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薇甘菊可溶性蛋白和抗氧化酶活性对田野菟丝子不同寄生密度的响应

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摘 要：为探求利用寄生植物田野菟丝子对入侵杂草薇甘菊进行生物控制的有效措施，研究了薇甘菊对0、1、2、4和8棵田野菟丝子幼苗寄生在可溶性蛋白和一些抗氧化酶活性方面的响应。寄生后30 d，1棵田野菟丝子/株薇甘菊(以下简称棵/株)以上的寄生密度导致薇甘菊可溶性蛋白含量显著降低。和对照相比，在寄生密度为1棵/株时，超氧物歧化酶(SOD)和过氧化物酶(POD)活性显著增强；但随着寄生密度的加大而下降，而且在寄生密度为4棵/株时，SOD和POD分别等于和小于对照，在8棵/株时均显著小于对照。在各寄生密度下，寄主的过氧化氢酶(CAT)活性均小于对照，而SOD/CAT，SOD/POD和SOD/(CAT+POD)比率均大于对照。这些结果表明，田野菟丝子的寄生对薇甘菊可溶性蛋白和抗氧化酶活性的影响依赖于寄生密度，在野外利用田野菟丝子控制薇甘菊的最理想寄生密度是4棵/株，从而可为野外利用田野菟丝子控制薇甘菊的技术体系提供参考。

关键词：生物防治；入侵杂草；寄生植物；抗氧化酶

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Responses of *Mikania micrantha* to parasitization of *Cuscuta campestris* in total soluble protein content and activities of antioxidant enzymes

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Abstract: To develop efficient biocontrol techniques for the invasive weed *Mikania micrantha*, the use of the obligate parasitic plant, *Cuscuta campestris* Yuncker as a biological control was investigated. In this experiment, whether the impacts of the parasite on host soluble protein content and activities of some antioxidant enzymes were affected by the density of the parasite was tested. The responses of *M. micrantha* to parasitic densities of 0, 1, 2, 4 and 8 individual seedlings of *C. campestris* per host plant were examined. On the 30th day of parasitization, infection with more than 1

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C. campestris seedling significantly lowered soluble protein content. Compared with control, activities of superoxide dismutase (SOD) and peroxidase (POD) significantly increased at parasitic density of 1 parasite per host plant; but as parasitic density increased, both SOD and POD activities decreased. Moreover, SOD activity was not changed but POD activity was significantly decreased at parasitic density of 4 parasites per host, and both SOD and POD activities were significantly decreased at parasitic density of 8 parasites per host, compared with control. The infected plants had significantly lower catalase (CAT) activity but higher SOD/CAT, SOD/POD and SOD/ (CAT + POD) ratios than the control at all parasitic densities. The results indicated that the effects of *C. campestris* infection on *M. micrantha* were density dependent, which provided a basis for refining this strategy for biological control of *M. micrantha*. The optimal cost-effective number of parasites to control *M. micrantha* was 4 per host plant in the field.

Key words: biological control; invasive weed; parasitic plant; antioxidant enzymes

1 Introduction

Biological invasion is one of the major threats to native biodiversity, economic development and biological safety (Mack *et al.*, 2000; Pimentel *et al.*, 2005) and it is an important element of global change (Vitousek *et al.*, 1997). The problems of invasive species and their control have been one of the most pressing applied issues in ecology today (Hastings *et al.*, 2006). Therefore, many researchers have tried to develop effective strategies to control invasive species in affected areas (Zavaleta *et al.*, 2001; Taylor & Hastings, 2004; Buhle *et al.*, 2005; Culliney, 2005; Hulme, 2006). These strategies include cultural, mechanical, chemical, and biological control. Among these, biological control is permanent, energy-efficient, non-polluting, inexpensive and ecologically safe relative to other methods (Culliney, 2005). Thus, it has been widely recognized as one of the most promising methods of controlling invasive weeds (Culliney, 2005), especially when native species are used to control exotic invasive weeds (Shen *et al.*, 2005).

Mikania micrantha is a fast-growing perennial climbing vine of the family Asteraceae, and is native to Central and South America (Holm *et al.*, 1977). However, in its palaeotropic exotic ranges such as moist tropical forest zones of the Pacific region, India, and Asia, particularly South-east Asia, it has become a horrific invader and a notorious weed, severely damaging forestry and plantation crops (Zhang *et al.*, 2004). It climbs up on other plants to reach the canopy for better sunlight, and smothers other plants, thus it is named "plant killer" in China. It sprawls out rapidly in spring and summer, showing a vigorous, fast and rampant growth habit, that is why it is named "mile-a-minute weed" (Waterhouse, 1994). Moreover, the weed can reproduce vigorously by both vegetative and sexual reproduction (Zhang *et al.*, 2004). It has been listed as one of the 100 worst invasive alien species in the world (Lowe *et al.*, 2001), and is one of the top 10 worst weeds in the world (Holm *et al.*, 1977). *M. micrantha* entered South China after 1910. Since the 1980s, it has spread and invaded widely, causing severe damage to many ecosystems, and leading to significant economic loss in South China including Hong Kong, Guangdong, and Hainan (Feng *et al.*, 2002; Zhang *et al.*, 2004). Thus, it has been listed as one of the 16 most invasive species by the State Environmental Protection Administration (Zhang *et al.*, 2004).

To biologically control *M. micrantha*, we have tried to use the obligate parasite *Cuscuta campestris* Yuncker in South China (Shen *et al.*, 2005, 2007). We found that *C. campestris* infection significantly reduced total biomass and photosynthesis, changed the biomass allocation patterns and completely inhibited flowering of *M. micrantha* plants. At the community level, field studies (Lian *et al.*, 2006) showed that *C. campestris* significantly reduced biomass and cover of *M. micrantha*, but had only minor effects on the growth of other plants. Thus, *C. campestris* might reduce the harmful effects of *M. micrantha*, and hence increase species diversity and help re-establishment of native species. These results indicated that the use of *C. campestris* could be a potentially effective and relatively safe way to control *M. micrantha*.

In this study, the effects of parasitic density of *C. campestris* on *M. micrantha* were investigated in the field in South China. In order to test whether the effects of the parasite on host soluble protein content and activities of some antioxidant enzymes are affected by the density of the parasite, we examined the responses of *M. micrantha* to parasitic densities of 0, 1, 2, 4 and 8 individual seedlings of *C. campestris* per host plant. The work will provide useful and practical information for the deployment of *C. campestris* for the biological control of the invasive species *M. micrantha*.

2 Materials and methods

2.1 Experimental materials and design

The study was conducted during the May-December 2004 growing season at the field station of South China Botanical Garden (23°10′ N, 113°21′ E, elevation 40 m a. s. l.) in Guangzhou, Guangdong Province, China. The region is characterized by a typical south subtropical monsoon climate. On 31 May 2004, whole *M. micrantha* plants were collected from a *M. micrantha* population in the suburb of Dongguan, Guangdong Province, China. Similar-sized two-node segments were selected from the middle of the stems to minimize the influence of phenotypic maternal effects. The segments were planted in 89 L pots filled with a mixture of pool mud and paddy field clay (1 : 2, v/v). The mixed soil had pH 6. 5 ± 0. 1, organic mater content 3. 3 ± 0. 09%, total nitrogen 0. 182±0. 08%, ammonia nitrogen 103. 57±5. 86 mg kg-1, available P 23. 98±1. 36 mg · kg^{-1}, and available K 132. 83 ± 6. 32 mg kg^{-1} (mean±SE). In each pot, three segments were planted with the lower node buried below and the upper one about 5 cm above the soil surface. The upper nodes began to sprout 3 d later. When the plants were about 350 cm in height (23 August), they were thinned to one per pot, and 100 individuals, similar in height and stem diameter, were selected and placed at random in an open field uniform in environmental conditions. Of these, 80 were randomly chosen as host plants (infected group), leaving the remaining 20 uninfected (control group). To prevent *M. micrantha* from climbing from one pot to another, pots were separated at least 1 m from each other and a bamboo cane about 5 m long was placed vertically in each pot for *M. micrantha* to climb on.

On 12 August, *C. campestris* seeds were sown in pots filled with sands at a depth of about 1 cm and they completed germination on 20 August. On 26 August, when *M. micrantha* plants were about 370 cm in height and the mean number of leaves was 450, and *C. campestris* seedlings were about 5 cm in height, *C. campestris* seedlings with wet sands were placed on the soil surface of each *M. micrantha* pot in the infected group. Density treatments (1, 2, 4 or 8 *C. campestris* seedlings per host plant) were randomly assigned to *M. micrantha* plants in the infected group, 20 host plants per treatment density. By 29 August, all the *M. micrantha* plants in the infected group had become infected with *C. campestris* stems. The experiment ended on 27 December, 120 d after parasitization (DAP) or 210 d after planting, when the uninfected *M. micrantha* plants had started to wither. During the experiment, the pots were weeded when necessary and watered twice daily with tap water at 600 h and 1800 h, except on rainy days. No fertilizer was added throughout the experimental period.

2.2 Soluble proteins and enzyme assays

On 30 DAP, the 8th fully expanded sun leaf from four randomly selected *M. micrantha* plants per infection density was collected for determination of soluble protein content and enzyme assays, four samples of fresh leaves per treatment. Approximately 0. 5 g of fresh leaves (midvein excluded) per sample was homogenized in 5 mL of ice-cold 50 mM potassium phosphate buffer (pH7. 8) in an ice-cold mortar. The homogenate was centrifuged at 16 000 g for 15 min at 4 ℃ (CR22G Ultracentrifuge, Hitachi, Japan), and the supernatant was collected and stored at 4 ℃ for soluble protein determination and enzyme assays. Total soluble protein content in the samples was determined by the protein dye-binding method of (Bradford, 1976), using bovine serum albumin as standard. Superoxide dismutase (SOD) activity was determined by measuring percent inhibition of nitroblue tetrazolium (NBT)

reduction by SOD (Giannopolitis & Ries, 1977). Activity was expressed in units where 50% inhibition is equivalent to one unit of SOD activity. Peroxidase (POD) activity was determined spectrophotometrically as described by Chance & Maehly (1955). Catalase (CAT) activity was assayed spectrophotometrically by following the decrease in absorption at 240 nm due to the disappearance of hydrogen peroxide (H_2O_2) (Chance & Maehly, 1955).

2.3 Statistical analysis

All tests were carried out at $\alpha=0.05$ level using SPSS (version 11.5, SPSS Inc., Chicago, IL, USA). One-way analysis of variance (ANOVA) was used to determine statistical significance for the effects of infection density on plants for the variables of total soluble protein content, and enzyme activities. Means for significant ANOVA effects were compared using Tukey *post hoc* comparisons.

3 Results

3.1 Soluble protein content

At 30 DAP, inoculation with 1 parasite had no significant effect on soluble protein content of *M. micrantha* plants; however, infection with more than 1 parasite significantly reduced soluble protein content (Fig. 1a). Soluble protein contents at 2 and 4 parasites per host plant were not significantly different, but significantly higher than that at 8 parasites per host. The soluble protein content in the infected *M. micrantha* plants with 8 parasites per host was only about half that of uninfected control.

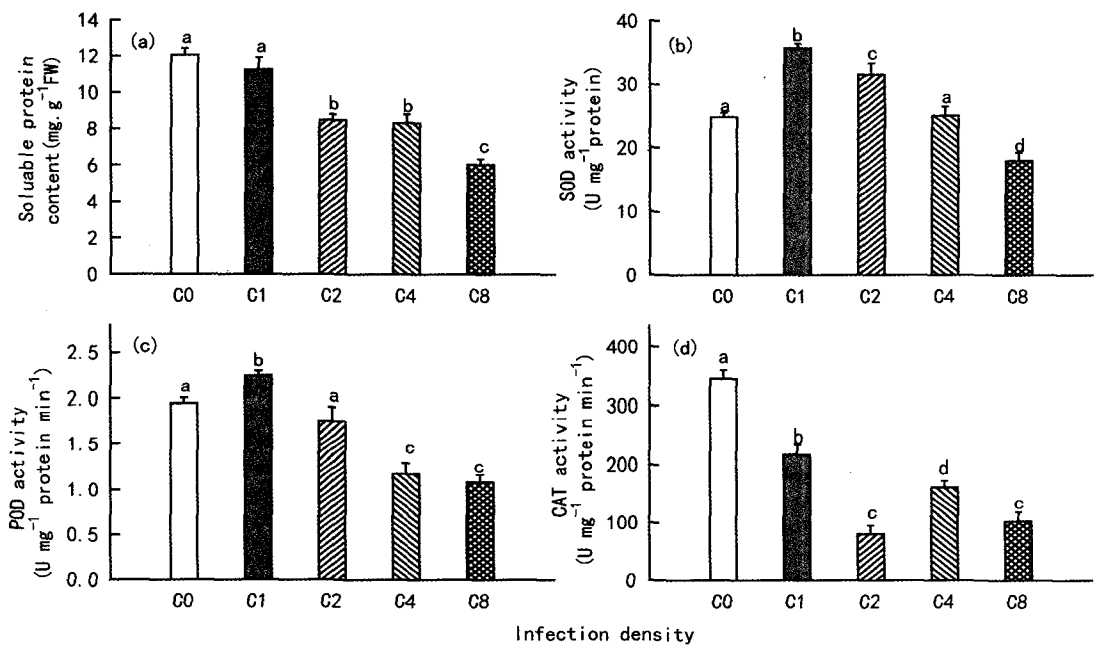

Fig. 1 Means (±SE, $n=4$) of soluble protein content (**a**), superoxide dismutase (SOD) activity (**b**), peroxidase (POD) activity (**c**) and catalase (CAT) activity (**d**) of *Mikania micrantha* 30 days after parasitization by different densities of *Cuscuta campestris*

Bars not sharing a common superscript letter are significantly different ($P<0.05$). Results of ANOVA: a, $F_{(4,15)}=29.447$, $P<0.001$; b, $F_{(4,15)}=28.095$, $P<0.001$; c, $F_{(4,15)}=21.815$, $P<0.001$; d, $F_{(4,15)}=45.750$, $P<0.001$. C0, C1, C2, C4 and C8: infection density at 0, 1, 2, 4 and 8 *C. campestris* per *M. micrantha* plant.

3.2 Activities of SOD, POD and CAT

Cuscuta campestris had significant effects on activities of SOD, POD and CAT of *M. micrantha* plants (Fig. 1: b-d). SOD activities were significantly higher at parasitic density of 1 or 2 parasites per host than that of the control, similar between 4 and control, and significantly lower at 8 than that of the control. For infected treatments, SOD activities decreased signifi-

cantly with increasing parasitic density. Compared with control, POD activity was not changed at parasitic density of 4 parasites per host, but significantly increased at 1 and decreased at 4 or 8 parasites per host plant. As parasitic density increased, POD activity decreased. The infected plants had significantly lower CAT activity than the control at all parasitic densities. CAT activities at infection density of 4 parasites per host were significantly lower than that at 1 but higher than those at 2 or 8 parasites per host. Compared with the control, infection with *C. campestris* led to significant increases in the ratios of SOD/CAT, SOD/POD, and SOD/ (CAT+POD) activities in *M. micrantha* plants (Table 1).

Table 1 Ratios of superoxide dismutase(SOD) activity to catalase(CAT) activity, SOD activity to peroxidase (POD) activity, and SOD activity to the sum of CAT activity and POD activity in *M. micrantha* 30 days after parasitization by different densities of *C. campestris*

	C0	C1	C2	C4	C8
SOD/CAT	0.07a	0.17b	0.39c	0.16b	0.18b
SOD/POD	12.69a	15.86b	18.04bc	21.25c	16.66b
SOD/(CAT+POD)	0.07a	0.16b	0.39c	0.16b	0.17b

No. followed by the same superscript in each row are not significantly different, according to Tukey *post hoc* comparisons ($P<0.05$). Refer to Fig. 1 for definitions of C0, C1, C2, C4 and C8.

4 Discussion

4.1 Response of *M. micrantha* to infection density of *C. campestris* in soluble protein content

It has been shown that *Cuscuta* can form a strong sink to redirect the flow of host resources to itself, and these resources include water, nitrogen, mineral nutrients and 99% of the carbon that it uses (Jeschke *et al.*, 1994a, b; Jeschke & Hilpert, 1997). Parasitic plants generally have high rates of transpiration (Stewart & Press, 1990) which may predispose hosts to water stress and thus stomatal closure (Frost *et al.*, 1997). There have been reports that parasite infection results in water stress in host plants (Taylor *et al.*, 1996; Frost *et al.*, 1997). Soluble proteins play an important role in osmotic adjustment; and high soluble protein content can sustain low osmotic potential to reduce damage caused by water stress (Yu & Tang, 1999). In this study, infection with more than 1 parasite per *M. micrantha* plant significantly reduced soluble protein content of the host. This reduction in soluble protein content may be the reason that *C. campestris* infection reduces gs and hence decreases *Pn* of *M. micrantha* host plants (Shen *et al.*, 2007).

On the other hand, in C3 plants, Rubisco generally accounts for 30-60% of the soluble proteins (Ellis, 1979). The rate of photosynthesis and biomass accumulation depend largely on the quantity and activity of Rubisco (Lorimer, 1981). Therefore, in this study, the reduced soluble protein content due to infection might have resulted in reduced Rubisco content in the infected *M. micrantha*, and such a reduced Rubisco content would have contributed to the reduced photosynthesis of the host.

4.2 Response of *M. micrantha* to infection density of *C. campestris* in activities of SOD, POD and CAT

In the present study, there was a complex relationship among activities of SOD, POD, CAT and infection densities. At low infection densities (1 or 2 parasites per host plant), SOD and POD activities increased or maintained, indicating the protective enzyme system was relatively well balanced. However, at relative high infection densities (4 or 8 parasites per host), such a balance was broken. These indicated that it's possible *C. campestris* infection resulted in high levels of reactive oxygen species (ROS), and at low infection density, the infected *M. micrantha* plants in response increased the activities of SOD to minimize the damage from ROS, which promoted POD to get rid of H_2O_2 and hydroxyl. However, when the infection densities became too high, the infected plants were unable to do so.

Furthermore, ratios of SOD/CAT, SOD/POD, and SOD/ (CAT+POD) were significantly higher in the infected at all infection densities than in the control. These ratios might be suggested as markers of H_2O_2 content (Shah *et al.*, 2001). Together, these might result in an imbalance of antioxidant enzyme systems in the infected *M. micrantha* plants, and such an imbalance might lead to excessive H_2O_2. It had been shown

that if only SOD activity was increased, while the activities of other antioxidant enzymes such as POD and CAT were not enhanced enough, plants can not prevent damage caused by oxygen free radicals (Pitcher *et al.*, 1991), or they might even suffer more serious damage brought by hydroxyl (Gossett *et al.*, 1994). Furthermore, the increased level of H_2O_2 caused by UV-B radiation increased the degradation of Rubisco by activation of proteolytic systems (He *et al.*, 2004). Therefore, in the present study, the *C. campestris* infection might have resulted in high level of ROS production and imbalance of the antioxidant enzymes. These would lead to Rubisco degradation and cell damage and thus reduced net photosynthesis of the infected *M. micrantha* plants (Shen *et al.*, unpublished data).

In conclusion, the results indicated that different levels of *C. campestris* infection had significantly different effects on the performance of *M. micrantha* plants. Host soluble protein content was significantly decreased when infected with more than 1 *C. campestris* seedling. For the infected treatments, as parasitic density increased, soluble protein content, activities of SOD and POD decreased. The protective enzyme system was relatively well balanced at low infection densities (1 or 2 parasites per host plant) but unbalanced at relative high infection densities (4 or 8 parasites per host). Thus, the minimum number of *C. campestris* for optimum control of *M. micrantha* in the field was 4 per host plant.

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伤组织形成，但效果相对较差，这可能是多种激素混合形成“复合启动因子”，对花药愈伤组织的形成有促进作用。

3.4 低温预处理时间对愈伤组织形态结构的影响

陈红等(2007)研究发现，低温预处理 8 d 左右的材料诱导的愈伤组织(结构紧密且略泛白色)好于低温预处理 10 d 以上的材料花药培养出的愈伤组织(松散，成分散小米状)。本试验低温预处理 7～10 d，结果两种材料试验所得的愈伤组织大都松散成小米粒状，转接时较为困难。其原因是否与处理时间过长有关有待进一步研究。

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