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Photosynthesis, chlorophyll fluorescence, and antioxidant enzyme responses of invasive weed *Mikania micrantha* to *Bemisia tabaci* infestation

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Abstract

In a glasshouse, *Bemisia tabaci* infestation largely reduced response of photosynthesis to irradiance and CO_2 concentration of *Mikania micrantha* compared with the non-infested control (C) ones. The maximum irradiance-saturated photosynthetic rate (P_{max}) and saturation irradiance (SI) of the infested *M. micrantha* were only 21.3 % and 6.5 % of the C-plants, respectively. *B. tabaci* infestation led to the reduction of contents of chlorophyll and carotenoids in *M. micrantha*, which was accompanied with the decrease of actual photosystem 2 (PS2) efficiency (Φ_{PS2}), efficiency of excitation energy capture by open PS2 reaction centres (F_v'/F_m'), electron transport rate (ETR), and photochemical quenching (q_P). Moreover, superoxide dismutase and catalase activities significantly decreased while proline and glutathione contents significantly increased in infested *M. micrantha*. Hence *B. tabaci* infestation not only induced direct damage of photosynthetic apparatus but also altered the antioxidant enzymes activities in *M. micrantha*, which might as consequences accelerate senescence of this weed.

Additional key words: carotenoids; catalase; chlorophyll fluorescence; electron transport rate; glutathione; photochemical quenching; photosystem 2 efficiency; proline; superoxide dismutase.

Introduction

Mikania micrantha Kunth is an herbaceous weed vine belonging to the family Asteraceae and is native to tropical Central and South America (Holm *et al*. 1977). It is known as "mile a minute weed" and has caused serious harms to forestry, pastures, and plantations in a wide range of areas in subtropical China (Zan *et al*. 2000). Various ways were used to control *M. micrantha*, including cultural, mechanical, chemical, and biological methods, from which biological control is considered as one of the most promising ways (Parker 1972).

Bemisia tabaci is a kind of pest of plants, distributed throughout field crop systems of the tropics and subtropics, where it feeds on vegetables, broadleaf field crops, and ornamentals (Perring *et al*. 1993, Bellows *et al*. 1994). *B. tabaci* damages plants not only *via* the direct feeding in phloem, but also by producing honeydew that causes stickiness and supports the growth of sooty mold (Zalom *et al*. 1995). In China, *B. tabaci* was first recorded by Zhou (1949) and was included into the serious economic pests till the late 1990s. Recently, it is one of the primary pests on cottage, tobacco, and several vegetable crops, especially in Northern China (Xu 1996).

Numerous studies have been carried out on the relationships of insects and plants. Insects feeding damages mesophyll, reduces photosynthesis, alters chlorophyll (Chl) content in plants (Haile and Higley 2003) and secondary metabolism, including phenols, tannin, and volatile compounds (Uritanic 1980). In addition, superoxide dismutase (SOD) activity increased but catalase (CAT) activity decreased in *M. micrantha* after being infested by *Actinote thalia pyrrha* for 48 h (Zhang *et al*. 2006).

Being a kind of pest, *B. tabaci* has choices of its host plants and they suffer serious damages due to large multiplication of the pest population. Though the approaches by using this pest for *M. micrantha*'s control remains uncertain, we first noticed that *B. tabaci* infestation posed severe damages on *M. micrantha* in the wild with symptoms of leaf discoloration, sooty mould, dryness, and early abscissions, but the relevant mechanisms were not clear. This is why we studied them (*1*) to determine the changes in gas exchange and antioxidant enzyme activities of *M. micrantha* in response to *B. tabaci* infestation; and (*2*) to find possible explanations for early senescence of *M. micrantha* induced by *B. tabaci* infestation.

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Materials and methods

Plants and insects: The experiment was conducted in the field glasshouse located in South China Botanical Garden, Guangzhou, China (23°08′N, 113°17′E). In early July 2006, thirty seedlings (about 90 d old) of *M. micrantha* were planted in a plot (1 m length×1 m width×0.5 m height). Populations of *B. tabaci* used in the experiment were from natural infestation, and were naturally introduced into the plot at the end of September, 2006. The *M. micrantha* plants with about 40–60 % of leaves affected were selected as the infested plants and those without visible infestation (healthy plants) as the control (C) ones.

Irradiance- and CO_2-response curves: On October 11 and 12, 2006, portable photosynthesis system (*LI-6400*, USA) was used to determine the response curves of photosynthesis-irradiance (P_N-PPFD) and photosynthesis-CO_2 (P_N-C_i). Uppermost fully expanded sun leaves of infested plants characterized by flaccid, yellow-green mottled appearance and about 40–60 % leaf area covered by sooty mold and C-leaves from the uppermost fully expanded sun leaves of healthy plants were sampled. Leaf surfaces were cleaned before measurement. The P_N-PPFD curves were obtained by using a quartz halogen unit coupled to leaf chamber following the order of 1 200, 1 000, 800, 500, 300, 200, 120, 50, 20, and 0 μmol m^{-2} s^{-1} under the fixed [CO_2] of 380 μmol mol^{-1}. P_N-C_i curves were finished at the same leaves under a saturation irradiance (SI) of 1 200 μmol m^{-2} s^{-1}, and [CO_2] reduced by the sequence of 350, 200, 100, and 50 μmol mol^{-1} and then increased from 500, 700, 1 000 to 1 400 μmol mol^{-1}. The air temperature was 30±1 ºC, air humidity 60–70 %, and vapour pressure difference (VPD) 2.0±0.5 kPa during the measurements.

The maximum radiant energy-saturated photosynthetic rate (P_{max}), compensation irradiance (CI), SI, and apparent quantum yield (Φ) were obtained according to the non-rectangular hyperbola model of Lambers *et al*. (1998). CI was assessed when PAR approached zero and SI was calculated as the lowest value of PAR for which photosynthesis reaches 90 % of P_{max}.

At relatively low C_i and high irradiance, carboxylation is limited by the amount and kinetic properties of ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBPCO (Farquhar *et al*. 1980, Harley and Sharkey 1991). The equations of Farquhar and Caemmerer (1982) were used to fit the P_N-C_i curves. At low C_i and high irradiance, RuBPCO activity, V_{cmax} was calculated ignoring CO_2 diffusion limitation within the leaf as:

$$V_{cmax} = (P + R_D)\,[P_i + K_c\,(1 + O/K_o)]\,(P_i - \Gamma)^{-1}] - R_D \quad (1)$$

where P is the rate of CO_2 assimilation, K_c and K_o are the Michaelis-Menten constants for CO_2 and O_2, p(CO_2) and p(O_2), respectively. Γ is the CO_2 compensation concentration in the absence of non-photorespiratory mitochondrial CO_2 release (R_D), and O is the oxygen partial pressure. R_D was determined from the P-C_i curve near the compensation concentration with the rate at $C_i = \Gamma$.

As C_i increases and/or irradiance decreases, carboxylation becomes limited by the rate of RuBP regeneration in the Calvin cycle (Harley and Sharkey 1991), electron transport rate J, was calculated from data at higher C_i as:

$$J_{max} = (P + R_D)\,(4\,P_i + \Gamma)\,(P_i - \Gamma)^{-1} \quad (2)$$

The values derived for *Nicotiana tabacum* by Caemmerer *et al*. (1994) are K_c = 40.4 Pa, K_o = 24.8 kPa, and Γ = 3.69 Pa, O = 20.5 kPa.

Chl fluorescence was measured on the same leaves that were used for photosynthesis measurements with a portable Chl fluorometer (*PAM 2100*, *Walz*, Effeltrich, Germany). Determinations were made of dark-adapted minimum and maximum fluorescence yields F_0 and F_m, irradiance-adapted minimum and maximum fluorescence yield F_0' and F_m', steady-state fluorescence yield F_s, and incident photosynthetic photon flux density (PPFD) on leaf surfaces. The maximum efficiency of PS2 photochemistry (F_v/F_m) was calculated as $(F_m - F_0)/F_m$. The actual PS2 efficiency (Φ_{PS2}), the efficiency of excitation energy capture by open PS2 reaction centres F_v'/F_m', the apparent electron transport rate (ETR), photochemical quenching coefficient (q_P), and non-photochemical quenching coefficient (NPQ) were calculated as described by Souza *et al*. (2004) and Han *et al*. (2005).

Chl content and antioxidant levels: In the same leaves as photosynthesis and Chl fluorescence were measured, Chl content and enzyme activities were determined. The cleaned leaf disks (6 mm in diameter) were extracted with 80 % acetone. Absorption was measured at 663 and 645 nm using an ultraviolet (UV)-visible spectrophotometer (*Unico*, *UV-3802*, China). Chl and carotenoid (Car) contents were calculated according to Lin *et al*. (1984).

SOD and CAT activities were assayed by the methods of Giannopolitis and Ries (1977) and Zeng *et al*. (1991), respectively. Malondialdehyde (MDA) and proline (Pro) contents were measured as described by Lin *et al*. (1984) and Hao *et al*. (2004), respectively. Glutathione (GSH) was distilled according to Tanaka *et al*. (1985) and measured by Ellman's way (1959).

Statistical analyses: The infested leaves and the healthy ones were considered as paired samples. Multiple comparison of means for Chl fluorescence parameters (*post hoc* Unequal *N* Tukey's Honestly Significant Difference test) was carried out between different times of day at one treatment. One-way analysis of variance (ANOVA) was used to test the significant differences of other parameters between the treatments. All the statistical analysis was performed using *SPSS 13.0 for Windows* (*SPSS*, Chicago, IL, USA).

Results

***P_N*-PPFD and *P_N*-*C_i* response curves**: The P_N-PPFD curve of infested *M. micrantha* was obviously lower than that of C-plants with P_{max} and SI being 21.3 and 6.5 % of C, respectively (Fig. 1*A*, Table 1). However, CI of control was only 44.9 % of infested *M. micrantha* (Table 1). Compared with the healthy plants, the infested ones were much less responsive to increasing CO_2 concentration (Fig. 1*B*). The V_{cmax} and J_{max} of the healthy plants were 2.7- and 1.5-fold of the infested ones, respectively (Table 1).

Table 1. Average parameters calculated from the photosynthesis-irradiance and photosynthesis-CO_2 response curves, activities of superoxide dismutase (SOD) and catalase (CAT), and contents of malondialdehyde (MDA), proline (Pro), and glutathione (GSH) in control (C) and infested *M. micrantha*. Means±SE ($n = 5$ for photosynthesis parameters, $n = 3$ for other parameters). ns = not significant; $^{**}p<0.01$; $^{***}p<0.001$. P_{max} − maximum irradiance saturated photosynthetic rate; SI − saturation irradiance; CI − compensation irradiance; Φ − apparent quantum yield; V_{cmax} − maximum carboxylation rate; J_{max} − maximum electron transport rate.

	C plants	Infested plants	*p*
P_{max} [μmol(CO_2) m^{-2} s^{-1}]	18.58±0.54	3.96±0.20	***
SI [μmol(photon) m^{-2} s^{-1}]	1196.4±148.20	76.99±5.78	***
CI [μmol(photon) m^{-2} s^{-1}]	12.05±1.15	26.84±3.88	**
Φ [mol(CO_2) mol^{-1}(photon)]	0.068±0.005	0.070±0.008	ns
V_{cmax} [μmol m^{-2} s^{-1}]	59.48±3.51	21.84±3.21	***
J_{max} [μmol m^{-2} s^{-1}]	101.57±4.91	66.24±3.82	***
SOD [U g^{-1}(FM)]	341.92±2.70	303.26±4.39	**
CAT [mmol kg^{-1}(FM)]	0.49±0.01	0.27±0.00	***
MDA [μmol kg^{-1}(FM)]	20.73±0.17	14.46±0.17	***
Pro [mg kg^{-1}(FM)]	33.38±0.87	38.42±0.27	**
GSH [mg kg^{-1}(FM)]	304.76±14.55	673.02±3.17	***

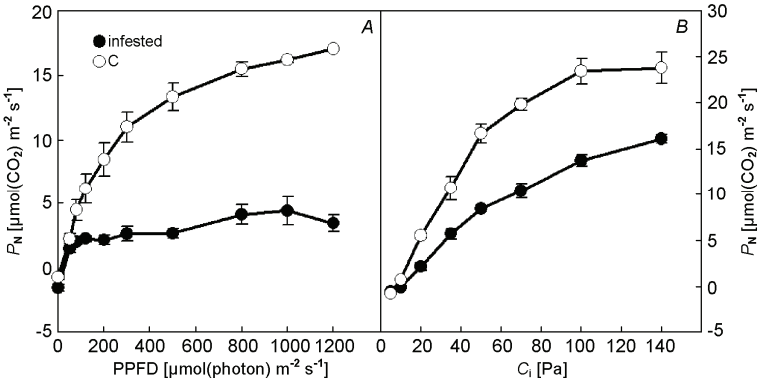

Fig. 1. Average irradiance (*A*) and CO_2 (*B*) response curves of the infested (●) and control (○) *M. micrantha* plants. P_N − net photosynthetic rate; PPFD − photosynthetic photon flux density; C_i − intercellular [CO_2]. Means±SE ($n = 5$).

Chl fluorescence: Incident PPFD on leaf surfaces revealed diurnal variations with peaks at noon and the values in infested *M. micrantha* were generally lower than those of C-plants (Fig. 2). Diurnal Φ_{PS2} in infested plants was consistently lower than that of healthy ones, and significant difference was only observed at 10:00 h when Φ_{PS2} in infested plants was 62.5 % of C-plants (Fig. 3*A*). F_v/F_m in infested plants showed a midday depression, and no significant differences were observed between different measurement times (Fig. 3*B*). F_v/F_m in the healthy plants showed a reversible significant midday depression (Fig. 3*B*) and had similar diurnal changes but was more dynamic than Φ_{PS2} in both C and infested *M. micrantha* (Fig. 3*C*).

ETR of infested *M. micrantha* were 58.8, 43.5, and 58.8 % of C-plants at 06:00, 10:00, and 12:00 h, respec-

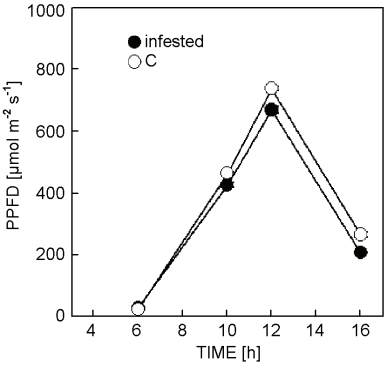

Fig. 2. Diurnal changes in incident photosynthetic photon flux density (PPFD) on the leaf surfaces of infested (●) and control, C (○) *M. micrantha* plants during the chlorophyll fluorescence measurements. Means±SE ($n = 10$).

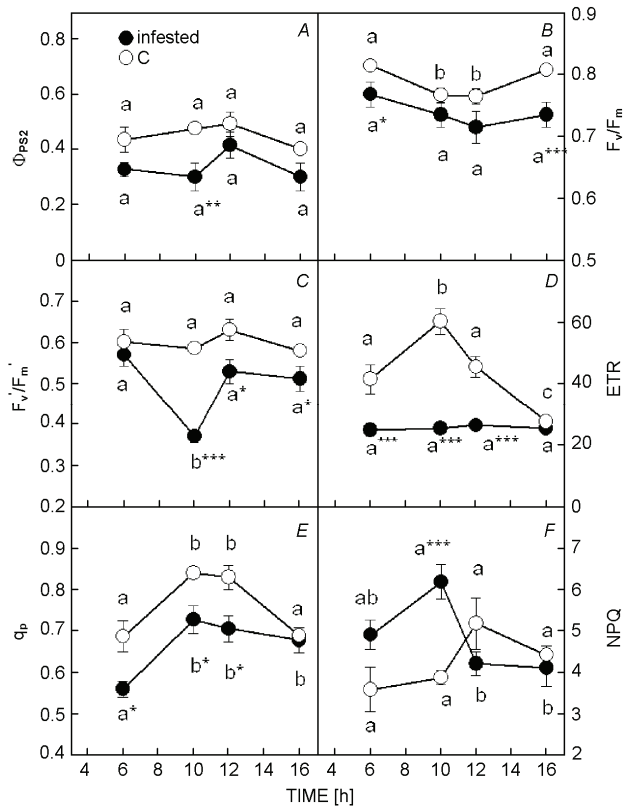

Fig. 3. Φ_{PS2} (*A*), F_v/F_m (*B*), F_v'/F_m' (*C*), ETR, (*D*), q_P (*E*), and NPQ (*F*) of the infested (●) and control (○) *M. micrantha*. Means±SE ($n = 5$). *Different lower case letters* indicate differences between different time of a day in infested or control *M. micrantha* according to Tukey's range tests ($p<0.05$), while * shows the difference between the treatments at the same time of the day according to one way-ANOVA (*$p<0.05$; **$p<0.01$; ***$p<0.001$).

tively, which were all significantly lower than those of C. Furthermore, no significant differences were observed between diurnal ETR in infested *M. micrantha* (Fig. 3*D*). NPQ in infested plants showed highest value of 6.2 at 10:00 h and q_P approached the highest value of 0.73. Similarly, NPQ in the C-plants had a peak value of 5.2 at midday when its q_P was 0.83 (Fig. 3*E,F*).

Chl content and antioxidant levels: Contents of Chl *a* and Car and Chl *a/b* ratio in infested *M. micrantha* were significantly lower than those of C-plants, while no significant difference was observed in Chl (*a*+*b*)/Car ratio (Fig. 4).

Activities of SOD and CAT in infested *M. micrantha* decreased by 11.3 and 44.9 %, while contents of Pro and GSH increased by 20 and 120 %, respectively, compared with C (Table 1). Moreover, the measured MDA content in infested *M. micrantha* was very significantly lower than that of C-plants (p=0.00001) (Table 1).

Discussion

We found that *M. micrantha* suffered damages from *B. tabaci* infestation as concerns decreased photosynthetic capacity, Chl content, and PS2 photochemistry, and altered activities of antioxidant enzymes, which would consequently cause growth reduction and senescence acceleration of *M. micrantha*. The pronounced symptoms of leaf discoloration, kraurosis, growth reduction, and early abscission were observed in the infested individuals. Similarly, Costa *et al*. (1993) reported that *B. tabaci* infestation induced reduction of photosynthetic rates and Chl content in plants, shortened plant growth, and disturbed their physiological metabolisms.

Sances *et al*. (1982) and other authors indicated that *B. tabaci* infestation caused water deficiency and loss of leaf Chl content, which resulted in the decrease of photosynthetic activity of infested plants. In our study, decreases in photosynthetic rate could not only be related to the reduction of Chl content, but also with the reduction of SI, V_{cmax}, and J_{max} in infested *M. micrantha*, in addition with the decrease of PS2 photochemistry.

The reduced SI would decrease adaptability to high irradiance and decrease P_N in infested *M. micrantha*, which would result in the growth reduction of *M. micrantha*. Significant reductions in V_{cmax} and J_{max} (Table 1) indicated that ribulose-1,5-bisphosphate carboxylase/oxygenase amount and activity were depressed and the regeneration capacity of this enzyme was reduced. ETR in infested *M. micrantha* also showed significant decreases before 16:00 h compared with C (Fig. 3*D*), suggesting that the Chl molecules were passive.

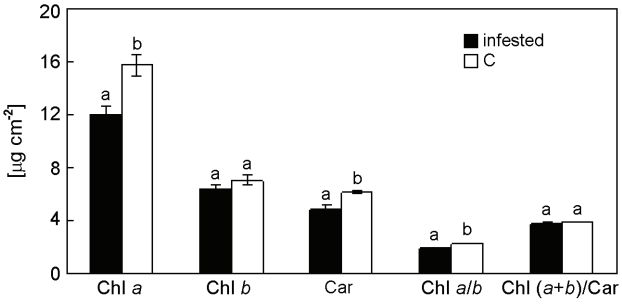

Fig. 4. Contents of chlorophyll (Chl) *a* and *b* and carotenoids (Car) and ratios of Chl *a/b* and Chl (*a*+*b*)/Car in infested (■) and control (□) *M. micrantha*. *Different lower case letters* indicate differences between treatments on the same parameter ($p<0.05$). Means±SE ($n = 3$).

The reduction of Φ_{PS2} in infested *M. micrantha* could be the consequence of decreased PS2 photochemistry since the decreased Φ_{PS2} was a result of decrease in F_v'/F_m' and q_P (Genty *et al*. 1989). F_v/F_m is an indicator of photoinhibition, which is 0.80−0.85 in healthy leaves

(Brennan and Jeferies 1990). In our study, the reversible diurnal F_v/F_m in healthy plants suggested that the midday photoinhibition was a normal photoprotective process in response to changes in environmental factors. However, all the F_v/F_m values were below 0.80 in infested *M. micrantha*, indicating that damage of PS2 reaction centre occurred with *B. tabaci* infestation. NPQ in infested *M. micrantha* reached its maximum value (6.2) at 10:00 h (Fig. 3*F*) and then decreased significantly with the increasing PPFD at midday (Fig. 2). This suggests that capacity of excess excitation energy dissipation of the infested *M. micrantha* at high irradiance was restrained which would result in photodamage.

Compared with the healthy ones, the infested plants showed serious damages in enzymatic protective system since the activities of SOD and CAT significantly decreased, resulting in the reduction of ability to eliminate active oxygen. However, the contents of non-enzymatic protective factors Pro and GSH of infested *M. micrantha* increased at various magnitudes compared with those of C-plants, indicating that both Pro and GSH were relatively sensitive and active in response to *B. tabaci* infestation.

MDA is a decomposition product of polyunsaturated fatty acid hydroperoxides and is widely used as indicator of lipid oxidative damage (Halliwell and Chirico 1993). In our study, MDA content in infested *M. micrantha* was very significantly lower than that in C-plants, implying that the non-enzymatic antioxidants such as GSH may play certain role in scavenging the active oxygen.

B. tabaci is a polyphagous insect, and many weeds are its host (Muñiz 2000). Pests and disease organisms' reorganization and control weeds may prevent weed outbreaks (Yassin and Bendixen 1982). Behavioural diversity is a common phenomena within a population of insects, but variation may occur at different points in the behavioural sequences that influence host selection (Bernays and Chapman 1994). We found that *B. tabaci* infestation made serious damages to *M. micrantha via* altering photosynthetic apparatus and disrupting anti-oxidant enzymes, which might as consequences accelerate the senescence of this weed. Nevertheless, issues on whether *B. tabaci* could be used to control *M. micrantha* and how it would be applied in field practice need further study, as *B. tabaci* also feeds on some important economic crops.

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