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Photosynthetic responses of *Jatropha curcas* to spider mite injury

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Abstract

The spider mite *Tetranychus urticae* Koch is emerging as a major problem in *Jatropha curcas* cultivation. The goal of this study was to investigate the photosynthetic responses of *Jatropha* to spider mite infestation. Leaf CO_2 assimilation rate, stomatal conductance, transpiration, intracellular CO_2 concentration, and instantaneous carboxylation efficiency significantly decreased in mite-infested leaves compared with controls. Lower water content and specific leaf area of the mite-infested leaves were positively related to symptoms of wrinkling and curling. Leaf electrolyte leakage remained unchanged in the mite-infested leaves, revealing no effect on leaf membrane integrity. Leaves exhibited reductions in soluble protein and soluble sugar in association with photosynthetic impairment. Although decreases in photochemical activity and chlorophyll fluorescence parameters suggested damage to the photosynthetic apparatus, although there were no measurable reductions in chlorophyll or carotenoid contents associated with photosynthetic apparatus impairment. The decrease in the leaf CO_2 assimilation rate was partially attributed to stomatal and metabolic limitations in the mite-infested leaves.

Additional key words: biodiesel; gas exchange; membrane damage; photosynthetic pigments; physiological response.

Introduction

Fossil fuels, such as petroleum and natural gas, are our most important energy sources, and demand for them continues to increase as world population and economy grows. Energy supply is becoming increasingly problematic due to the depletion of fossil fuel reserves and the escalating price of oil. In addition, deleterious waste products produced by the combustion of fossil fuels create a number of ecological problems including the greenhouse effect. Recent oil crises and environmental concerns encourage search for fossil fuel substitutes to reduce our dependency on crude oil (Fischer and Schrattenholzer 2001). Bioenergy is a renewable source of primary energy and its sustainable use does not increase emissions of carbon dioxide. *Jatropha* (*J. curcas* L.) is a crop important for biodiesel production, being considered a potential, universally accepted source of energy (Kumar and Sharma 2008).

Jatropha, belonging to the family of Euphorbiaceae, is a large succulent shrub or small tree originating from Central America. It is drought resistant, thriving well in many tropical and subtropical regions throughout Africa and Asia, where an average annual rainfall ranges from 200 to 1,500 mm (Openshaw 2000). The nonedible seed oil content is about 30–40% and has multiple industrial applications (Pramanik 2003). Seed oil consists mainly of fatty acids, such as palmitic acid (14–15%), stearic acid (3.7–9.8%), oleic acid (34–45%), and linoleic acid (29–44%) (Berchmans and Hirata 2008).

Studies on the use of *Jatropha* seed oil for industrial applications have been recently carried out (Koh and Mohd Ghazi 2011). The oil is used for making candles, varnish, soaps, and lubricants, and for illumination. It can also serve as fuel for diesel engines or to be converted into

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Abbreviations: Car – carotenoids; CE – instantaneous carboxylation efficiency; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration; EL – electrolyte leakage; F_0 – initial fluorescence; F_m – maximum fluorescence; F_v – variable fluorescence; F_v/F_m – maximum quantum efficiency of PSII; g_s – stomatal conductance; MD – membrane damage; P_N – photosynthetic CO_2 assimilation; RWC – relative water content; SLA– specific leaf area; WUE – water-use efficiency.

biodiesel by the transesterification process (Berchmans and Hirata 2008). The seedcake that remains after oil extraction is used as an organic fertilizer (Kumar and Sharma 2008). Detoxification of seedcake could also allow its use as livestock feed, as it is rich in crude protein (Wang *et al*. 2011).

Jatropha has been assumed to suffer relatively little damage from pests and thus have minimal requirements for plant protection. However, in reality, when *Jatropha* is grown in continuous stretches as a monocrop, it is devastated by insect pests and diseases that are emerging as major problems for its cultivation (Terren *et al*. 2012). Mites (*Tetranychus urticae* Koch and *Polyphagotarsonemus latus* Banks) are considered important pests that reduce *Jatropha* yield and seed quality. The spider mite, *T. urticae*, has a very broad range of host plants with economic importance, including beans, soybean, castor bean, cotton, grape, rose, strawberry, tomato, peach, and papaya (Greco *et al*. 2006). Spider mites feed primarily on the undersurfaces of leaves (Jeppson *et al*. 1975). The feeding apparatus of this mite penetrates leaves to withdraw plant sap, specifically disrupting mesophyll cells under the epidermis (Hislop and Jeppson 1976). Infested leaves are distorted, which is followed by complete defoliation if mites are not controlled.

The photosynthetic responses of plants to spider mite injury have been studied (Sadras and Wilson 1997, Haile and Higley 2003, Bueno *et al*. 2009). Evaristo *et al*. (2013) reported that the damage to *Jatropha* growth due to broad mite (*P. latus*) injury is caused by reductions in the photosynthetic rate, stomatal conductance, and leaf transpiration. However, the impact of leaf-feeding spider mites on *Jatropha* leaf photosynthesis has not been investigated. Our hypothesis was that *Jatropha* plants had distinct photosynthetic and physiological behavior in the presence of infestation by spider mite compared to uninfested plants. We studied the effect of spider mite infestation on field grown *Jatropha* with respect to CO_2 assimilation, transpiration, stomata behavior, and physiological responses.

Materials and methods

***Jatropha* cultivation**: Experiments were carried out under field conditions at Kaohsiung, Taiwan. *Jatropha* seeds collected from Taiwan-grown plants were sown in pots and seedlings were raised in a greenhouse. After the second leaves had expanded, healthy seedlings were transplanted into the field under 3 × 2 m spacing in March 2012. Each plant received 60 g of slow-release fertilizer (*Hi-Control*, Japan; N:P:K ratio = 14:12:14). Plants were infested with spider mites in October 2012. Infestation by *T. urticae* Koch was carried out by transferring 50–70 spider mites collected from naturally infested plants onto leaves of the experimental plants. Fully expanded 6th-position leaves were used for photosynthetic response measurements two weeks after the spider mite infestation. Uninfested plants comprised the controls.

Determination of photosynthesis and chlorophyll (Chl) fluorescence: Photosynthetic CO_2 assimilation (P_N), stomatal conductance (g_s), transpiration (E), and intercellular CO_2 concentration (C_i) were measured by an open portable photosynthesis system (*LI-6400XT*, *LI-COR*, USA) equipped with a CO_2 injector and LED light source. Water-use efficiency (P_N/E) and instantaneous carboxylation efficiency (P_N/C_i) were also calculated. Light-response curves were obtained by varying the PPFD between 0–2,000 μmol m^{-2} s^{-1} with the following settings: temperature of 26°C, CO_2 concentration of 400 μmol mol^{-1}, and chamber humidity of 45–55%. Chl fluorescence was evaluated with a leaf chamber fluorometer (*6400-40*, *LI-COR*, USA). Initial (F_0), maximum (F_m), variable ($F_v = F_m - F_0$) fluorescence, the F_v/F_0 ratio, and maximum quantum efficiency of PSII (F_v/F_m) were measured from dark-adapted (30 min) leaves.

Water content and specific leaf area: Leaves were collected and fresh mass (FM) was determined. Leaf samples were dried in a drying oven for 48 h at 70°C to constant mass and their dry mass (DM) was determined. Relative water content (RWC [%]) was calculated as (FM – DM)/FM × 100. Leaf area (LA) was measured with a leaf area meter (*LI-3100*, *LI-COR*, USA), and then specific leaf area (SLA = LA/DM) was calculated.

Electrolyte leakage, a measure of cell membrane damage, was assessed as described by Lutts *et al*. (1996). Leaf discs were placed in test tubes containing 10 mL of deionized water and incubated at 25°C in a water bath for 6 h, after which the electrical conductivity of the solution (L1) was determined. Samples were then boiled at 100°C for 1 h, and the last electrical conductivity (L2) reading was obtained after equilibration at 25°C. Electrolyte leakage (EL) was defined as EL [%] = (L1/L2) × 100.

Photosynthetic pigments: In order to assay pigments, soluble proteins, and soluble sugars, fresh leaves were ground to fine powder in liquid nitrogen. Photosynthetic pigments, Chl and carotenoids (Car), were eluted from leaf samples (DM of 0.05 g) with 80% acetone at 4°C overnight and determined by the methods of Porra *et al*. (1989) and Holm (1954), respectively. Samples were centrifuged at 13,000 × *g* for 5 min, and their supernatants were used to determine the absorbances of Chl *a*, Chl *b*, and Car in acetone, as measured with a spectrophotometer (*U-3010*, *Hitachi*, Tokyo, Japan) at wavelengths of 663, 645, and 470 nm, respectively.

Soluble proteins were determined by the Bradford (1976)

method. Samples (DM of 0.05 g) were added to 3 ml of a phosphate-buffered solution (pH 7.0). Extracts were centrifuged at 13,000 × *g* for 15 min at 4°C, and 0.1 ml of the supernatants were combined with 4.9 ml of a Coomassie Brilliant Blue G-250 solution (0.1 g L^{-1}). After 2 min, the soluble protein content was determined at a wavelength of 595 nm with a *Hitachi U3010* (Japan) UV-visible spectrophotometer, using crystalline bovine serum albumin as standard.

Soluble sugar content was measured by the method of Fairbairn (1953). Each sample (0.05 g of DM) was put in a test tube and 5 ml of distilled water was added and mixed. After 30 min in a water bath at 85°C, the supernatant was collected. This step was repeated twice, and then distilled water was added to a volume of 10 ml. Soluble sugar content was determined with the sulfuric acid anthrone method at a wavelength of 620 nm and with a *Hitachi U3010* UV-visible spectrophotometer, using glucose as standard.

Statistical analysis: Data were analyzed using the *SAS 9.1* (*SAS Institute*, Cary, USA). The means of six replicates were assessed for significant differences by a *Student*'s *t*-test.

Results

Physiological parameters: Spider mites feed on the lower surfaces of *Jatropha* leaves and cause visual symptoms of wrinkling with leaf margins curled downwards (Fig. 1). *Jatropha* plants also showed distinct physiological responses to spider mite infestation (Table 1). RWC and SLA significantly decreased by the spider mite infestation. Membrane damage (MD) as measured by leaf electrolyte leakage, a membrane integrity indicator, remained unchanged in the spider mite-infested plants compared with controls. Chl *a* contents were higher than Chl *b* contents in leaves of both control and infested plants. However, no significant differences were observed in pigments (Chl *a*, Chl *b*, and Car) regardless of the spider mite infestation. In contrast to membrane integrity and pigment content, soluble proteins and sugars decreased significantly under the spider mite infestation, exhibiting 26 and 20% reductions, respectively, in comparison with controls (Table 1).

Photosynthetic characteristics: P_N decreased markedly in the infested plants at PPFD over 250 µmol m^{-2} s^{-1}, while no significant difference was found between the control and infested plants at lower PPFD levels (Fig. 2*A*). P_N in the control plants became light-saturated over approximately 1,000 µmol(photon) m^{-2} s^{-1} with a maximum CO_2 assimilation rate of 19.0 µmol m^{-2} s^{-1}. In contrast, the infested leaves showed lower P_N with saturation points at approximately 500 µmol(photon) m^{-2} s^{-1} and a maximum value of 11.4 µmol(CO_2) m^{-2} s^{-1}. Stomatal conductance (g_s) and *E* increased as PPFD increased in the control and infested plants. Compared with the controls, g_s and *E* decreased significantly in the infested plants at PPFD of 0–2,000 µmol m^{-2} s^{-1} (Fig. 2*B*,*C*). C_i decreased drastically at lower PPFD, whereas values remained steady at higher PPFD. As observed for P_N, C_i decreased significantly in the infested plants at PPFD over 250 µmol m^{-2} s^{-1} when compared with the controls (Fig. 2*D*).

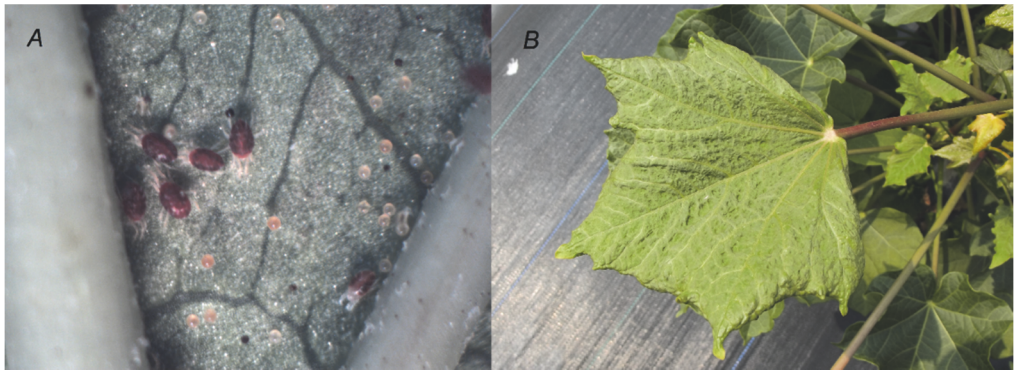

Fig. 1. Spider mites feed on the lower surfaces of leaves (*A*), and infested leaves exhibit wrinkling with margins curled downwards (*B*).

Table 1. Water content (RWC), specific leaf area (SLA), membrane damage (MD), and concentrations of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), carotenoids (Car), soluble proteins, and soluble sugars in control and mite-infested *Jatropha curcas* leaves. Values are mean ± SD of six replicates. * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$ (*t*-test).

Treatment	RWC [%]	SLA [m^2 kg^{-1}]	MD [%]	Chl *a* [mg g^{-1}(DM)]	Chl *b* [mg g^{-1}(DM)]	Car [mg g^{-1}(DM)]	Soluble protein [mg g^{-1}(DM)]	Soluble sugar [mg g^{-1}(DM)]
Control	74.4 ± 0.9	15.9 ± 1.1	11.8 ± 2.3	4.80 ± 0.82	1.38 ± 0.24	1.16 ± 0.16	15.8 ± 1.0	123.5 ± 12.1
Mite-infested	71.5 ± 3.5*	12.9 ± 1.0***	10.7 ± 0.7	4.59 ± 0.20	1.59 ± 0.19	1.13 ± 0.08	11.7 ± 3.7*	98.9 ± 11.0**

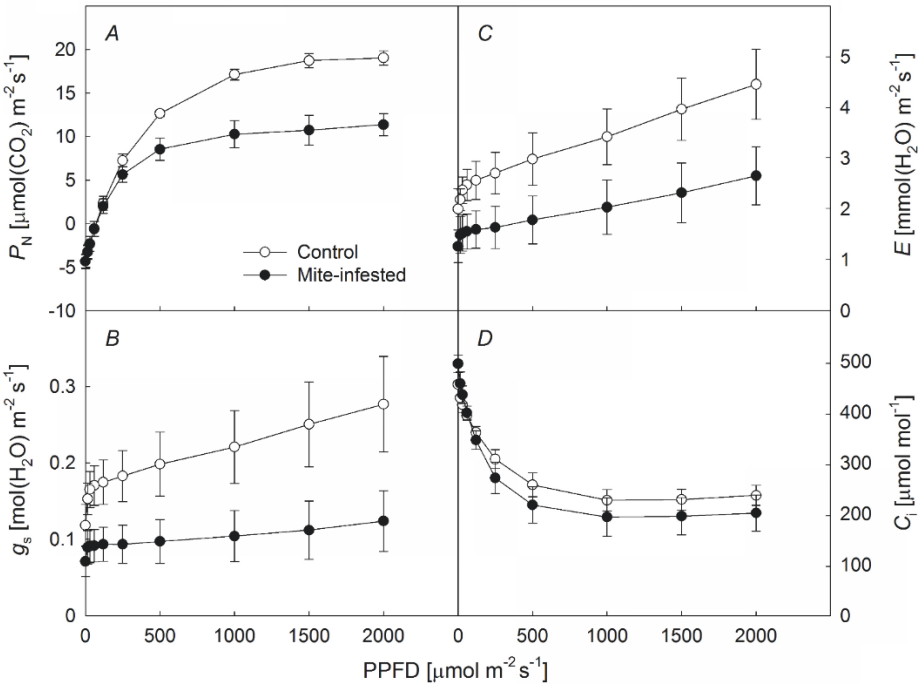

Fig. 2. Light-response curve of leaf CO_2 assimilation rate (P_N) (*A*), stomatal conductance (g_s) (*B*), transpiration (*E*) (*C*), and intracellular CO_2 concentration (C_i) (*D*), in control and mite-infested *Jatropha curcas* leaves. Values are means ± SD of six replicates.

There was no significant difference in the WUE (P_N/E) ratio between the infested and control plants (Fig. 3*A*). The CE (P_N/C_i) ratio of the infested plants decreased by 19.2–32.3% at PPFD over 500 μmol m^{-2} s^{-1} in comparison with the controls (Fig. 3*B*).

Photochemical activity: Photochemical activity was evaluated by initial (F_0), maximum (F_m), and variable (F_v) fluorescence values, the F_v/F_0 ratio, and the maximum quantum efficiency of PSII (F_v/F_m). F_0 showed a slight decrease in the infested plants, but it was not significant. F_m and F_v values decreased markedly by 16.5 and 18.7%, respectively, in the plants subjected to the spider mite infestation. Additionally, F_v/F_0 and F_m/F_0 decreased significantly in the infested plants as compared with the controls (Table 2).

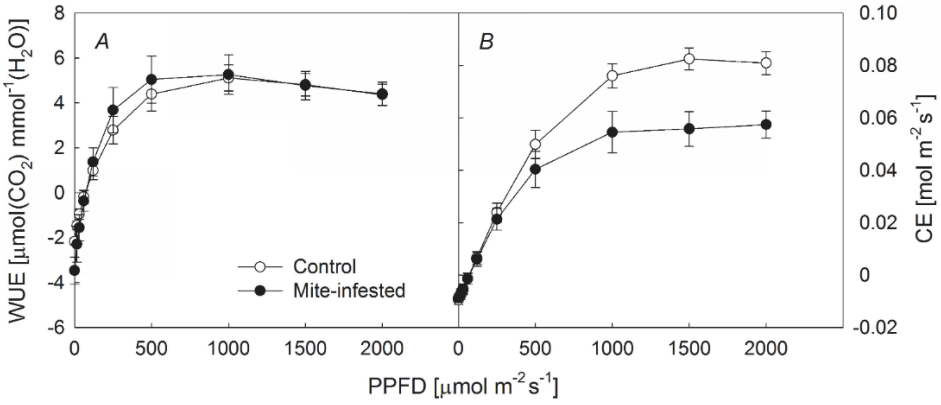

Fig. 3. Light-response curve of water-use efficiency (WUE) (*A*) and instantaneous carboxylation efficiency (CE) (*B*) of control and mite-infested *Jatropha curcas* leaves. Values are means ± SD of six replicates.

Table 2. Initial (F_0), maximum (F_m), and variable (F_v) fluorescence, F_v/F_0 ratio, and maximum quantum efficiency of PSII (F_v/F_m) in control and mite-infested *Jatropha curcas* leaves. Values are mean ± SD of six replicates. * – $p<0.05$; ** – $p<0.01$; *** – $p<0.001$ (*t*-test).

Treatment	F_0	F_m	F_v	F_v/F_0	F_v/F_m
Control	124.7 ± 4.5	708.1 ± 26.0	583.3 ± 26.5	4.68 ± 0.29	0.82 ± 0.01
Mite-infested	117.3 ± 9.0	591.6 ± 25.5***	474.3 ± 23.9***	4.06 ± 0.38**	0.80 ± 0.01**

Discussion

Physiological responses: The present study indicates that spider mite infestations induced significant changes in physiological processes associated with water relations, leaf gas exchange, and photochemical activity in *Jatropha* plants. Spider mite damage is similar to that of the broad mite; initially, infested leaves are slightly wrinkled with their margins curled downwards; the curling increases over time and later leaves exhibit a crepe paper appearance (Lopes 2009, Evaristo *et al*. 2013). RWC and SLA values in *Jatropha* leaves were lower in the spider mite-infested plants than those in the controls. The infested leaves appeared to be collapsed due to leaf water loss, reflecting their wrinkled and curled symptoms. Spider mites penetrate the lower surface of *Jatropha* leaves to suck fluids from mesophyll cells. Indirect damage also occurs to surrounding epidermal cells during feeding, resulting in their collapse (Reddall *et al*. 2004).

Tissue electrolyte leakage has long been used to evaluate membrane damage in plants induced by stress. The observed increased electrolyte leakage suggests that the injuries induced in the plasma membrane were a consequence of oxidative damage (Silva *et al*. 2010). Several studies have reported that injuries caused by pest stresses on plant cells are triggered in part by oxidative stress (Leitner *et al*. 2005, Khattab 2007, Sivritepe *et al*. 2009). However, this study showed that spider mite-induced biotic stress caused no membrane damage in *Jatropha* plants. Though spider mites pierced and sucked fluids from plant cells, membrane integrity was not damaged by the mite infestation.

Numerous investigations have demonstrated that chlorosis is the most obvious symptom of injury by spider mites and is indicative of Chl loss (Landeros *et al*. 2004, Reddall *et al*. 2004, Sivritepe *et al*. 2009). The decrease in Chl content was possibly due to mechanical damage to the chloroplast during mite infestation and due to the effect of ROS-mediated lipid peroxidation (Khattab 2007, Sivritepe *et al*. 2009). However, the present study showed that Chl *a*, Chl *b*, and Car were little affected by the spider mite infestation. Bueno *et al*. (2009) also reported no significant reduction in leaf Chl content in soybeans infested with spider mites. The unchanged Chl content in mite-infested leaves may be due to the short exposure time to pest attack (Evaristo *et al*. 2013). Therefore, mite exposure time might be insufficient to cause membrane damage or reduce Chl content. Grinberg *et al*. (2005) reported that interaction between cucumber plants and the broad mite, *P. latus*, feeding causes dramatic morphological, structural, and ultrastructural changes. Infested plants showed growth inhibition and a decrease in the leaf number and leaf area. The infested leaves also became firmer. Severe infestation led to a complete loss of epidermis and to increase in a mesophyll cell size and number. The entire epidermal tissue seemed to collapse and the mesophyll cell walls appeared thick and distorted. Moreover, Bueno *et al*. (2009) demonstrated photosynthetic response of soybean interacted with spider mite *T. urticae* Koch. A significant photosynthetic rate reduction was observed due to stomatal limitation. However, plants did not show Chl content reduction associated with photosynthetic impairment and *T. urticae* injury did not impair the function of light harvesting and electron transport.

Spider mites suck water and nutrients from leaf cells. Mite feeding continually influences the contents of metabolic substances in surrounding tissues. Therefore, spider mite infestations may also impair the transport and distribution of nutrients, assimilates, water, and hormones (Poskuta *et al*. 1975, Sances *et al*. 1979, Reddall *et al*. 2004). This is supported in the current work where the soluble protein content of leaves was significantly changed by spider mites. The soluble protein content was reported to decrease in plants subjected to water stress (Sharma and Dubey 2005). This study showed that the spider mite-infested leaves contained significantly less water than the controls, suggesting that protein degradation in infested leaves might occur due to spider mite-induced water stress. In the mite-infested plants, the contents of soluble sugar in leaves were lower than in the controls. The effect of mite feeding on soluble sugars has been also reported in grape, chrysanthemum, bean, and cucumber plants (Fairbairn 1953, Tomczyk 2001, Sivritepe *et al*. 2009). This effect might be due to the drain of assimilates towards the mites and/or a decrease in photosynthesis induced by mites.

Gas exchange: Spider mite injury has been found to reduce leaf CO_2 assimilation, g_s, and E in apple (Ferree and Hall 1980, Lakso *et al*. 1996), cotton (Brito *et al*. 1986, Sadras and Wilson 1997, Reddall *et al*. 2007), peach (Mizell *et al*. 1986), soybean (Haile and Higley 2003, Bueno *et al*. 2009), and strawberry (Sances *et al*. 1982). The decrease in P_N and E of *Jatropha* infested with the spider mite seems to be caused by stomata limitation, which inhibits the exchange of CO_2 and H_2O. Decreased g_s might be caused by the suction of fluids from the intracellular leaf water content, reducing total leaf water content, which in turn reduced total leaf water content, and other biochemical factors, such as enzymatic activity interact in spider mite-infested plants. Spider mites suck the contents of mesophyll cells and then injury occurs to epidermal cells through dehydration of mesophyll. Epidermal cells, including stomatal guard cells, consequently dehydrate, which results in closing the stomatal pores and it prevents gas exchange. Thus, CO_2 is not transported into mesophyll cells for conversion to sugar *via* the photosynthetic process (Reddall *et al*. 2004, 2007). Photosynthesis is also dependent on biochemical carbon fixation, which takes place inside leaf tissues. Biochemical impairment of leaf tissues by spider mites can therefore also affect photosynthesis. In the present study, reductions in instantaneous carboxylation efficiency (P_N/C_i) indicated

some metabolic limitation on the photosynthesis in the injured plants. The activity and/or quantity of Rubisco carboxylation might be lower in the mite-infested leaves in correlation with reduced soluble proteins, which constitute 40% of Rubisco. In addition, an effective quantum yield of PSII in response to light and in relation to P_N values need to be compared between control and infested plants. This would facilitate our understanding of the mite's effects on the photochemical processes in PSII and thylakoid membrane components involved in linear photosynthetic electron transport in *J. curcas*.

Photochemical response: Although spider mite infestation had little effect on the leaf Chl content in *Jatropha*, it affected photochemical activity significantly, suggesting that the photosynthetic apparatus is highly susceptible to such pest stress. The present study showed significantly lower F_v, F_m, F_v/F_0, and F_v/F_m values in the spider mite-infested leaves relative to controls, indicating that the infested leaves had a lower PSII efficiency. Among these four parameters, F_m is the main factor showing the significant decrease in the spider mite-infested leaves. When plants are subjected to stress, the quenching of F_v and F_m is involved in alterations in fluorescence parameters under unfavorable environmental conditions (Baker and Horton 1987). F_v/F_0 reflects the efficiency of the water-splitting complex on the donor side of PSII (Schreiber *et al*. 1995) and is the most sensitive component in the photosynthetic electron transport chain. Impairment of photosynthetic electron transport would result in the decline of F_v/F_0 (Pereira *et al*. 2000). The F_v/F_m ratio in most higher plants is close to 0.83 and is a measure of the potential quantum yield of PSII (Demmig and Björkman 1987). F_v/F_m reflects the maximum efficiency of excitation energy capture by open PSII reaction centers. A decrease in this parameter indicates downregulation of photosynthesis, or photoinhibition (Öquist *et al*. 1992). Therefore, the decrease in F_v/F_m and F_v/F_0 suggests the loss in photosynthesis is due to damage of the photosynthetic apparatus (Tan *et al*. 2008). Furthermore, a lowered yield of F_0' is also an important reference value, and therefore further characterization of the background chlorophyll fluorescence quenching, $(F_0 - F_0')/F_0$ (Bilger *et al*. 1986, Roháček *et al*. 1999) will be helpful in elucidating the photosynthetic decline manifested as inhibiting LHC function. In the study, the mite-infestation mainly reduced F_m rather than F_0, and F_m caused the significant decrease of F_v, F_v/F_0, and F_v/F_m in the spider mite-infested leaves.

Conclusion: Our study suggests that the lower photosynthetic activity of infected *Jatropha* plants might be caused by reduced stomatal conductance and possibly also by low carboxylation activity, but more detailed information is needed to determine conclusively the mechanism by which photosynthesis is reduced by spider mite feeding. The reduction in leaf photosynthesis by spider mites would undoubtedly lower photosynthetic production in infested plants, which eventually could be expected to reduce *Jatropha* growth and productivity.

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