those in C_3 rice plants. Optimum temperature for photosynthesis was approximately at 25–30°C and the maximum rate was 20 $\mu mol\,m^{-2}\,s^{-1}$. Application of varying vapor pressure difference (from 1 to 3 kPa) did not affect the photosynthetic rate. Photorespiration in Jatropha was 28.5%, which is within the range of typical C_3 plants. Based on the photosynthetic parameters presented in this study, field performance of Jatropha under severe environmental condition is discussed.

Key words: *Jatropha curcas* L., photosynthesis, photorespiration, leaf position, vapor pressure difference.

In history, fossil fuels have been serving as a central driving force for the development of civilization and industrialization of mankind. However, world oil reserves are being exhausted at an ever increasing rate, which is accompanied by a sharp increase of atmospheric CO_2, one of the major greenhouse gases. The recent oil crises and growing public awareness of global energy issue have prompted the development of alternative, renewable sources of energy (Ndong et al. 2009). Biomass is a recyclable energy source that is expected to replace fossil fuels (Dyer and Mullen 2008). The use of biomass as a fuel is generally recognized as 'Carbon Neutral', and hence it is considered to mitigate global warming. Biomass from agricultural products and its by-products can be collected more easily than other biomass. However, the agricultural products are consumed as foodstuffs in most instances. Jatropha (*Jatropha curcas* L.) is an energy plant in which between 28% and 38% of the seeds consists of oil (Kaushik et al. 2007) that can be converted into a good quality biodiesel by esterification with methanol. The seeds also include phorbol-ester which has been reported to be toxic to humans and domestic animals (Goel et al. 2007). For this reason, oil extracted from Jatropha seeds is not suitable for food use at present. Since Jatropha can grow in marginal soils and semiarid climates, this plant has gained increasing attentions as a promising alternative for the production of biodiesel that does not compete with food production. By 2008, Jatropha originals from Mexico had already been planted over an estimated 900,000 ha across the globe (Kant and Wu 2011).

Moreover, several Jatropha extension programs have been or being underway in sub-Saharan African countries, such as Tanzania, Zambia, Burkina Faso, Cameroon, Gambia, Kenya, Liberia, Sierra Leone, Mozambique and Botswana, which are promoted by national policies for bioenergy and/or international co-operations. If an energy crop is grown in the arable

Abbreviations: *A/Ci*, photosynthesis against intracellular CO_2 concentration; $A_{2\%}$, CO_2 assimilation rates at 2%; $A_{21\%}$, CO_2 assimilation rates at 21%; *Ci*, internal CO_2 concentration; *PFD*, photon flux density; *VPD*, vapor pressure difference.

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land, it will compete with food productions and causing food price to rise. It is necessary to expand cultivation of Jatropha at the area where food crops are comparatively difficult to grow, such as semiarid zones. Photosynthesis was often used as an alternative guide for plant production, stress tolerance, effect of fertilizer and response of environments (Kawamitsu et al. 2002; Uehara et al. 2009). Although Jatropha is able to adapt to variable conditions including semi-arid climates, little is known of its photosynthetic responses to these various environments. Several research on photosynthesis in Jatropha have been studied focusing on the effects of soil salinity and water stress, fertilizer application (e.g. Silva et al. 2010; Yong et al. 2010) and night chilling (Zheng et al. 2009). However photosynthetic responses to the atmospheric environment such as temperature and vapor pressure difference (*VPD*) weren't reported so far.

In this study, major photosynthetic responses (photosynthesis, transpiration, and leaf conductance) of Jatropha to light, temperature, *VPD*, CO_2 and O_2 concentration and nitrogen nutrient supply were investigated, in order to better understand its photosynthetic responses against various atmospheric environment and basic gas exchange characteristics. Transpiration performance was discussed in the context of the extension of Jatropha cultivation to the arid and semiarid regions of the world.

Materials and methods

Plant materials and growth conditions

A strain of Jatropha (*Jatropha curcas* L.) used in this study was derived from Thailand. The seeds were sown in sandy soil in April 2009 and May 2011 for the experiments on photosynthetic responses to light, CO_2 concentration, temperature, VPD and photorespiration, and photosynthetic responses to light at different leaf positions, respectively. In both experiments, seedlings were grown in a green house in University of the Ryukyus, Okinawa, Japan. After the second leaves had expanded, the healthy seedlings were transplanted to 1/5,000 Wagner pots containing a dark-red soil : sand : peat moss=1 : 1 : 1, v/v soil mixture. The seedlings were watered as required, and fertilized twice a week with 500 ml of modified Hoagland solution at each pots. Composition of the nutrient solution was 6 mM $Ca(NO_3)_2$, 12 mM KNO_3, 2 mM KH_2PO_4, 2 mM $MgSO_4$, 25 µM H_3BO_3, 10 µM $MnSO_4$, 2 µM $ZnSO_4$, 0.5 µM $CuSO_4$, 0.5 µM H_2MoO_4, and 0.1 mM $FeC_6H_5O_7$.

Photosynthetic responses to light, CO_2 concentration, temperature, VPD

Leaf gas exchange measurements were conducted in September 2009. Leaves of 7th to 13th of leaf position were used. Gas exchange was determined using an open gas-exchange system essentially as described previously (Agata et al. 1986; Du et al. 1996; Kawamitsu et al. 2002). This photosynthesis/transpiration simultaneous measurement system is able to control various parameters within an assimilation chamber in a flexible manner, such as photon flux density (PFD; 0–2,500 µmol m^{-2} s^{-1}), leaf temperatures (10–45°C), *VPD* (0–3 kPa), oxygen concentration (0–30%) and CO_2 concentration (0–2,000 ppm) with high-precisely and also optionally. In brief the measurement system operated, and the modifications of the settings from the previous reports were as follows. First, atmospheric air taken in through an air compressor was adjusted with a mass flow controller (SEC-4400, ESTEC), and then passed through silica gel and soda lime to prepare CO_2-free gas. This gas was then passed through a humidity control device (a bubbling device connected to a Coolnics circulator; CTE-82W, Yamato-Komatsu) that was able to regulate humidity of the introduced air. To obtain desired CO_2 concentration, the CO_2-free air was mixed with 5% CO_2 gas balanced with N_2 gas and adjusted with the mass flow controller (SEC-4500, ESTEC) and then agitated sufficiently in a gas mixing box before finally being introduced into the assimilation chamber (26×30×9 cm, see Figure 1). In the assimilation chamber, the inlet air was mixed well by a small fan so that a uniform atmospheric condition was achieved. The flow rate through the chamber was set at 0 to 20 L per min, depending on the leaf area and photosynthetic activity. Three metal-halide lamps (D-400, Toshiba) were used as a light source and a water filter (7 cm-depth) was inserted between the light source and the assimilation chamber to reduce thermal rays. Leaf temperature was measured by thermocouples (T type) attached to the abaxial surface with a clip. Difference in CO_2 concentration and relative humidity between inlet and outlet of assimilation chamber were monitored using an infrared gas analyzer (LI-6251, Li-COR), and a relative humidity sensor (HMP-112Y, Vaisala), respectively. Signals from these sensors were processed with an A/D transformation device (DL-100, Yokogawa) and connected to a personal computer that could simultaneously calculate all related photosynthesis parameters and display them on the screen. Stomatal conductance and internal CO_2 concentration (*Ci*) were calculated from the data according to von Caemmerer and Farquhar (1981) and Boyer and Kawamitsu (2012), respectively. Shortly after each gas exchange measurement, the measured leaf was cut and leaf area was measured with a leaf area meter (LI-3100, LI-COR). The recalculation of photosynthesis and related parameters was then performed using the measured leaf area.

Photorespiration

Photorespiration was determined using the open gas-exchange system described above by manipulating O_2 concentration into the assimilation chamber. To obtain different O_2 concentration, atmospheric air containing 21% O_2 was diluted by mixing with 99% N_2 gas before adjusting the CO_2 concentration. The O_2 concentration inside the assimilation chamber was monitored with a nondestructive portable O_2 analyzer (Fibox type PSt3, PreSens).

Measurement was carried out for four potted plants, and the

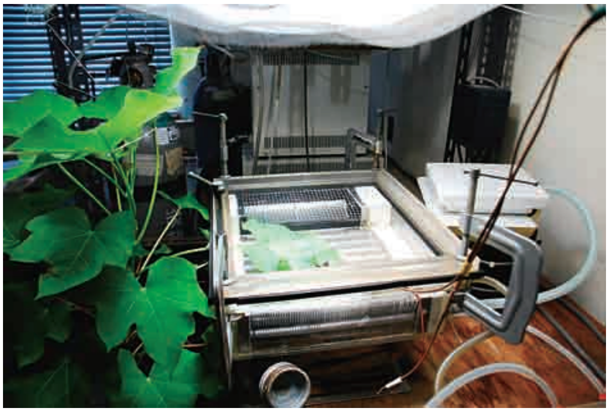

Figure 1. The CO_2 assimilation chamber which accommodate whole region of a leaf of Jatropha. The fan in the chamber eliminates boundary layer resistance and suppresses the fluctuations in CO_2 and humidity.

result showing the maximum photosynthetic rate at 21% O_2 was plotted as representative of the Jatropha response.

Gas exchange rate at different leaf positions

Jatropha seeds from Thailand were sown in sandy soil in May, 2011. Thereafter, healthy seedlings were transplanted in 1/5000 a Wagner pots filled with the same soil mixture as described above and the grown in a greenhouse. Seedlings were fertilized and watered in the same manner as described above. Gas exchange measurements were carried out in October 2011. The 3rd, 8th, 13th and 18th leaf from the top position were measured using a portable photosynthesis system (LCpro-SDADC) with a broad leaf chamber window area of 6.25 cm^2. The source of light was an LCpro+ red and blue LED lamps placed on top of the leaf clip. Measurements were performed at the environmental humidity and CO_2. The infra-red gas analyzer was checked before measurement using a compressed air cylinder with a known CO_2 concentration (400 ppm; Sumitomo Seika Chemicals), and calibration was adjusted as necessary. Photosynthetic light response curves were constructed by reducing the PFD in 7 steps. Leaf temperature was maintained at 30°C using a thermostat.

Gas exchange rate at different nitrogen levels

Jatropha seeds from Thailand were sown in June, 2008 and transplanted into 1/5,000 a Wagner pots filled with sand. The weekly-supplied nutrient solution contained the same components as described above but with modified NO_3^- concentration (64, 32, 16, 8 and 0 mM). Gas exchange measurements were started in November 2008. Light response carves were then measured under a leaf temperature of 30°C, a dew point 21°C and a CO_2 concentration of 380 ppm.

Results and discussion

The mature leaf area of the Jatropha ranged from approximately 100 to 200 cm^2 depending on the growth conditions and leaf positions. To date, photosynthetic rates reported in the literatures dealing with Jatropha were all determined using a conventional portable photosynthesis system (such as LI-6400, Li-COR) which focuses on a smaller leaf area of approximately 6 cm^2. This value is only less than a 6% of the total area of one leaves in the case of Jatropha plant.

Since chambers of most commercially available gas exchange systems usually enclose only a small leaf surface (2–6 cm^2) of illuminated photosynthesizing leaf area, which is surrounded by gaskets of a certain width, a darkened area is observed to surround the illuminated photosynthesizing leaf area under the gaskets, the respiration from which and thus interferes with the measurement of photosynthetic flux (Flexas et al. 2007). Thus an underestimation of the net photosynthesis measured with clamp-on leaf chambers due to respiratory CO_2 produced under the gasket is inherent in these systems (Pons and Welschen 2002).

In our study, we developed a new assimilation chamber (Figure 1) into which a whole Jatropha leaf could be set thereby, avoiding this chamber 'edge' effect. Thus, the photosynthetic parameters obtained by this system should reflect more natural characteristics of photosynthesizing leaves. Moreover, the use of our larger chamber allowed us to disregard photosynthetic heterogeneity within a single leaf (e.g. Wong et al. 1979; Terashima et al. 1988; Buckley et al. 1997). Furthermore, the flow rate in this system can be modified in the range from 0 to 20 $L\,min^{-1}$, it was thought that the photosynthetic ability of a leaf could be evaluated more appropriately.

Light response curves

The photosynthetic rate became light-saturated over approximately 1,000 $\mu mol\,m^{-2}\,s^{-1}$ PFD, and the maximum rate of photosynthesis was 24.0 $\mu mol\,m^{-2}\,s^{-1}$ (Figure 2). In accordance with this result, Yong et al. (2010) found that the maximum photosynthetic rates for mature Jatropha leaves range 15 to 25 $\mu mol\,m^{-2}\,s^{-1}$ at a PFD of over 800 $\mu mol\,m^{-2}\,s^{-1}$ when N nutrition was not limited. Transpiration and leaf conductance showed sensitive responses under low light intensities, but were less responsive to the light intensities over 500 $\mu mol\,m^{-2}\,s^{-1}$ PFD. Their maximum values were 3.1 $mmol\,m^{-2}\,s^{-1}$ and 230 $mmol\,m^{-2}\,s^{-1}$, respectively.

CO_2 responses and A/Ci curves

The CO_2 response curves for the photosynthesis of mature leaves were determined between 0 and 1,000 ppm of ambient CO_2. Photosynthesis plotted against ambient CO_2 is shown in Figure 3. The photosynthetic rate was not saturated at CO_2 concentration below 1,000 ppm. At 800 ppm, twice the present atmospheric CO_2 concentration, photosynthesis increased up to 34 $\mu mol\,m^{-2}\,s^{-1}$. Similarly, photosynthesis against

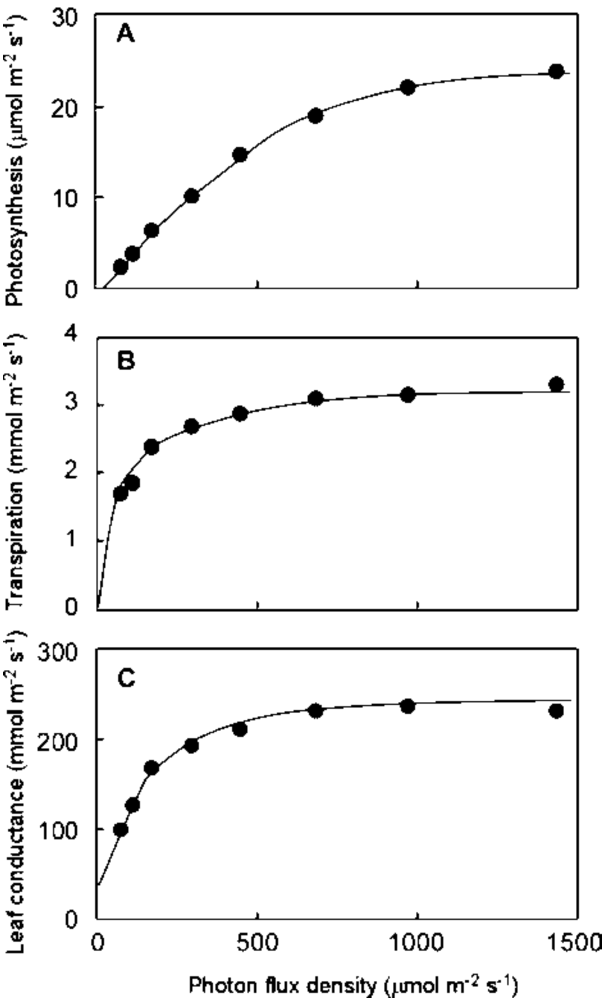

Figure 2. Light response curves of photosynthesis (A), transpiration (B) and leaf conductance (C) for the leaves of Jatropha. Gas exchange rate was measured at 380 ppm of CO_2, at a leaf temperature 30°C and a dew point of 21°C.

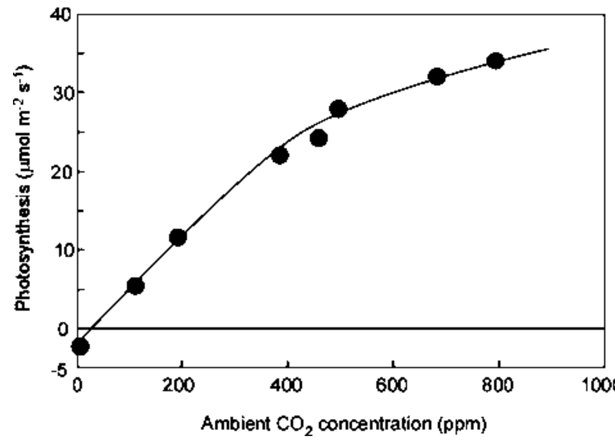

Figure 3. Photosynthesis versus atmospheric CO_2 for the leaves of Jatropha, Gas exchange rate was measured at a leaf temperature of 30°C, a dew point of 21°C and a PFD of 970 μmol m^{-2} s^{-1}.

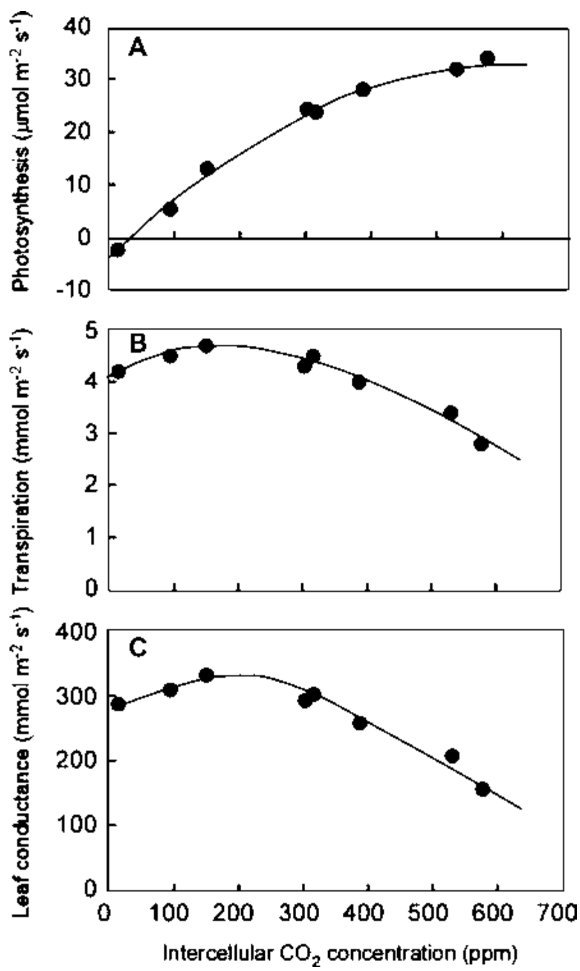

Figure 4. Responses of photosynthesis (A), transpiration (B) and leaf conductance (C) to intercellular CO_2 for the leaves of Jatropha.

intracellular CO_2 concentration (*A/Ci* curve) showed that it was not saturated up to 600 ppm (Figure 4). The initial slope of the *A/Ci* curve was similar to that in the other C_3 plant such as rice plants (Imai and Kobori 2008). Transpiration and leaf conductance vs. *Ci* showed peaks at approximately 200 ppm and thereafter decreased with increased *Ci*.

Temperature dependence curves

Photosynthesis showed a peak rate at leaf temperatures of 25 to 30°C and the optimum temperature for transpiration was approximately 35°C (Figure 5). However, leaf conductance fell rapidly with increases in temperature over 25°C. At low temperatures of around 15°C, photosynthesis and transpiration rates were decreased despite of higher leaf conductance probably due to the low *VPD*. At higher temperature, on the other hand, these three parameters were reduced because of the high *VPD*.

VPD dependence curves

Previous report demonstrated that, leaf photosynthesis in C_3 rice plants is usually reduced when the *VPD* is increased from 0.5 to 3 kPa (Kawamitsu et al. 1993).

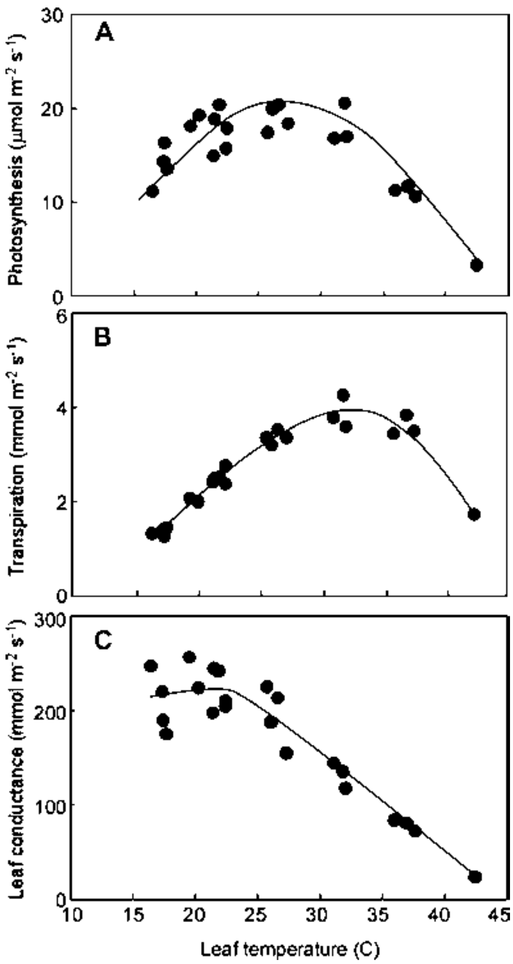

Figure 5. Temperature dependence curves of photosynthesis (A), transpiration (B), and leaf conductance (C) for leaves of Jatropha. Gas exchange rate was measured at a CO_2 concentration of 380 ppm, a dew point of 21°C and a PFD of 970 μmol m^{-2} s^{-1}.

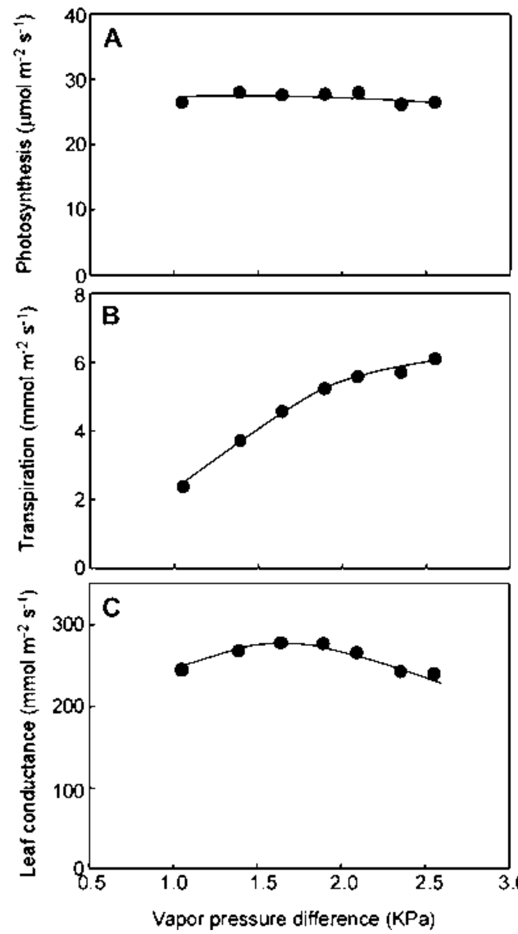

Figure 6. Responses of photosynthesis (A), transpiration (B) and leaf conductance (C) to vapor pressure difference (VPD) for leaves of Jatropha. Gas exchange rate was measured at a leaf temperature of 32°C, a dew point of 21°C and a PFD of 970 μmol m^{-2} s^{-1}.

However, *VPD* has no effect on photosynthesis in C_4 plants. In the case of Jatropha, photosynthesis vs. *VPD* responses curves was similar to those in C_4 plants (Figure 6). In both C_3 and C_4 plants, the transpiration rate linearly increased with *VPD* because of increases in the driving force of evaporative demands. Leaf conductance decreased at large *VPD* with a peak at approximately 1.5 kPa.

The above results suggested that, if the enhancement of leaf transpiration by large *VPD* is accompanied with restricted water absorption from the roots, it may pose severe impacts on the leaf water relation, which is potentially detrimental to growth and survival of Jatropha in such environments. In a semiarid zone such as Southern Africa, the *VPD* frequently reaches to 4 or 5 kPa in summer (data not shown). Because of the limitation of maximum flow rate of the measurement system, photosynthetic performance under *VPD* over 3kPa was not investigated in this study. Future work, however, it will be important to examine whether photosynthesis and leaf conductance decrease or not at very high *VPD* values.

Photorespiration

C_3 photosynthesis is sensitive to oxygen concentration because of photorespiration. Photorespiration can be calculated simply using gas exchange data as follow (Sage and Sharkey 1987);

$$\text{Photorespiration} = (A_{2\%} - A_{21\%}) / A_{2\%} \times 100\ (\%)$$

where, $A_{2\%}$ and $A_{21\%}$ are the CO_2 assimilation rates at 2% and 21% O_2, respectively. In Jatropha, the $A_{2\%}$ and $A_{21\%}$ were 35 and 25 μmol m^{-2} s^{-1}, respectively (Figure 7). Accordingly, the calculated photorespiration was 28.5%, which is within the typical range for C_3 plants (Sage and Sharkey 1987). There were no changes observed in transpiration rate or leaf conductance with decreasing oxygen concentration. Concerning the effect of low O_2 on Jatropha photosynthesis, it is interesting to note that natural inhabitation of Jatropha are frequently observed in higher altitudes in the world (Igamberdiev et al. 2004).

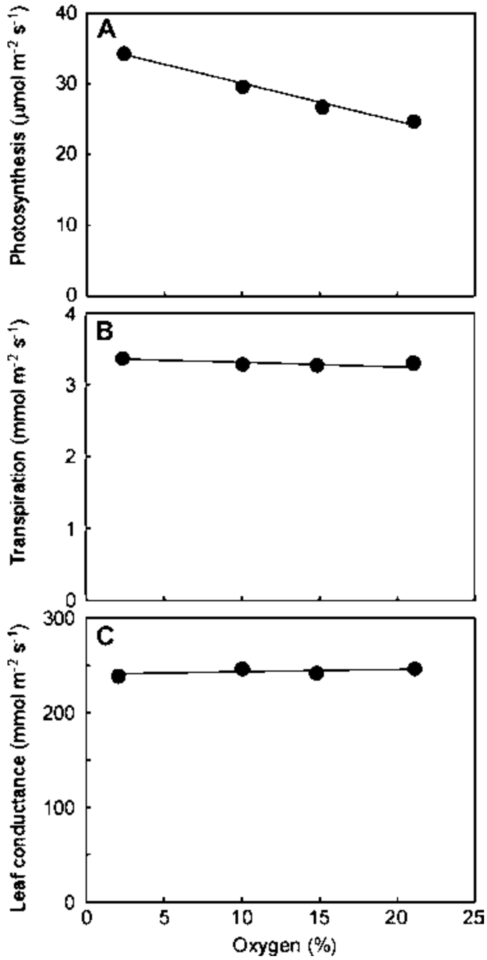

Figure 7. Oxygen dependence of photosynthesis (A), transpiration (B) and leaf conductance (C) for leaves of Jatropha. Gas exchange rate was measured at a leaf temperature of 32°C, a CO_2 concentration of 380 ppm and a PFD of 970 $\mu mol\, m^{-2} s^{-1}$.

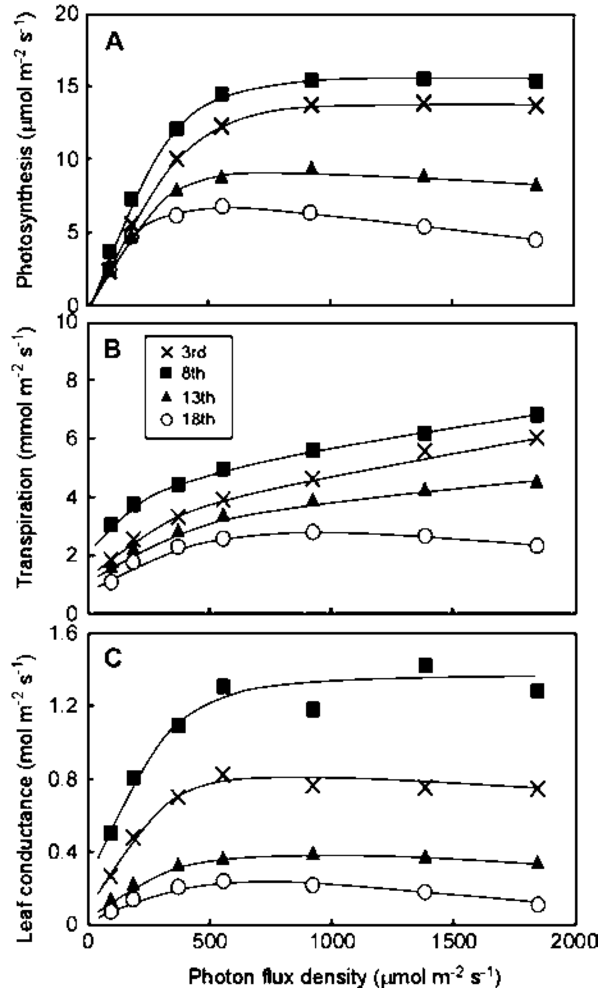

Figure 8. Light response curves of photosynthesis (A), transpiration (B) and leaf conductance (C) for leaves at different leaf position in Jatropha. Leaf temperature was set at 30°C and CO_2 at 380 ppm.

Since O_2 concentration at high altitudes is low, it will be interesting to examine whether the photorespiration is suppressed and consequently photosynthesis is promoted in higher altitudes in Jatropha.

On the other hand, an increased allocation of energy to photorespiration could mitigate deleterious effects such as photoinhibition by allowing metabolism to continue using photosynthetic electron transport products (Osmond and Grace 1995). A plant grow in dry area is often exposed to strong light. The photorespiration of Jatropha is higher than C_4 plants meaning that Jatropha is able to withstand photoinhibition, as other C_3 plants.

Leaf gas exchange rates at different leaf positions

Maintenances of increased photosynthesis for long periods are very important to increased biomass and seed productions. In addition to the leaf age, it has been shown that leaf position also influences the leaf gas exchange characteristics. Therefore, different light requirements among the different leaf positions in potted Jatropha plants was investigated by means of photosynthetic light response curves (Figure 8).

Consequently, the 8th leaf from the top showed higher photosynthesis, transpiration and leaf conductance with saturation points at approximately 500 $\mu mol\, m^{-2} s^{-1}$ PFD. The maximum photosynthesis decreased in younger 3rd, then older 13th and 18th leaves in this order. This result indicated that photosynthesis of older leaves within the Jatropha canopy is saturated at very low light intensities thus liable to have photo-inhibitions if exposed to higher PFD levels. To examine whether different leaf position may affect photosynthetic performance also in the field condition, we measured the gas exchange parameters at different leaf positions under field, using a portable gas exchange measurement system. Consequently, almost the same trend was observed in the field-grown plants (data not shown).

These observations suggested that, due to the nature of lower photosynthetic capacity, wide ranges of light intensities in the field may occasionally cause

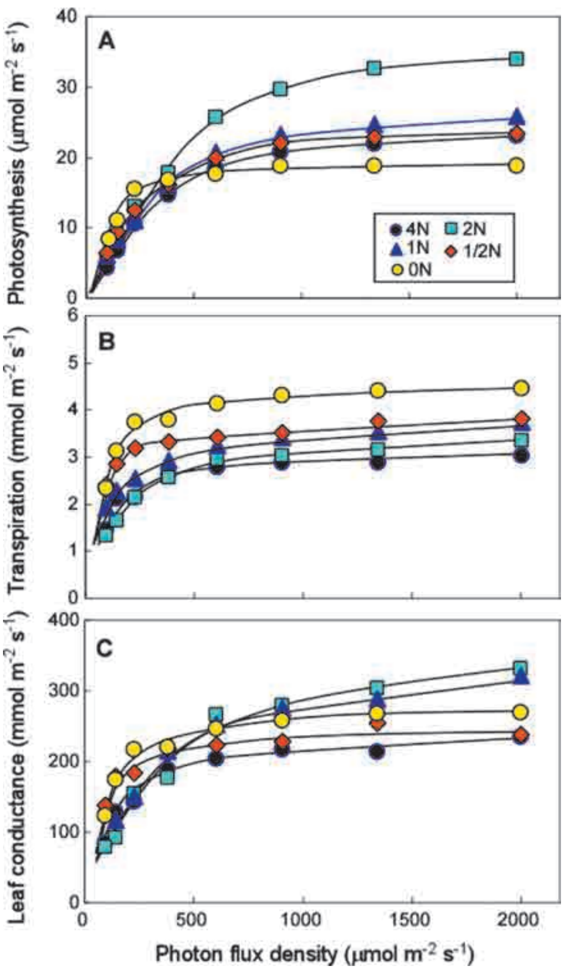

Figure 9. Light response curves of photosynthesis (A), transpiration (B) and leaf conductance (C) in Jatropha grown under different nitrogen concentrations. Leaf temperature was set at 30°C and CO_2 at 380 ppm.

absorption of excessive light energy, in particular in the lower positions of Jatropha leaves. The resultant risk of photodamage can be substantial in the Jatropha plantation in the semiarid regions, where frequent water deficits may exacerbate the photodamage derived from excessive photon energy. To overcome these problems and extend Jatropha cultivation in such areas, multilateral researches will be required in the future. Moreover, future research directions should include not only the selection and breeding of resistant Jatropha strains, but also the establishment of suitable farming methods which may involve optimization of the spacing of the plants, and introduction of inter-cropping systems in Jatropha fields to mitigate photoinibition of lower canopy.

Gas exchange performance in relation to the leaf nitrogen content

In many crop plants, application of higher amount of nitrogen fertilizer generally results in the increase of biomass production. However, an optimal amount of fertilizer is different among crop plants, and if applied beyond this optimum, the biomass production decreases. To address this issue, Jatropha plants were grown in five conditions (0N, 1/2N, 1N, 2N and 4N) that differed in the nitrogen supply, and were subjected to photosynthetic measurement. The 1N plant represents a control plant grown at 16 mM NO_3^-, and 2N, 4N and 1/2N are twice, four-times and half of the nitrogen supply, respectively. Photosynthetic measurement revealed that the maximum photosynthesis was the highest in 2N plants, followed by the order of 1N, 4N, 1/2N and 0N plants (Figure 9). At lower PFD levels, on the other hand, photosynthesis was higher in 0N plants and followed by 1/2N plants. Maximum transpiration rate was higher in 0N plants and then in 1/2N plants. Maximum leaf conductance was higher in 2N plants and lower in 4N plants. At low PFD levels, however, 0N and 1/N plants showed higher leaf conductance, which was in accordance with the rates of photosynthesis. On that occasion, 2N of leaf nitrogen content became 3.4% which is highest of the other treatments. In contrast, 1N and 4N of leaf nitrogen content was 2.5 and 3.0%, respectably.

These facts provide evidence that Jatropha is capable of growing in both barren and eutrophic soils. However, the results also suggested that application of optimal nitrogen fertilization has positive effects on the photosynthesis in Jatropha.

Although there are some reports arguing that Jatropha can grow even in denuded land (Heller 1996; Openshaw 2000; Francis et al. 2005), quantitative investigation on the potential and/or practical yield of Jatropha in such non-cultivated lands has been scarce so far. Since the ultimate objective of Jatropha research and development is to obtain maximum yield of Jatropha in arid lands that do not compete with food production (Divakara et al. 2010), study on the agricultural performance of Jatropha in such severe arid climate, together with the physiological performance of Jatropha which eventually leads to its biomass production, will be the important research directions in the future. Characteristics of gas exchange measurement in Jatropha is therefore one of the basic physiological data towards establishment of Jatropha cultivation in the arid and semiarid zones.

From the above results, it is clear that the optimal environmental condition for Jatropha photosynthesis were a PFD of 500~1,000 μmol $m^{-2} s^{-1}$, a VPD of 1.5 kPa or less and a leaf temperature of 25–30°C. Moreover, it also became clear that the optimum condition for nitrogen supply was the one which maintains leaf nitrogen content as approximately 3.4%. Furthermore, present study revealed significant differences of the gas exchange characteristic at different leaf positions in Jatropha.

Since CO_2 and H_2O concentrations and air temperature are substantially different within a canopy of the plant from the atmosphere above the tree to the soil surface at the ground level (Al-said et al. 2009; Tominaga et al. 2010), it is possible that these factors may interact each other and affect biomass production of individual Jatropha plants in the field. Therefore, the plant density during Jatropha cultivation is potentially one of the determinant factors for maximizing the Jatropha yield. It was suggested that establishment of cultivation management so as to maintain the photosynthetic gas exchange characteristic to the maximum level is very important in Jatropha.

References

Agata W, Kawamitsu Y, Hakoyama H, Shima Y (1986) A system for measuring leaf gas exchange based on regulating vapour pressure difference. *Photosynth Res* 9: 345–357

Al-Saidi A, Fukuzawa Y, Furukawa N, Ueno M, Baba S, Kawamitsu Y (2009) A System for the measurement of vertical gradients of CO_2, H_2O and air temperature within and above the canopy of plant. *Plant Prod Sci* 12: 139–149

Beckley TN, Farquhar GD, Mott KA (1997) Qualitative effects of patchy stomatal conductance distribution features on gas-exchange calculations. *Plant Cell Environ* 20: 867–880

Boyer JS, Kawamitsu Y (2011) Photosynthesis gas exchange system with internal CO_2 directly measured. *Environ Control Biol* 49: 193–207

Divakara BN, Upadhyaya HD, Wani SP, Gowda CLL (2010) Biology and genetic improvement of *Jatropha curcas* L. *Appl Energy* 87: 732–742

Du YC, Kawamitsu Y, Nose A, Hiyane A, Murayama S, Wasano K, Uchida Y (1996) Effects of water stress on carbon exchange rate and activities of photosynthetic enzymes in leaves of sugarcane (*Saccharum* sp.). *Aust J Plant Physiol* 23: 719–726

Dyer JM, Mullen RT (2008) Engineering plant oils as high-value industrial feedstocks for biorefining: the need for underpinning cell biology research. *Physiol Plant* 132: 11–22

Flexas J, Díaz-Espejo A, Berry JA, Cifre J, Galmés J, Kaldenhoff R, Medrano H, Ribas-Carbó M (2007) Analysis of leakage in IRGA's leaf chambers of open gas exchange systems: quantification and its effects in photosynthesis parameterization. *J Exp Bot* 58: 1533–1543

Francis G, Raphael E, Klaus B (2005) A concept for simultaneous wasteland reclamation, fuel production, and socio-economic development in degraded areas in India: Need, potential and perspectives of Jatropha plantations. *Nat Resour Forum* 29: 12–24

Goel G, Makkar HP, Francis G, Becker K (2007) Phorbol esters: structure, biological activity, and toxicity in animals. *Int J Toxicol* 26: 279–288

Heller J (1996) Physic nut *Jatropha curcas* L. IPGRI, Rome, Italy

Igamberdiev AU, Mikkelsen TN, Ambus P, Bauwe H, Lea PJ, Gardeström P (2004) Photorespiration contributes to stomatal regulation and carbon isotope fractionation: a study with barley, potato and Arabidopsis plants deficient in glycine decarboxylase. *Photosynth Res* 81: 139–152

Imai K, Kobori K (2008) Effects of the interaction between ozone and carbon dioxide on gas exchange, ascorbic acid content, and visible leaf symptoms in rice leaves. *Photosynthetica* 46: 387–394

Kant P, Wu S (2011) The extraordinary collapse of Jatropha as a global biofuel. *Environ Sci Technol* 45: 7114–7115

Kaushik N, Kumar K, Kumar S, Kaushik N, Roy S (2007) Genetic variability and divergence studies in seed traits and oil content of Jatropha (*Jatropha curcas* L.) accessions. Biomass. *Bioenerg* 31: 497–502

Kawamitsu Y, Hiyane S, Tamashiro Y, Hakoyama S (2002) Regulation of photosynthesis and water use efficiency in relation to stomatal frequency and interveinal distance in C_3- and C_4-grass species. *Environ Control in Biol* 40: 365–374

Kawamitsu Y, Yoda S, Agata W (1993) Humidity pretreatment affects the responses of stomata and CO_2 assimilation to vapor pressure difference in C_3 and C_4 plants. *Plant Cell Physiol* 34: 113–119

Ndong R, Mireille MV, Olivier SG, Benoit G, Roland P, Marjorie D, Caroline S (2009) Life cycle assessment of biofuels from Jatropha curcas in West Africa: a field study. *GCB Bioenergy* 1: 197–210

Openshaw K (2000) A review of Jatropha curcas: an oil plant of unfulfilled promise. *Biomass Bioenergy* 19: 1–15

Sage RF, Sharkey TD (1987) The Effect of Temperature on the Occurrence of O_2 and CO_2 Insensitive Photosynthesis in Field Grown Plants. *Plant Physiol* 84: 658–664

Silva EN, Ribeiro RV, Ferreira-Silva SL, Viégas RA, Siveira J A G (2010) Comparative effects of salinity and water stress on photosynthesis, water relations and growth of Jatropha curcas plants. *J Arid Environ* 74: 1130–1137

Terashima I, Wong SC, Osmond CB, Farquhar GD (1988) Characterisation of non-uniform photosynthesis induced by abscisic acid in leaves having different mesophyll anatomies. *Plant Cell Physiol* 29: 385–394

Tominaga J, Kawasaki S, Yabuta S, Fukuzawa Y, Suwa R, Kawamitsu Y (2010) Eclipse effects on CO_2 profile within and above sorghum canopy. *Plant Prod Sci* 13: 338–346

Uehara N, Sasaki H, Aoki N, Ohsugi R (2009) Effects of the temperature lowered in the daytime and night-time on sugar accumulation in sugarcane. *Plant Prod Sci* 12: 420–427

von Caemmerer S, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376–387

Wong SC, Cowan IR, Farquar GD (1997) Stomatal conductance correlates with photosynthetic capacity. *Nature* 282: 424–426

Yong JWH, Ng YF, Tan SN, Chew AYL (2010) Effect of fertilizer application on photosynthesis and oil yield of *Jatropha curcas* L. *Photosynthetica* 48: 208–218

Zheng YL, Feng YL, Lei YB, Yang CY (2009) Different photosynthetic responses to night chilling among twelve populations of Jatropha curcas. *Photosynthetica* 47: 559–566