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Growth and photosynthetic responses in *Jatropha curcas* L. seedlings of different provenances to watering regimes

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Abstract

Seedlings from four provenances of *Jatropha curcas* were subjected to 80, 50, and 30% of soil field capacity in potted experiments in order to study their responses to water availability. Our results showed that with the decline of soil water availability, plant growth, biomass accumulation, net photosynthetic rate, stomatal conductance (g_s), and transpiration rate (E) decreased, whereas leaf carbon isotope composition ($\delta^{13}C$), leaf pigment contents, and stomatal limitation value increased, while maximal quantum yield of PSII photochemistry was not affected. Our findings proved that stomatal limitation to photosynthesis dominated in *J. curcas* under low water availability. The increase of $\delta^{13}C$ should be attributed to the decrease in g_s and E under the lowest water supply. *J. curcas* could adapt to low water availability by adjusting its plant size, stomata closure, reduction of E, increasing $\delta^{13}C$, and leaf pigment contents. Moreover, effects of provenance and the interaction with the watering regime were detected in growth and many physiological parameters. The provenance from xeric habitats showed stronger plasticity in the plant size than that from other provenances under drought. The variations may be used as criteria for variety/provenance selection and improvement of *J. curcas* performance.

Additional key words: carotenoids; chlorophyll fluorescence; gas exchange; water-use efficiency.

Introduction

It is well known that either excessive or insufficient soil water content leads to stress (waterlogging or drought) for plants. Accordingly, plants possess genetically controlled mechanisms that allow them to live and grow under stress (Boyer 1982) including changes in structure, photosynthesis, osmotic adjustment, antioxidative protection, organ, whole-plant hydraulics (Dichio *et al.* 2013), and water-use efficiency (WUE) (Kheira and Atta 2009). Plant establishment and productivity are tightly related to leaf carbon gain and its response to drought. Under water stress, a reduction in photosynthesis was attributed to both stomatal and/or nonstomatal limitations (Varone *et al.* 2012). Generally, stomatal limitations are invoked by stomatal closure and nonstomatal limitations include both diffusive (reduced mesophyll conductance) and metabolic (photochemical and enzymatic limitations) processes (Galmés *et al.* 2007, Varone *et al.* 2012). As a photochemical parameter, maximal quantum yield of PSII photochemistry (F_v/F_m) of dark-adapted leaves by chlorophyll (Chl) fluorescence measurements is often used to indicate plant photosynthetic

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Abbreviations: C_a – ambient chamber CO_2 concentration; Car – carotenoids; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; FC – soil field capacity; FM – fresh mass; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; L_s – stomatal limitation value; P_N – net photosynthetic rate; R_s – root/shoot ratio; WUE – water-use efficiency; $\delta^{13}C$ – carbon isotope composition.

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performance (Maxwell and Johnson 2000). Carbon isotope composition ($\delta^{13}C$) of plant was found to be related to WUE (Farquhar and Richards 1984) and was used widely as a proxy of WUE to evaluate plant adaptability (Bartholomé *et al.* 2015).

Jatropha curcas Linnaeus is a bush/small tree that belongs to the family Euphorbiaceae. It is a valuable, multipurpose plant and receives specific attention as a biodiesel feedstock (Kumar and Sharma 2008). As a green and popular renewable fuel plant, many studies were focused on the technique (Kumar *et al.* 2013), quality of its seed oil (Samsuri and Zoveidavianpoor 2014), *etc*. However, to our knowledge, it is still an undomesticated crop and its basic agronomic properties have not been thoroughly understood (Achten *et al.* 2008) until now. *J. curcas* was accepted as a drought-resistant plant (Maes *et al.* 2009b). Previous studies showed that it can grow without irrigation in a broad spectrum of rainfall regimes from 200 to 3,000 mm annually (Kheira and Atta 2009, Trabucco *et al.* 2010) and give a high production with 900–1,200 mm rainfall (Maes *et al.* 2009c). Additionally, *J. curcas* has a relatively high WUE (Maes *et al.* 2009b) and most probably a relatively low water footprint (Jongschaap *et al.* 2009, Maes *et al.* 2009a). Although these above-mentioned studies have shed new insights on the water requirements of *J. curcas*, only a few studies reported its tolerance to drought (Fini *et al.* 2013, Sapeta *et al.* 2013) or salinity (Rajaona *et al.* 2012). Further study is needed to gain knowledge about its physiological adaptations to drought. Moreover, *J. curcas* has been cultivated in many countries with marginal and poor soils (Fairless 2007, Divakara *et al.* 2010), therefore physiological traits and the adaptation capacity to drought are vital for selecting proper genotypes of *J. curcas*.

It was reported that plants, which photosynthesis is reduced due to stomatal limitation under drought, could recover their maximum photosynthetic rate rapidly upon rewatering, while the recovery was slow and incomplete in plants mainly due to nonstomatal limitations (Varone *et al.* 2012). Thus, we hypothesized that stomatal limitation to photosynthesis is an acclimation to low water availability in *J. curcas* due to its high drought tolerance. Furthermore, we expected that *J. curcas* provenances from xeric habitats should show different behavior under lower water supply compared to those from relatively mesic environments. Although three studies have compared the behavior of accessions from different provenances (Maes *et al.* 2009b, Achten *et al.* 2010, Sapeta *et al.* 2013), none or small differences were found in these provenances. But in many other plants, physiological responses to drought vary with the genotype or provenance (Yin *et al.* 2009a, 2009b; Costa *et al.* 2012). In our study, *J. curcas* of four provenances from different natural habitats were used as a study material. The overall goal was to investigate the adaptability of *J. curcas* to different water regimes. The specific objectives were (*1*) to study the effects of soil water availabilities on the growth and physiological characteristics of *J. curcas*; (*2*) to compare the differences between different provenances in response to water regimes.

Materials and methods

Plants and experimental design: Four local provenances of *J. curcas* were used and their specific differences were shown. Hainan is located in southeastern China with a tropical maritime climate, while the other three are from the dry-hot valleys along the Jinshajiang River in southwestern China where the subtropical monsoon climate dominates.

Provenance	Origin	Latitude [°N]	Longitude [°E]	Altitude [m]	Annual rainfall [mm]	Annual mean temperature [°C]
P1	Hainan	19°10'	109°36'	300	1,500	24.0
P2	Yanbian	27°28'	101°46'	1,100	1,065	19.2
P3	Panzhihua	26°23'	101°54'	1,300	800	20.9
P4	Jinyang	27°26'	103°08'	580	800	16.9

Seeds collected from 30 trees of each provenance in October 2007 were sown in 10-L plastic pots (one seed per pot) filled with the same amount of homogenized soil at the beginning of March 2008. The soil was collected from *J. curcas* plantation and mixed with 10% (w/w) farm manure. It was torrid red soil with average nutrient concentrations at local *J. curcas* plantations. The average germination rate of seeds was about 89 ± 4%. After germination, seedlings grew for about two months before the experiment started in a naturally lit greenhouse under semicontrolled conditions (only shelter from rain) with a temperature range of 20–38°C and relative humidity range of 50–70% from 1 June to 20 September 2008 at Panzhihua, Sichuan Province, China. Panzhihua falls into the subtropical monsoon climate with dry winter and hot summer, and its annual rainfall, mean temperature, and mean relative humidity are 800 mm, 20.9°C, and 61%, respectively. Plants had 7–9 leaves at the beginning of the experiment and 23–32 leaves at the end. There was no difference in their developmental stage between the plants of various origins.

Uniform seedlings (75) of each provenance (in total 300 seedlings) were randomly subjected to three watering treatments, *i.e.*, 80, 50, and 30% of field capacity (FC) with their respective soil water contents of 25.6, 16, and 9.6% (w/w). The procedure used to maintain the soil water content was described by Yin *et al.* (2009b); the pots were weighed every two days and rewatered to their expected soil water content by replacing the amount of water that had transpired. Before the experiment, an empirical relationship between seedling fresh mass (Y [g]) and seedling height (X [cm]): $Y = 3.061\ X - 13.533$ ($R^2 = 0.874$, $P<0.001$) (Yin *et al.* 2012) was obtained from 38 plants with different sizes of four provenances. During the experiment, it was used to adjust the amount of water in each pot following changes in plant biomass. In the greenhouse, each combination of the treatment and provenance was arranged parallel to the arch of greenhouse. To avoid systematic error due to the possible differences caused by marginal effects in the greenhouse, the plants were rotated every ten days during the experiment.

Growth, biomass, and δ^{13}C measurements: Plant height and basal diameter of five representative (in their height, diameter, and biomass) seedlings from each treatment were measured at the end of the experimental period. Afterwards, the plants were harvested and divided into leaves, stems, and roots followed by drying up all samples to constant mass (first 15 min at 105°C and then 48 h at 70°C). Samples were then weighed and a root/shoot ratio (R_s) was calculated. For δ^{13}C analysis, the third mature and exposed leaves from the top of plant, which became fully expanded during the imposition of the watering regimes, were harvested (five harvested seedlings of each provenance and treatment). Samples were ground to fine powder for δ^{13}C analysis (Li *et al.* 2000) using a mass spectrometer (*Finnegan MAT Delta V Advantage*, Germany).

Gas exchange, Chl fluorescence, and Chl concentration measurements: Gas exchange was measured with a portable photosynthesis system (*LI-6400*, *Li-cor*, Lincoln, NE, USA) from the third to the fifth fully-expanded leaves of the main stem during 14–16 August, 2008. Net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured at a reference ambient chamber CO_2 concentration (C_a) (400 ± 1 μmol mol^{-1}) by using a CO_2 injector mixer. The environmental conditions during the measurements were: air temperature of 30–31°C; leaf-air vapor pressure deficit of 1.8 ± 0.2 kPa; relative air humidity of 59 ± 2%; PAR of 1,600 μmol(photon) m^{-2} s^{-1} in the leaf chamber using a *6400-02B LED* light source. The stomatal limitation value (L_s) was calculated according to Berry and Downton (1982) using the following formula:
$L_s = 1 - C_i/C_a$.

Chl fluorescence measurements were performed with a portable fluorometer (*PAM-2100*, *Walz*, Effeltrich, Germany). Leaves were darkened for 30 min before measurements. The parameters were determined according to Rosenqvist and van Kooten (2003). Maximal quantum yield of PSII photochemistry was estimated from the variable to maximum fluorescence ratio (F_v/F_m). Determination of leaf Chl *a* and Chl *b* was carried out according to the method of Inskeep and Bloom (1985). Leaf tissues were homogenized in chilled acetone (volume fraction 80%), after centrifugation, the absorbance of the supernatant was determined with a spectrometer (*UV330*, *Unicam,* UK). Total carotenoids (Car) were measured as described by Lichtenthaler and Wellburn (1983).

Statistical analysis: Statistical significance of effects of the provenance, watering regime, and their interaction (as "Pr", "W", and "Pr × W") were assessed with *SPSS 11.5* for *Windows* statistical software package by two-way analysis of variance (*ANOVA*) using General Linear Model procedure (specify model: full factorial; sum of squares: type III) and means of five replicates from each treatment were compared by the *Tukey*'s test. Data were plotted using *OriginPro 8.5* for *Windows* and the relationships between g_s and other parameters were performed by regression or exponential fitting.

Results

Growth, biomass accumulation, and R_s: The growth and biomass accumulation were affected by the provenance, watering regime, and their interaction (Table 1). For each provenance, plant height, basal diameter, and biomass accumulation significantly decreased with the decline of the soil water content. Compared with other provenances, the P1 showed the largest plant height and total biomass under the same watering regime, while P4 showed the lowest total biomass under 30% FC. However, R_s was not affected by the provenance, but by the watering regime and provenance × watering interaction (Table 1). With the decrease of the soil water content, R_s was not affected by watering treatment except a decrease in P4.

Gas exchange and Chl fluorescence: Regarding the gas-exchange parameters, P_N was marginally affected by the watering regime, and significantly affected by the provenance and the provenance × watering interaction (Table 2). Only P_N in P4 decreased with the decline of the soil water content. However, g_s, E, and L_s were only affected by the provenance and watering treatment. Namely, g_s and E significantly decreased, and L_s significantly increased with the decline of the soil water content in all four provenances. Compared to other provenances, P4 exhibited the lowest g_s and E and the highest L_s, especially, at 30% FC. In addition, F_v/F_m was not significantly affected by watering, but by the provenance and their interaction.

Pigment contents and δ^{13}C: Except for Chl *a*, which was not affected by the provenance, the pigment contents were significantly affected by the provenance, watering, and their interaction (Table 3). Contents of Chl *a*, Chl *b*, and Car increased with the decline of the soil water content; P4 showed the highest pigment contents under 30% FC. Overall, δ^{13}C was only affected by the watering regime; it increased significantly with the decline of the soil water content (Table 3).

Table 1. Effects of watering regimes on plant growth and biomass accumulation in *Jatropha curcas* provenances. Data are shown as means of five replications of each provenance or each watering regime at the end of a 2-month experimental period. *Different letters* indicate significant differences between the provenances or treatments ($P<0.05$). FC – soil field capacity; Pr – provenance effect; W – watering effect; Pr × W – interaction effect of provenance and watering as determined by two-way analyses of variance.

Provenance	Treatment	Total biomass [g]	Plant height [cm]	Basal diameter [mm]	Root/shoot ratio
P1	80% FC	110.3^{a}	73.5^{a}	30.1^{a}	0.37^{cde}
	50% FC	83.2^{c}	51.5^{cd}	27.9^{b}	0.45^{bc}
	30% FC	46.0^{e}	45.8^{e}	23.1^{d}	0.34^{de}
P2	80% FC	96.6^{b}	55.9^{bc}	30.1^{a}	0.50^{ab}
	50% FC	63.1^{d}	47.4^{de}	27.3^{b}	0.41^{bcde}
	30% FC	37.1^{f}	39.1^{f}	21.2^{e}	0.45^{bc}
P3	80% FC	97.9^{b}	51.9^{cd}	30.8^{a}	0.46^{bc}
	50% FC	58.0^{d}	44.2^{e}	27.4^{b}	0.46^{bc}
	30% FC	28.8^{g}	39.2^{f}	19.8^{e}	0.36^{cde}
P4	80% FC	94.3^{b}	57.8^{b}	29.7^{a}	0.57^{a}
	50% FC	47.7^{e}	44.0^{e}	24.8^{c}	0.44^{bcd}
	30% FC	17.6^{h}	29.4^{g}	15.6^{f}	0.31^{e}
Significance	Pr	< 0.001	< 0.001	< 0.001	0.093
	W	< 0.001	< 0.001	< 0.001	< 0.001
	Pr × W	0.018	< 0.001	< 0.001	0.002

Table 2. Effects of watering regimes on gas-exchange characteristics and chlorophyll fluorescence in *Jatropha curcas* provenances. Data are shown as means of five replications of each provenance or each watering regime at the end of a 2-month experimental period. *Different letters* indicate significant differences between provenances or treatments ($P<0.05$). P_N – net photosynthetic rate; g_s – stomatal conductance; L_s – stomatal limitation value; E – transpiration rate; F_v/F_m – maximal quantum yield of PSII photochemistry.

Provenance	Treatment	P_N [μmol m^{-2} s^{-1}]	g_s [mol(H$_2$O) m^{-2} s^{-1}]	L_s	E [mmol(H$_2$O) m^{-2} s^{-1}]	F_v/F_m
P1	80% FC	10.92^{a}	0.15^{ab}	0.37^{cd}	2.19^{ab}	0.825^{abcd}
	50% FC	10.61^{a}	0.11^{ab}	0.49^{abcd}	1.83^{ab}	0.834^{ab}
	30% FC	7.61^{abc}	0.06^{ab}	0.61^{abcd}	1.14^{ab}	0.845^{a}
P2	80% FC	11.02^{a}	0.18^{a}	0.35^{d}	2.85^{a}	0.820^{abcde}
	50% FC	10.90^{a}	0.13^{ab}	0.43^{bcd}	2.30^{ab}	0.829^{abc}
	30% FC	11.88^{a}	0.08^{ab}	0.65^{abc}	1.76^{ab}	0.809^{bcde}
P3	80% FC	9.78^{ab}	0.15^{ab}	0.37^{cd}	2.58^{a}	0.795^{e}
	50% FC	11.46^{a}	0.10^{ab}	0.56^{abcd}	1.95^{ab}	0.814^{bcde}
	30% FC	9.82^{ab}	0.07^{ab}	0.69^{ab}	1.47^{ab}	0.802^{de}
P4	80% FC	10.08^{ab}	0.14^{ab}	0.58^{abcd}	2.36^{ab}	0.804^{cde}
	50% FC	2.61^{bc}	0.02^{b}	0.55^{abcd}	0.52^{b}	0.795^{e}
	30% FC	1.52^{c}	0.01^{b}	0.77^{a}	0.34^{b}	0.798^{e}
Significance	Pr	< 0.001	0.033	0.011	0.006	< 0.001
	W	0.051	< 0.001	< 0.001	< 0.001	0.202
	Pr × W	0.030	0.802	0.637	0.649	0.014

Discussion

In the present study, 10-L pots (bigger than 6.5-L pots used by Maes *et al.* 2009b) were used in order to cultivate *J. curcas* seedlings. No limitations of root development by the pot size were found when plants were harvested. The root biomass (data not shown) was the highest in P4 under 80% FC (34.16 ± 2.05 g) and smallest in P4 under 30% FC (4.18 ± 0.58 g) across all provenances and treatments, and the similar trend was detected also in R_s. Therefore, we can conclude that the pots did not limit the root development of other provenances and treatments. The most possible limitation occurred in P4 under 80% FC, which did not impact our results.

Table 3. Effects of watering regimes on gas-exchange characteristics in *Jatropha curcas* provenances. Data are shown as means of five replications of each provenance or each watering regime at the end of a 2-month experimental period. *Different letters* indicate significant differences between provenances or treatments ($P<0.05$). Chl – chlorophyll; Car – carotenoids; $\delta^{13}C$ – carbon isotope composition.

Provenance	Treatment	Chl *a* [mg g^{-1}(FM)]	Chl *b* [mg g^{-1}(FM)]	Car [mg g^{-1}(FM)]	$\delta^{13}C$ [‰]
P1	80% FC	1.07^{d}	0.24^{d}	0.24^{d}	-27.84^{e}
	50% FC	1.46^{c}	0.36^{bc}	0.34^{c}	-26.90^{cd}
	30% FC	1.59^{bc}	0.37^{bc}	0.37^{c}	-26.61^{bcd}
P2	80% FC	0.81^{d}	0.18^{d}	0.19^{d}	-28.13^{e}
	50% FC	1.59^{bc}	0.39^{bc}	0.38^{c}	-27.30^{de}
	30% FC	1.86^{b}	0.44^{b}	0.41^{c}	-26.10^{abc}
P3	80% FC	0.91^{d}	0.21^{d}	0.21^{d}	-28.04^{e}
	50% FC	1.52^{c}	0.36^{bc}	0.38^{c}	-26.33^{bcd}
	30% FC	2.16^{a}	0.57^{a}	0.49^{b}	-25.77^{ab}
P4	80% FC	0.99^{d}	0.21^{d}	0.24^{d}	-28.04^{e}
	50% FC	1.40^{c}	0.35^{c}	0.36^{c}	-26.54^{bcd}
	30% FC	2.31^{a}	0.64^{a}	0.55^{a}	-25.28^{a}
Significance	Pr	0.096	0.007	0.007	0.079
	W	< 0.001	< 0.001	< 0.001	< 0.001
	Pr × W	0.003	< 0.001	0.003	0.236

Significant provenance effects on plant growth (biomass, height, and stem diameter) were detected in this study (Table 1), which was similar to a previous report (Rao *et al.* 2008). Regarding to gas-exchange and Chl fluorescence parameters (P_N, g_s, E, L_s, and F_v/F_m, Table 2), provenance differences were detected in the present study. In contrast, only drought, but not accession effect was found by Maes *et al.* (2009b) and Sapeta *et al.* (2013). As one of the possible reasons, we suggest that *J. curcas* is an undomesticated plant for above mentioned regions (Rao *et al.* 2008, Maes *et al.* 2009c) and has low genetic diversity (Popluechai *et al.* 2009, Ovando-Medina *et al.* 2011). In contrast, *J. curcas* has been grown in China for more than 300 years and it has become naturalised (Ye *et al.* 2009). In this study, three provenances (P2, P3, and P4) were from the southwest of the Sichuan province with the subtropical monsoon climate in the Jinshajiang River, dry-hot valley southwest of China, while P1 is from the Hainan province with the tropical maritime climate in southeast of China. Thus, we suggest the provenance differences in responses to watering regimes could be explained by their contrasting origins, which needs to be further confirmed by their genetic differences.

Plant biomass was affected by the provenance, watering, and their interaction (Table 1). Growth decreased significantly by the low soil water content, which was observed also by others (Achten *et al.* 2010). The largest plant height and total biomass were observed in the P1; P4 exhibited the smallest height and biomass under the same watering regime. For P4, the total biomass at 30% FC was only 18.7% of that at 80% FC with the largest reduction in biomass under the low soil water among all four provenances. It indicated that the P4 from the xeric habitat possesed stronger plasticity in the plant size than other provenances under drought. Moreover, R_s was affected by the watering regime and the interaction with the provenance. R_s decreased due to the decline of the soil water content and this effect was most pronounced in P4 (Table 1). This observation implied that root growth was lower than shoot growth under low water availability. Although the increase in R_s has been reported for *J. curcas* in response to drought (Díaz-López *et al.* 2012), this effect was not observed in this experiment, which is in agreement with the previous report of Sapeta *et al.* (2013). The probable reasons were that plant acclimations may have occurred with appropriate reduction in a plant size (Sapeta *et al.* 2013) and/or R_s was adjusted by soil water and nutrient availability (Yin *et al.* 2012).

In all provenances, g_s and E significantly decreased, and L_s increased following the reduced soil water contents (Table 2). Furthermore, P_N was affected by the provenance and the interaction of provenance and watering (Table 2). In particular, P1 had higher P_N under 80 and 50% FC compared to that under 30% FC. P_N of P2 and P3 was not affected by watering while P_N in P4 decreased gradually by the low soil water content. P4 had the lowest g_s and

E, highest L_s and less negative $\delta^{13}C$, especially under 30% FC (Tables 2, 3), while these parameters were similar in the other provenances. F_v/F_m is widely used as a reliable diagnostic indicator of photoinhibition of plants in response to stresses (Maxwell and Johnson 2000). In the present study, F_v/F_m ranged from 0.795 to 0.845 and was not affected by water availability, which indicated that the low soil water content did not inhibit PSII. Regarding to possible relationships among gas-exchange parameters, the fitting analysis revealed that P_N increased exponentially to its maximum with the increase of g_s while g_s was correlated negatively with L_s (Fig. 1). Therefore, in *J. curcas*, changes in P_N could be partially attributed to stomatal limitation at least. This was additionally confirmed by the observation that photosynthesis limitation was not affected by photochemical processes (F_v/F_m, Table 2). The inhibition of photosynthesis due to stomata closure is a reversible process since photosynthesis can recover from stress when enough water is supplied again (Varone *et al.* 2012). Moreover, pigment concentrations can reflect the level of photosynthesis (Jiang *et al.* 2007). Chl *a*, Chl *b*, and Car concentrations significantly increased with the decrease of the soil water content and the significant effect of interaction was also detected (Table 3). This may be the reason for nearly unaffected gas exchange for P2 and P3 under 30% FC. $\delta^{13}C$ increased significantly with the decline of the soil water contents in each provenance, which should be attributed to the decrease in g_s and *E* under the lowest water supply.

The present findings pointed to stomatal limitation of P_N and finally a reduction of growth in *J. curcas* under low water availability. The increase of $\delta^{13}C$ should be attributed to the decrease in g_s and *E* under the lowest water supply. *J. curcas* could adapt to low water availability by adjusting its plant size, stomata closure, decreasing transpiration rate, increasing WUE, and leaf pigment concentrations. Effects of the provenance and the interaction with the watering regime were detected in growth and many physiological parameters. The provenance from the xeric habitat showed the stronger plasticity in the plant size than other provenances under drought. The variations may be used as criteria for variety/provenance selection and improvement of *J. curcas*.

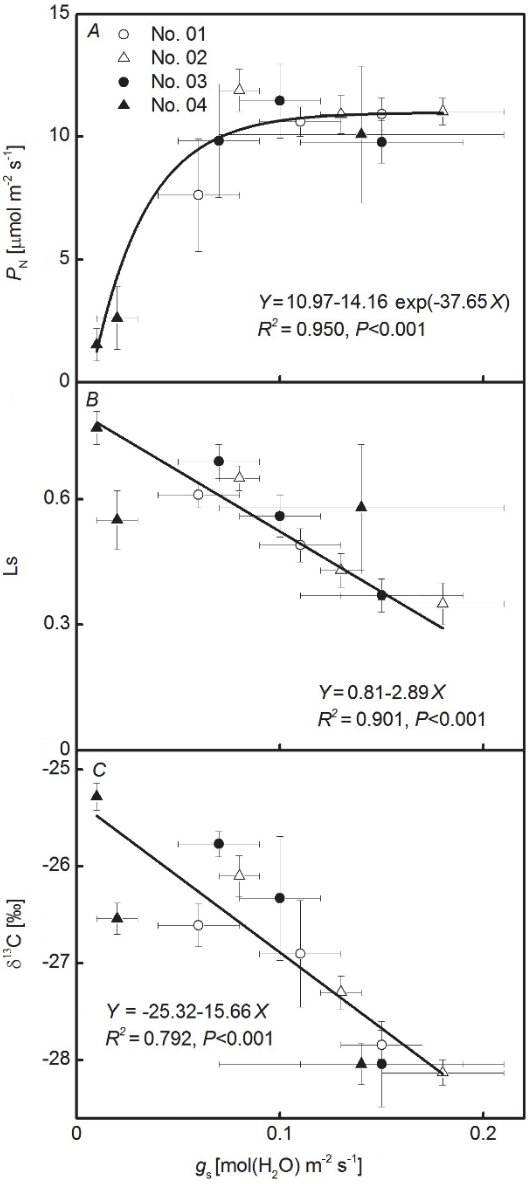

Fig. 1. Exponential and linear regressions of net photosynthetic rate (P_N) (*A*), stomatal limitation value (L_s) (*B*), and carbon isotope composition ($\delta^{13}C$) (*C*) on changes of stomatal conductance in *Jatropha curcas*. Fitting equations, determination coefficients, and significance levels were given.

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