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Effects of *Mikania micrantha wilt virus* on endogenous hormones and interspecific competitive ability in *Mikania micrantha* H.B.K.

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ABSTRACT

We compared the content of endogenous hormones [indole-3-acetic acid (IAA), cytokinin (CTK), gibberellin (GA_3), abscisic acid (ABA)] and auxin in *Mikania micrantha wilt virus* (MMWV) infected and healthy plants using enzyme-linked immunosorbent assay (ELISA) 1, 4, 7, 10, 13 and 16 days after infection. The results showed that there was positive correlation between the magnitude of plant disease and the content of IAA, GA_3, CTK and auxin in MMWV-infected plants. The content of ABA in MMWV-infected plants accumulated continuously with the increase in inoculation time and was constantly higher than in healthy plants. The ratios of IAA/ABA and GA_3/ABA in the MMWV-infected plants were significantly lower than in healthy plants, which indicated that MMWV infection disrupted the balance of endogenous hormones and altered the growth and development of plants. Furthermore, the competition experiment was done to investigate the effects of MMWV on the interspecific competitive ability of *M. micrantha* with its coexisting plant *Bidens pilosa* L. The results indicated that MMWV-infected plants were less competitive against *B. pilosa* than healthy plants. These results suggested that the poor growth of *M. micrantha* after infection may be closely related to the decrease in IAA, GA_3, CTK and auxin and the increase in ABA, which weakened the competitive ability.

Key words: Auxin, *Bidons pilosa*, ELISA, Endogenous hormones, healthy plants, infected plants, interspecific competitive ability, *Mikania micrantha* wilt virus.

INTRODUCTION

Mikania micrantha H.B.K. (Compositae, Origin : South and Central America) is most aggressive weed worldwide and caused serious ecological problems in Southeast Asia and South China (28,34). Its strong allelopathy has been considered as a novel weapon, which facilitate its successful invasion (34). *Bidens pilosa* L. (Compositae), an annual herbaceous weed originated from tropical South America, has also caused

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substantial damage to the ecosystem in Southern China (19,27). In field conditions, the *B. pilosa* co-exists with *M. micrantha*.

Plant hormones are key regulators of plant responses to biotic and abiotic stresses, they change the responses to different environmental stresses (6,7,8,12). For example, salicylic acid (SA), jasmonic acid (JA) and ethylene (Et) are tuners of plant responses to biotic stress. The Auxins (Auxs), cytokinins (CKs) and abscisic acid (ABA) affects the plant growth, development and plant-pathogen interactions (6,10,12). The ethylene, gibberellins (GA) and ABA also influence the normal growth and development under flooding stress (7).

Previous studies indicated that there was a positive correlation between the magnitude of plant disease and the content of IAA in *Turnip mosaic virus* (TuMV)-infected Chinese cabbage ″Aijiaohuang″. In plants with severe symptoms, the content of GA_3 is lower, while, ABA content is higher. The ratios of IAA/ABA and GA_3/ABA in infected plants were both significantly lower than the healthy plants. These results indicated that TuMV infection disrupts the balance of endogenous hormones (29). The GAs content in banana plants inoculated with *Banana bunchy top virus* (BBTV) at different infecting periods was lower than healthy plants, but the ABA content became higher and got accumulated. BBTV infected plants show the highest content of ABA (3.34 folds) after inoculation for 35 days compared to healthy plants. Thus the symptoms of banana bunchy top disease were closely related to the imbalances of endogenous hormones in BBTV-infected plants (33). *Mikania micrantha wilt virus* (MMWV), is the new isolate of *Gentian mosaic virus* (GeMV). This virus can infect *M. micrantha* plants and cause wilt, crimpled and malformation (25,26,30). However little information is available about the effects of MMWV infection on endogenous hormones and interspecific competition of *M. micrantha*.

Our previous field observations and laboratory experiments found that MMWV-infected *M. micrantha* displays wilt and leaf crimpling which inhibit the growth of *M. micrantha* (25,26,30). The information about the changes in the contents of endogenous hormones in *M. micrantha* and the interspecific competitive ability of *M. micrantha* is not known. We hypothesize that MMWV infection may change the content of endogenous hormones in *M. micrantha* and the interspecific competitive ability of *M. micrantha* against *B. pilosa*, which would inhibit the invasion of *M. micrantha*. To test this hypothesis, we measured the content of endogenous hormones in healthy and MMWV-infected plants of *M. micrantha* at different times after inoculation. Besides, competition experiment was also done to compare the competitive ability between MMWV-infected plants of *M. micrantha* and *B. pilosa*. These results could aid in developing new strategies for biocontrol of invasive plants.

MATERIALS AND METHODS

Plant species

Seeds of *B. pilosa* were collected in April 2017 from a wild population from our Research Farm, South China Agricultural University (N 23°16′, E 113°34′), Guangzhou. Plants of *M. micrantha* (10.5 m height) at the vegetative stage were collected in April 2018 from the same farm. The plants of *M. micrantha* were cut into 8 cm-long pieces and planted into plastic pots (9 cm dia, 12.5 cm high, one plant per pot). They were grown in greenhouse (14/10 h D/N cycle, 75% ± 2% relative humidity) and watered twice a week.

Virus inoculation and symptoms

MMWV was also obtained from the same farm as mentioned above in May 2017 and was inoculated to *M. micrantha* in the same greenhouse, which means that both healthy and infected plants were under the same conditions as described above. MMWV was mechanically inoculated to the fourth and fifth leaves (counted basipetally from the apex) of the plants using a cotton tipped applicator (25). The symptoms were observed and recorded 15 and 30 days after inoculation, respectively.

Endogenous hormones

Enzyme-linked immunosorbent assay (ELISA) kits (Shenzhen ziker Biological Technology Co., Ltd, Shenzhen, China) was used to determine the content of indole-3-acetic acid (IAA), cytokinin (CTK), gibberellin (GA_3), abscisic acid (ABA) and auxin in the leaves 1, 4, 7, 10, 13 and 16 days, after the symptoms appeared.

Competition experiment

To evaluate the effects of MMWV on competitive ability of *M. micrantha*, a competition experiment was done to compare the competitive ability of MMWV-infected *M. micrantha* and *B. pilosa*. The seedling height of *M. micrantha* and *B. pilosa* was about 10 cm. The monocultures of healthy *M. micrantha*, MMWV-infected *M. micrantha* and *B. pilosa* were grown with four plants per pot. The proportion of healthy *M. micrantha* and *B. pilosa*, MMWV-infected *M. micrantha* and *B. pilosa* in mixed cropping was 1:1 (four plants per pot), respectively. Both monocultures and mixed-cropping plants were grown in the same greenhouse for 100 days. At the end of experiment, plants shoot height were measured, and the plant's aboveground parts were harvested, dried at 70°C for 48 h and then weighed. The treatments were replicated five times.

The relative yield total (RYT), relative competition intensity (RCI) and aggressivity (A) were calculated as under (23).

$$RYT = Y_{ab} / Y_{aa} + Y_{ba} / Y_{bb}$$

$$RCI = (Y_{aa} - Y_{ab}) / Y_{aa}$$

$$A_{ab} = Y_{ab} / (Y_{aa} \times Z_{ab}) - Y_{ba} / (Y_{bb} \times Z_{ba})$$

Where, Y_{ab} : Relative yield of species *a* in the mixture with species *b* and the relative yield of species *b* in the mixture with species *a*, Y_{ba}. Y_{aa} : Yield in monoculture and the relative yield of *b* in monoculture is Y_{bb}.

When, RYT > 1 : Species a and b occupied different ecological niches and showed symbiotic relationship. When RYT = 1 : Species a and b use common resources; When RYT < 1: It indicates antagonism and competition between species a and b (23).

When, 0 < RCI < 1, : It indicates the lower yield of specie in the mixed cropping, the greater the influence of another species on it, and the lower competitiveness in the mixed cropping. When RCI = 1, This species has been pushed out from the system; When RCI = 0, : Mixed cropping has no effect on the yield of this species. If RCI < 0,: Existence

of other species is beneficial to growth of this species, would thus promote its yield (23).
Z_{ab} : Ratio of specie *a* in the mixture to specie *b* and Z_{ba} : Ratio of specie *b* in the mixture to specie *a.* When $A_{ab} > 0$: Specie a is more competitive than b and is in a dominant position; When $A_{ab} = 0$, : Specie a and b have the same competitive capacity; When $A_{ab} < 0$, : Species a is less competitive than b (23).

Statistical analysis

All data were analyzed using SPSS 13.0 Software Package (SPSS Inc., Chicago, IL, USA). One-way ANOVA followed by Duncan's multiple range test was employed to analyze changes in the contents of endogenous hormones and the biomass of plants. The Student's t-test was used to analyze data from the competition experiment. All the data were presented as means ± standard error (SE). Statistical differences were considered significant at $p < 0.05$.

RESULTS AND DISCUSSION

I. Pathological characteristics of MMWV

After inoculation of *M. micrantha,* the pathological characteristics of MMWV were recorded after 15 and 30 days, respectively. There were no visible symptoms on seedlings in healthy plants (Figure 1). Mild shrinking and typical mosaic were observed during the 15 days after inoculation. While, 30 days after inoculation, the plants showed redness of leaves, dwarfness and severe mosaic. Different plant viruses have been identified based on viral disease symptoms, serology or molecular tools (3). The visual symptoms of plant diseases are easy to determine, whether plants are infected by the virus (2,3,18). Plant infected with *Cucumber mosaic virus* (CMV) commonly display mosaic, yellowing, chlorosis, leaf curling and severe stunting (2,3,22). While, papaya ring spot virus (PRSV) infection show severe leaf damage (4). *Soybean mosaic virus* (SMV) infection in soybean causes mosaic, leaf curling, chlorosis and necrosis in leaves (18). Our results may serve as the diagnosis criteria for MMWV diseases.

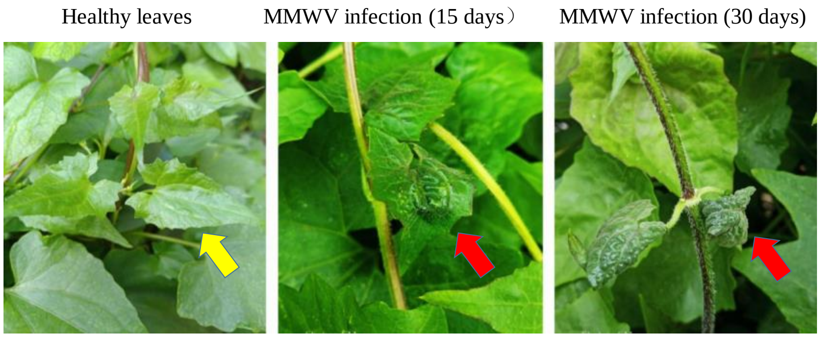

Figure 1. Red arrow indicate the symptoms of *Mikania micrantha* leaves infected with *Mikania micrantha* wilt virus (MMWV). Healthy leaves (Yellow arrows), Leaves in early stage of MMWV infection (15 days) and, Leaves in late stage of MMWV infection (30 days).

II. Interaction of MMWV with endogenous hormones

The contents of endogenous hormones in *M. micrantha* changed after inoculation with MMWV, which revealed the pathogenesis of MMWV. ELISA was applied to determine the dynamic changes in endogenous hormones (IAA, ABA, GA_3, CTK and auxin) 16 days after MMWV infection. The value of IAA/ABA and GA_3/ABA was analyzed (Figure 2). There were no significant differences in contents of IAA, ABA, GA_3, CTK, auxin, IAA/ABA and GA_3/ABA in healthy plants. However, the contents of IAA, GA_3, CTK and auxin were lower than in leaves of MMWV-infected plants than in healthy plants.

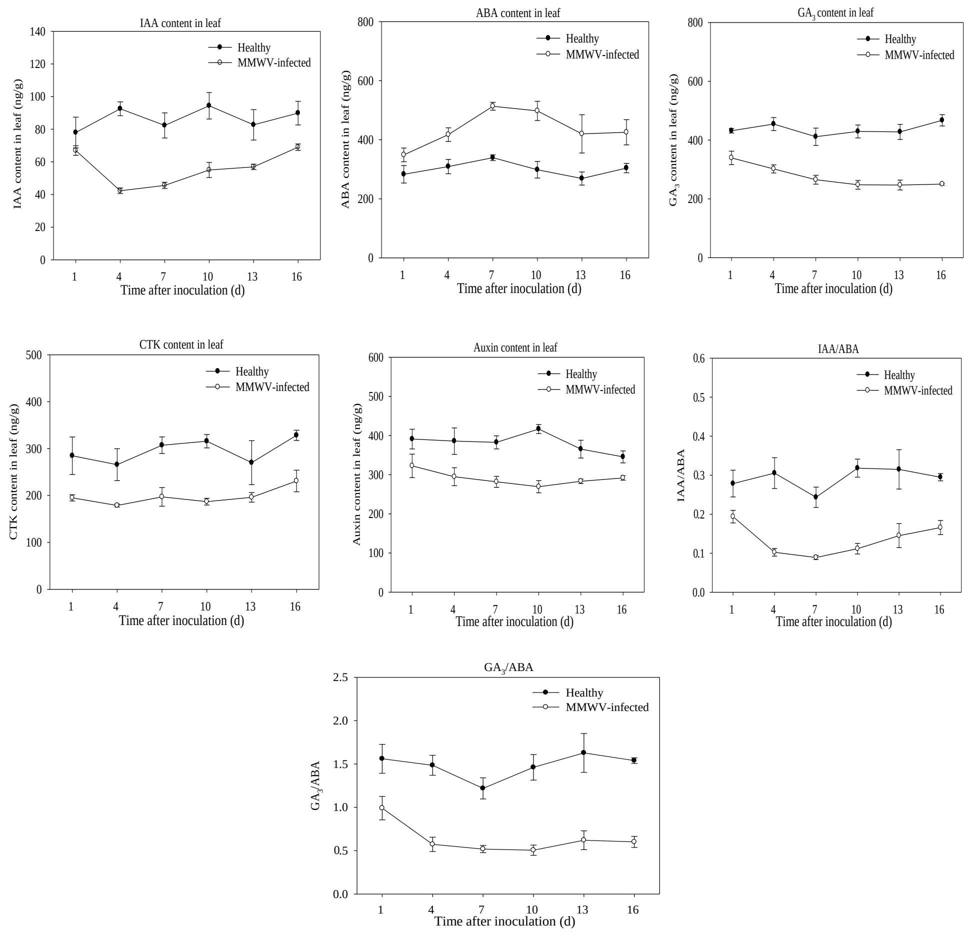

Figure 2. Contents of IAA, ABA, GA3, CTK, Auxin, IAA/ABA and GA3/ABA in the different time after infection of *Mikania micrantha* with *Mikania micrantha* wilt virus (MMWV). The data were analyzed using SPSS 13.0 Software Package using one-way ANOVA followed by Duncan's multiple range test. Data shown are mean ± SE.

The contents of IAA and GA_3 in MMWV-infected leaves were significantly lower (54.3 % and 48.2 %, respectively), 4-days after symptom appearance, respectively. Similarly, the content of CTK and auxin in infected leaves were significantly decreased by 40.9 % and 35.7 %, respectively, 10 days after symptom appeared. However, the content of ABA in infected plants was higher (66.8 %) than healthy plants 10 days after symptom appeared. MMWV infection also disturbed the balance of IAA/ABA or GA_3/ABA, the healthy plants contained more IAA/ABA and GA_3/ABA than infected ones. By analyzing the symptoms development and endogenous hormone contents in MMWV-infected leaves, we concluded that the higher level of ABA and the lower levels of IAA, GA_3, CTK and auxin reduced the plant growth and leaf shrivelling. It also suggested that the appearance and development of symptoms are strongly correlated with the contents of endogenous hormones.

Plant virus infections cause numerous disease syndromes in plants [induction of disease symptoms, such as chlorosis, necrosis, and developmental abnormalities (1,8,13,17,24,31)]. For example, the inoculation of *Plum pox virus* (PPV) significantly increased the contents of GA_3 and ABA in peach, resulting in chlorosis (9). At the later stage of infection, the flowers of red currant 'Vitan' plants infected with *Blackcurrant reversion virus* (BRV) had significantly more ABA than healthy plants and it indicated little correlation between the BRV infection and ABA levels in flowers (14). The infection by *Stem grooving virus* (SGV) reduced the contents of IAA, GA_3 and CTK in pear seedlings by 15 %, 19 % and 59 %, respectively, suggesting that the poor growth of pear seedlings might be closely related to the sharp decrease in these endogenous hormones after infection (15). In *Rice dwarf virus* (RDV)-infected rice l and 10 days after symptom appearance, the GA_3 content was significantly lower (6.28 and 5.92 folds), respectively, than in healthy plants. Similarly, the content of IAA in RDV-infected rice plants was always lower than in healthy plants but the contents of ABA in RDV infected rice plants was always higher, 1 and 13 days after symptom appearance (33). In rice varieties ‘Nipponbare’ and ‘Huaidao 5’ the content of ABA increased by 80.8 % and 45.3 %, 60-days after infection by *Rice black-streaked dwarf virus* (RBSDV). The RBSDV infection also affects the biosynthesis of ABA, which increased the growth of rice seedling (20). *Southern rice black-streaked dwarf virus* (SRBSDV) infection changed the balance of IAA/ABA and GA3/ABA in rice, which indicated that SRBSDV infection could change the contents of rice endogenous hormones (21). ABA accumulation was greater in plants of both *Bamboo mosaic virus* (BaMV)- and *Cucumber mosaic virus* (CMV)-infected *Nicotiana benthamiana* than in healthy plants (6). Our results showed that the contents of IAA, GA_3, CTK and auxin were decreased, while the content of ABA significantly increased. This study verified that the change in endogenous hormones in *M. micrantha* after infection by MMWV resulted in poor growth of MMWV-infected *M. micrantha*.

III. Competition study

As compared to healthy plants of *M. micrantha* in monoculture, MMWV infection significantly decreased the aboveground biomass and shoot height by 56.0 % and 78.9 %, respectively (Figure 3). When healthy *M. micrantha* was co-cultivated with *B. pilosa*, both aboveground biomass and shoot height were similar to healthy *M. micrantha* plants in monoculture. In contrast, when MMWV-infected *M. micrantha* in monocultures was co-cultivated with *B. pilosa* the aboveground biomass and shoot height decreased by 42.0 % and 18.9 %, respectively (Figure 3).

The aboveground biomass of *B. pilosa* was decreased by 6.1 %, when co-cultivated with healthy *M. micrantha*. When *B. pilosa* monoculture was co-cultivated with MMWV-infected *M. micrantha*, the aboveground biomass of *B. pilosa* was increased by 5.2% (Figure 3). However, the shoot height of *B. pilosa* was not influenced when co-cultivated with healthy *M. micrantha* and MMWV-infected *M. micrantha* (Figure 3).

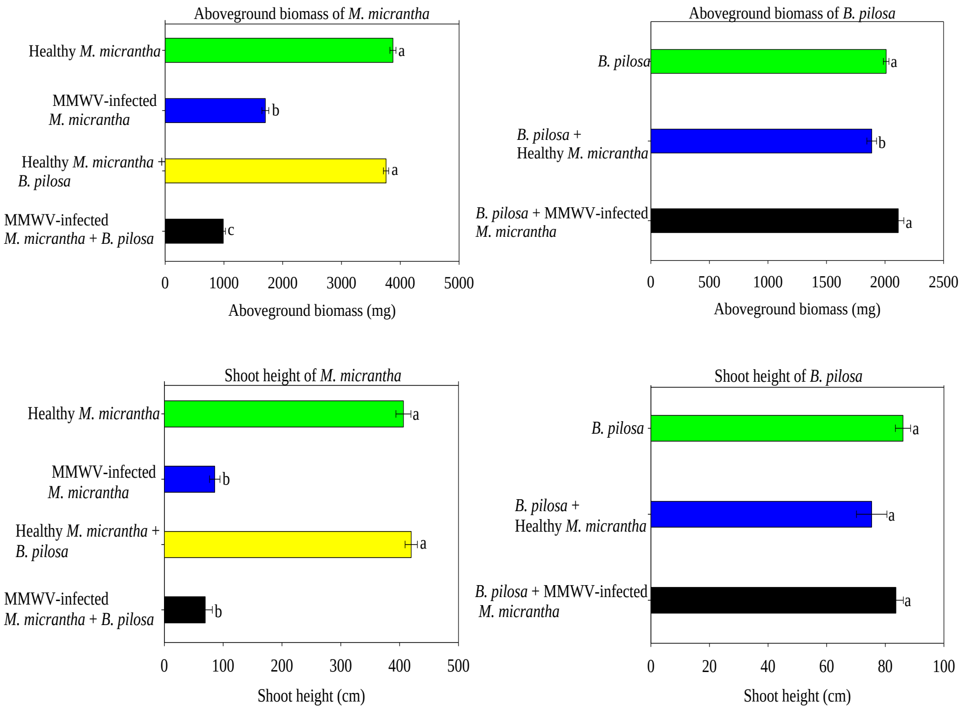

Figure 3. Effects of mixed cropping healthy *Mikania micrantha* with *Bidens pilosa*, and MMWV-infected with *B. pilosa* on the aboveground biomass and shoot height of *M. micrantha* and *B. pilosa*, respectively. Data shown are mean ± SE. Significant differences among treatments are indicated by different letters above bars (P<0.05 using Duncan' test).

In addition, MMWV infection decreased the relative yield total (RYT) by 14.3%, but increased the relative competition intensity (RCI) by 13.1% in *M. micrantha*. The aggressivity (A) value of healthy plants of *M. micrantha* (0.06) was significantly higher than infected plants (-0.94), which indicted that MMWV infection significantly weakened the interspecies competitive ability of *M. micrantha* (Figure 4).

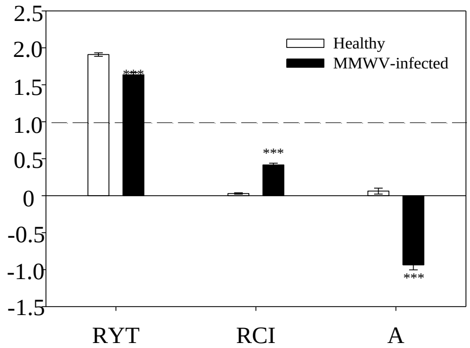

Figure 4. Comparison of the relative yield total (RYT), relative competition intensity (RCI) and aggressivity (A) values between healthy and MMWV-infected *Mikania micrantha* under different treatments. Data shown are mean ± SE. Asterisk indicates a significant difference between healthy and MMWV-infected plants ($p < 0.05$, Student's *t*-test, *** $p < 0.001$).

The invasive plant *M. micrantha* is usually controlled by different methods [biological control, chemical control, mechanical removal, integrated control and resource management strategies (25,26,34)]. Recently, the application of biological agents (bacteria, fungi and viruses) to control weeds has received greater attention (10,16,25). *Pepino mosaic virus* (PepMV) and *Óbuda pepper virus* (ObPV) agents reduced the population of noxious weed *Solanum nigrum* (10). In Florida *Tobacco Mild Green Mosaic Tobamovirus* (TMGMV) controlled the invasive tropical soda apple (*Solanum viarum*) (11). Although the MMWV infection did not significantly change the allelopathic potential of dried leaf litter or aqueous leaf leachates of *M. micrantha* on the target plants, but it changed their chemical contents (25). Further research is needed to explore the effects of MMWV on the allelopathic potential of *M. micrantha.* The MMWV infection significantly suppressed the growth (26) and decreased the floret number and seed production in *M. micrantha* (25). These results indicated that MMWV can be used as biocontrol agent against *M. micrantha*.

CONCLUSIONS

This is the first study reporting that the MMWV can significantly change the contents of endogenous hormones (IAA, CTK, GA_3, ABA and auxin) in *M. micrantha*. This reduced the growth and development of *M. micrantha* and decreased the interspecies competitive ability of *M. micrantha.* The appearance and development of symptoms are correlated to the contents of endogenous hormones. To conclude, our study provided an idea for new management strategies to control invasive plant *M. micrantha* with viruses.

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