

Effects of water stress on the growth and allelopathic potential of invasive plant *Mikania micrantha* H.B.K

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ABSTRACT

To reveal the ecophysiological mechanisms underlying the adaptation of *M. micrantha* to drought stress, three irrigation regimes [normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity)] were used in pot experiment. The results showed that: (i) The content of chlorophyll a, chlorophyll b and total chlorophyll decreased with the decreasing soil water content, (ii) The daily mean of photosynthetic rate (P_{day}), transpiration rate (T_r), stomatal conductance (G_s) increased with the increasing soil water content, while the water use efficiency (WUE) decreased, (iii) Soil infested by *M. Micrantha* showed the severe water stress and exerted the allelopathic inhibition in the seedling growth of *Brassica campestris* and *Raphanus sativus*, (iv) The activities of peroxidase, catalase and superoxide dismutase increased and then decreased with severe drought stress, while the soluble protein content increased. (v) Drought stress caused resulted in significant changes in morphology and biomass allocation of *M. micrantha*. These results indicated that *M. micrantha* has strong adaptability to water stress, which may be one of the reasons to explain its successful invasion.

Key words: Antioxidant enzymes, *Brassica campestris*, drought resistance, field capacity, invasion, irrigation, *Mikania micrantha*, mustard, pot culture, radish, *Raphanus sativus*, seedling growth, water deficit, Water use efficiency

INTRODUCTION

Invasive alien plants displace the native species, change the community structure and alter the fundamental processes (20) through interference (competition and allelopathy) (14). Invasive alien plants are adapted to diverse environmental conditions due to their high phenotypic plasticity (25,30). Successful invasions of alien plants depend on numerous factors, soil water content significantly affects the growth, morphological traits and allelopathy of invasive plants (1,10,19). The soil water content has positive correlations with invasion success (16). Water stress inhibits the growth of invasive plant

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Flaveria bidentis (6). The invasive species can tolerate high leaf temperature under water stress and can display higher plastic photosystem II thermal tolerance responses than Mediterranean natives (13). The native plant *Merremia boissiana* adjusts its resource allocation to competition (allelopathy) to adapt to various water conditions, which might be one of the reasons for its successful invasion in Hainan Province of China (15). Drought stress affects the photosynthesis in invasive tree (*Prosopis juliflora* (Sw.) DC.) more than in the native tree (*Anadenanthera colubrina* (Vell.) Brenan) (22). *P. juliflora* and *A. colubrina* have different capacities to tolerate low water availability (22). Thus invasive alien plants have higher adaptability to water stress than native plants, which may help them in invasion.

Mikania micrantha H.B.K. (Asteraceae), a fast-growing vine species originated from South and Central America (20,21,28), is listed as one of the world's most aggressive weeds (21,32). It dominates in wide range of habitats (lawns, orchards, agricultural land, watersides, waste ground and roadsides) and can rapidly form dense nearly monospecific stands quickly within few years (7,29,32). It releases the allelochemical compounds into the environment which suppress the growth and development of its neighboring plants (28,32). It is an invasive alien plant with strong invasiveness and has caused serious damages in South China and has wide range of habitats. It is known that the soil water content is one important environmental factor that could significantly effect the invasive of the alien plants (1,10,19). However, it is not clear whether the invasive plant *M. micrantha* also has higher ability to adapt to drought stress. This study aimed to understand the effects of water stress on the growth traits and allelopathic potential of invasive plant *M. micrantha*. For this we studied the biomass allocation, photosynthetic characteristics and allelopathic potential of this plant in 4-experiments: (i) Growth and morphology experiment, (ii) Bioassay experiment, (iii) Photosynthetic experiment and (iv) Enzyme activities.

MATERIALS AND METHODS

Growth and morphology

Plants of *M. micrantha* were collected in March 2014, from our University Farm (N 23°16', E 113°34'). They were cut into 8 cm long pieces and transplanted into plastic pots (25 cm dia, 30 cm high) at one plant per pot. When the seedlings were approximately 12 cm tall, uniform seedlings were selected to reduce the experimental error. Three irrigation regimes [(normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity)] were used. From May 2014, the plants were watered once a day to maintain various water stress levels until harvest. Plants were grown in glasshouse (25 ± 2°C, 75% ± 5% relative humidity, 14/10 h day/night). All plants were randomized weekly to avoid any positional effects. After 90 days, total leaf area (LA) was determined using leaf area meter (CI-203 Area-meter; CID, USA) and the

shoot length of each plant was measured. Plants were partitioned into leaves, stems and roots and separately dried at 75°C for 48 h, thereafter, these were weighed. The Root/shoot ratio was calculated as the ratio of roots biomass to shoots (leaves + stems). The specific leaf area (SLA) was calculated as the ratio of LA (leaf area) to leaf dry mass. The stem (leaf, root) mass ratio SMR (LMR and RMR) was calculated by dividing the dry mass to plant total dry mass. Growth and morphology experiment were replicated 5-times.

Photosynthetic and chlorophyll content: The photosynthesis of *M. micrantha* was determined from the youngest fully expanded leaves using a portable photosynthesis system (Li-6400, Li-Cor, Lincoln, NE, USA). The net photosynthetic rate (P_n), transpiration rates (T_r) and stomatal conductance (G_s) were measured from 08:00 to 18:00 at 2 h intervals. The daily average photosynthesis (P_{day}) was used to evaluate the effects of different soil relative water content treatment (25). Leaf water use efficiency (WUE) was calculated as the ratio between P_{day} and daily average T_r (25). One g fresh leaves of *M. micrantha* collected from different treatments was extracted with 80% cold acetone and quantized spectrophotometrically 645 and 663 nm (2). Chlorophyll a and b contents, total chlorophyll content and chlorophyll a/b were determined according to Arnon (2). There were five independent replicates.

Bioassays: After planting of *M. micrantha* under different drought stresses [normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity)] for 90 days, the allelopathic potential of the soil were determined. Soil (3 g) was collected from different drought stress treatments, air dried and mixed with 5 mL agar (0.5%, w/v) in 50 mL beaker. After the agar solidification another 3 mL water agar was added to each beaker. Five germinated seeds of receptor plants (*Brassica campestris* L. and *Raphanus sativus* L.) were placed on the surface of water agar. The beaker was then covered with plastic film and the seeds were incubated in climate chamber (25 ± 2 °C, in dark) (24). The shoot height and root length were recorded 4 d after incubation. The bioassay experiment was replicated five times.

Soluble proteins and enzyme assays: After 90 d in pot culture, fresh leaves of *M. micrantha* from each treatment plants were collected to determine the soluble protein content and the activity of defense-related enzymes [superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT)]. POD activity was determined by using spectrophotometer (18). SOD activity was determined using the method of Giannopolitis and Ries (12). Catalase activity was determined as per Bergmeyer (4). Total soluble protein content was assayed by the protein dye-binding method, using bovine serum albumin as standard (5). There were five independent replicates.

Statistical analysis: All data were shown as mean \pm standard error (SE). Data were analyzed statistically by one-way ANOVA followed by a Duncan's multiple range tests using the SPSS 13.0 software package (SPSS, Chicago, IL, USA). Differences were considered to be significant at a level of $P < 0.05$.

RESULTS AND DISCUSSION

I. *M. micrantha* growth

The water stress decreased the biomass due to changes in biomass allocation and morphology. Water stress significantly inhibited the *M. micrantha* growth [total biomass, shoot length and leaf area (Table 1)], especially under severe water stress (20%). Compared with the control (normal irrigation, 80% field capacity), severe water stress significantly decreased the total biomass, shoot length and leaf area by 50.3%, 46.3% and 42.5%, respectively. However, severe water stress (20% field capacity) increased the RMR and SLA by 30.0% and 17.2%, respectively than normal water content, SMR was not affected. Consequently, R/C increased by 16.6% with water stress. The higher phenotypic plasticity may be an important invasive mechanism of *S. canadensis* (11). Invasive grass *Poa pratensis* and *Bromus inermis* has higher biomass allocation to roots compared with two native species *Pascopyrum smithii* and *Stipa viridula*, these invasive plants might use their high competitive ability in terms of water uptake and root growth than their native counterparts (9). Bakker and Wilson (3) found that, the invasive species *Agropyron cristatum* had greater competitive ability than native *Bouteloua gracilis*, because *A. cristatum* had higher biomass allocation to roots than *B. gracilis*. The larger biomass in roots means the plants have higher ability to absorb soil water (3). Study also demonstrated that successful invasive species were plastic enough to cope with dry conditions of the Iberian Peninsula (13). Invasive plant *S. canadensis* has strong ability of drought resistance and endurance, but severe drought reduces the total biomass, root biomass, stem biomass and leaf biomass, but increased the root mass ratio, leaf mass ratio and root cap ratio (11). Our study showed that water stress significantly decreased the stem length and biomass of *M. micrantha*, which indicated that *M. micrantha* might change its morphology and biomass allocation to adapt to drought stress.

Table 1. Effects of 3-drought treatments on biomass, shoot length, leaf, stem or root mass ratio, total leaf area specific leaf area and the ratio of roots to shoots (leaves + stems) of *M. micrantha*.

Soil water (Field capacity %)	Biomass (g)	SL (cm)	RMR (g g ⁻¹)	SMR (g g ⁻¹)	LMR (g g ⁻¹)	LA (cm ²)	SLA (m ² kg ⁻¹)	R/C (g g ⁻¹)
20	1.93 c	247.59 c	0.10 a	0.53 a	0.37 b	507.75 c	71.42 a	0.18 a
40	2.43 b	313.68 b	0.08 b	0.52 a	0.40 a	617.51 b	64.02 b	0.16 b
80 (control)	3.89 a	460.54 a	0.07 c	0.55 a	0.38 ab	883.71 a	60.97 b	0.15 c

The leaf (stem, root) mass ratio (LMR, SMR and RMR) was calculated by dividing the dry mass by total plant dry mass, SL: shoot length, LA: total leaf area, SLA: specific leaf area, R/S: the ratio of roots to shoots (leaves + stems). All data represent means. Values followed by different letters in the same row indicate significant differences ($P < 0.05$) according to Duncan's multiple range test.

II. Photosynthetic characteristics and chlorophyll content

When *M. micrantha* was planted under severe water stress (20% field capacity), its P_n , T_r and G_s were decreased by 34.1, 50.8 and 57.3%, respectively, than control (normal irrigation (80% field capacity)). The P_n , T_r and G_s showed declining trends under

continuous drought stress, while *WUE* increased significantly (Table 2). Thus *M. micrantha* keep growing at > 20% soil relative water content and the *WUE* was highest. Compare to control (soil relative water contents was 80%), the drought stress (the soil relative water contents were 60% and 30%) reduces P_n , T_r , G_s and other physiological indices of invasive plant *Flaveria bidentis* (31). When the relative soil water content was between 38.9% and 70.5%, P_n , G_s and T_r of *Hippophae rhamnoides* significantly decreased with increasing drought stress, however, the stomatal limitation increased significantly, which indicated that stomatal limitation was responsible for reduction in P_n (23). Compared with control (100% soil water content), the P_n , the maximum photosynthetic rate and light saturation point of invasive plant *Solidago canadensis* are lower and light compensation point is higher at the relative soil water content of 80%, 60% and 40%, respectively (11).

2. Effects of 3-drought treatments on photosynthetic rate (P_{day}), transpiration rate (T_r), stomatal conductance (G_s) and water use efficiency (*WUE*) of *M. micrantha*.

Soil water stress (Field capacity %)	P_{day} ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	T_r ($\text{mmol m}^{-2}\text{s}^{-1}$)	G_s ($\text{mmol m}^{-2}\text{s}^{-1}$)	<i>WUE</i> ($\mu\text{mol mmol}^{-1}$)
20	3.16 c	0.56 b	20.14 b	5.98 a
40	4.01 b	0.65 b	23.38 b	6.36 a
80 (control)	4.80 a	1.14 a	47.16 a	4.28 b

All data represent means. Values followed by different letters in the same row indicate significant differences ($P < 0.05$) according to Duncan's multiple range test.

P_{day} : photosynthetic rate, T_r : transpiration rate, G_s : stomatal conductance, *WUE*: water use efficiency.

The contents of chlorophyll a, chlorophyll b, total chlorophyll and chlorophyll a/b in the leaves of *M. micrantha* were 7.06 mg g⁻¹ (Fig. 1A), 3.10 mg g⁻¹ (Fig. 1B), 10.16 mg g⁻¹ (Fig. 1C) and 2.28 (Fig. 1D), respectively, when planted *M. Micrantha* under no-water stress (80% field capacity). Chlorophyll a, Chlorophyll b and total chlorophyll in the leaves of *M. micrantha* decreased with the decrease in field capacity. The effect of progressing drought was more pronounced on chlorophyll a in the leaves of *M. micrantha* than chlorophyll b or total chlorophyll (Fig. 1). This is consistent with the findings that the contents of chlorophyll a, chlorophyll b and total chlorophyll of invasive plant *Solidago canadensis* decreased with the decrease of soil water content, while the ratio of chlorophyll a/b increased (11). This study has shown that *M. micrantha* seedlings were able to maintain high photosynthetic rate and regular growth under drought stress.

III. Soluble proteins and enzyme assays

At field capacity of 20%, 40% and 80%, the POD activity was 2.4, 3.2 and 1.7 U mg⁻¹ protein min⁻¹, respectively (Fig. 2A). The normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity) increased the POD activity by 58.9% and 41.2% over the control, respectively (Fig. 2A). Similarly, the activities of CAT and SOD increased and then decreased with the deepening of soil water stress (Fig. 2B and 2C). The content of soluble protein at normal irrigation and moderate water stress were not significantly different, but were higher than severe water stress (Fig.

2D). Compared to control (80% field capacity), severe water stress (20% field capacity) increased the soluble protein content by 13.9% (Fig. 2D). Our results showed that the activities of antioxidant enzyme were increased in all irrigation regimes (20% to 80% field capacity). *Populus pruinosa* accumulates the soluble protein to eliminate the reactive oxygen and alleviate the impairment of the photosynthetic apparatus under soil drought (27). Malondialdehyde, superoxide dismutase activity and peroxidase activity of invasive plant *Galinsoga parviflora* were max at 20% PEG-6000 treatment (8). Soluble protein mass fraction was max at 15% PEG-6000 treatment (8). POD activity of invasive *Ambrosia trifida* decreases significantly under mild drought stress and increases under severe drought stress (26). Under normal watering conditions, there are no significant changes in leaves of electrolyte leakage, MDA content and antioxidant enzymes (SOD, CAT and POD) activities. It is indicated that *A. trifida* is sensitive to drought stress and has strong adaptability to drought stress (26). The contents of MDA and chlorophyll changes in various degrees, indicating that invasive plant *Eupatorium catarium* has a mechanism to tolerate drought stress and benefit itself acclimatized to different habitats (17).

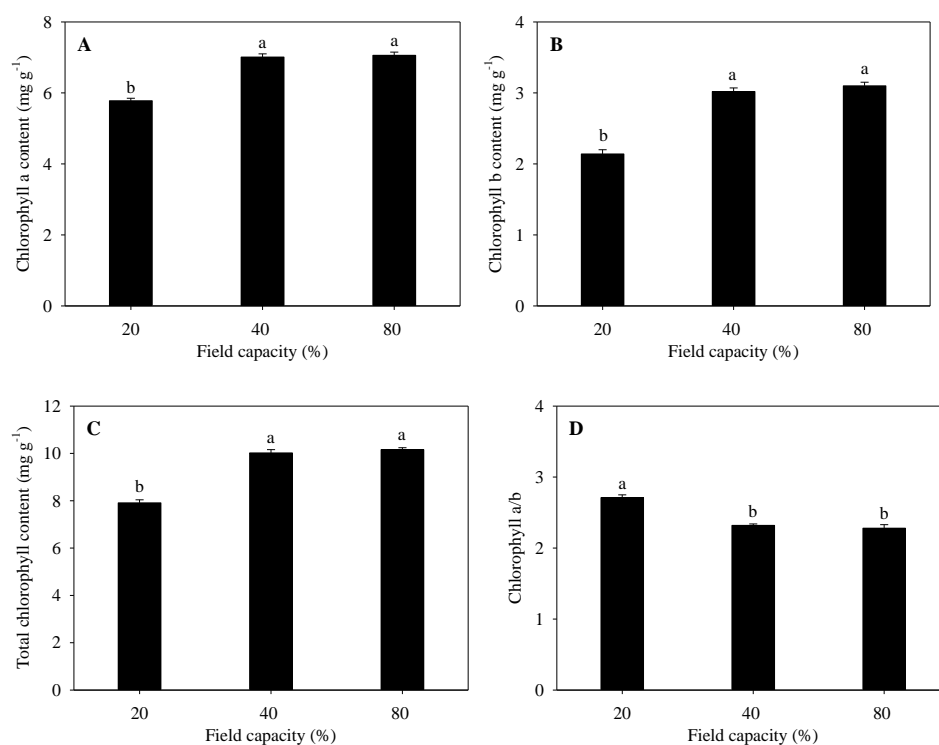


Figure 1. Effect of 3-drought treatments [(control: normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity)] on chlorophyll a content (A), chlorophyll b content (B), total chlorophyll content (C) and chlorophyll a/b (D) in the leaves of *M. micrantha*. Values are means \pm SE from five replicates. Significant differences ($P < 0.05$ using Duncan's multiple range test) among all treatments are indicated by different letters above bars.

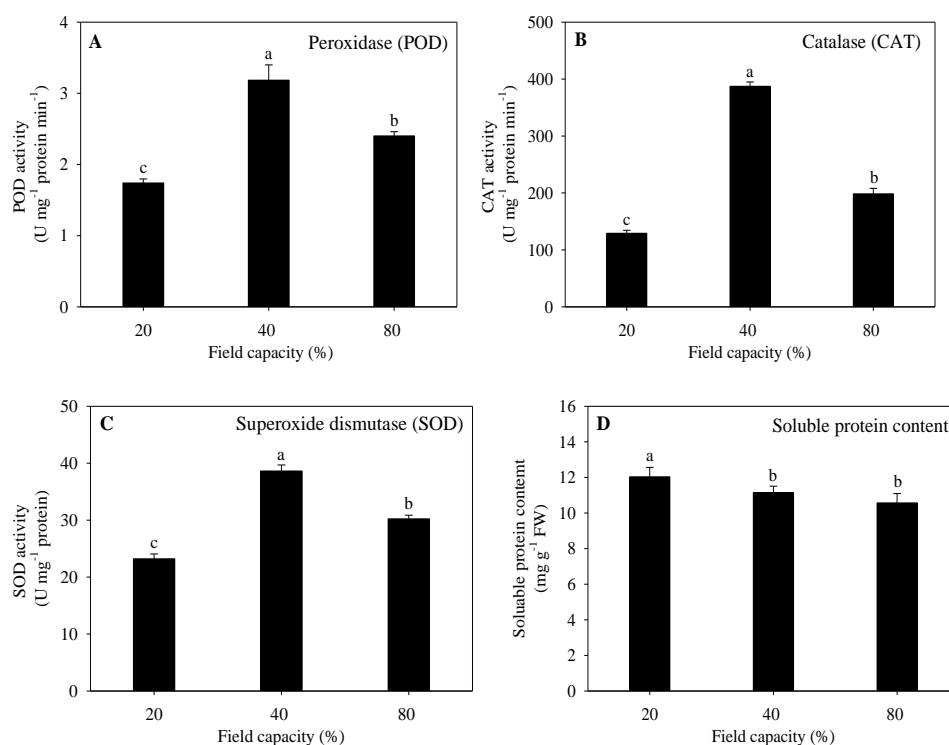


Figure 2. Changes in the peroxidase (POD) activity (A), catalase activity (B), superoxide dismutase (SOD) activity (C) and soluble protein content (D) of *Mikania micrantha* subjected to 3-drought treatments [control: normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity)]. All data represent means \pm SE. Different letters above bars indicate significant differences ($P < 0.05$) according to Duncan's multiple range test.

Temperature-induced drought stress disproportionately affects the rapidly growing white spruce (3). Our results suggested that *M. micrantha* protective enzyme system can regulate physiological indices under soil drought, has stronger ability to adapt drought stress.

IV. Bioassay

The shoot heights of *B. campestris* were 6.29, 6.78, and 6.79 mm when grown in soil samples from *M. micrantha* planted soil and treated with severe water stress (20% field capacity), moderate water stress (40% field capacity) and normal irrigation (80% field capacity), respectively. Compared with control (soil without *M. micrantha*), the shoot heights of *B. campestris* were inhibited by 11.61, 4.78 and 4.68% in the soil samples from *M. micrantha* planted soil and treated with severe water stress (20% field capacity), moderate water stress (40% field capacity) and normal irrigation (80% field capacity), respectively (Fig. 3A). Similarly, the root length of *B. campestris* was also inhibited by

16.86, 12.42 and 7.14%, when planted in the soil from *M. micrantha* planted soil samples were treated with the above irrigation regimes, respectively (Fig. 3B). The shoot height (Fig. 3C) and root length (Fig. 3D) of *R. sativus* showed similar trend with those of *B. campestris*. The allelopathic potential of soil samples (*M. micrantha* planted) on the receiver plants increased, when the same soil treatment with decreased field capacity. Aqueous leachates from the dry leaves of *Merremia boissiana* which poses a big threat to many secondary forests, showed higher inhibition effects on the seed germination and seedling growth of *Lactuca sativa* var. *ramose* under adequate light and drought (15). Plasticity in allelopathy indicates that *M. boissiana* might adjust its resource allocation to competition (allelopathy) which is beneficial for it to adapt to various water conditions (15). Our results showed that the *M. micrantha* grown soil under severe water stress (20% field capacity) drastically inhibited the seedling growth of recipient plants (Figure 3).

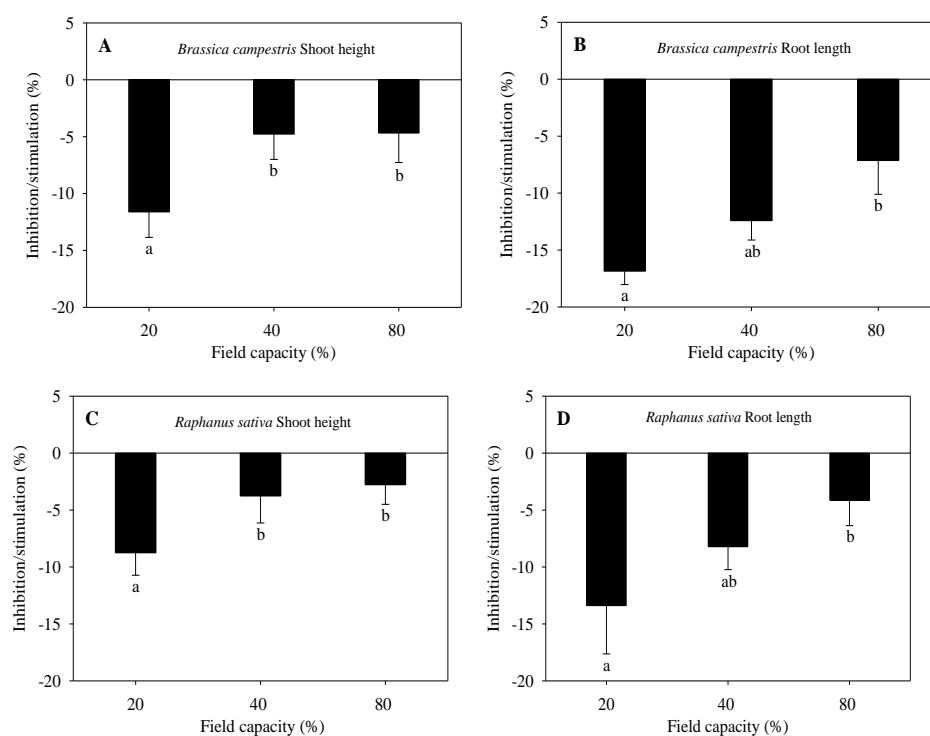


Figure 3. Effects of soil samples on the root length and shoot height of *Brassica campestris* (A, B) and *Raphanus sativus* (C, D). Soil samples were obtained from the pots after *M. Micrantha* subjected to 3- drought treatments [(control: normal irrigation (80% field capacity), moderate water stress (40% field capacity) and severe water stress (20% field capacity)]. Values are means \pm SE from five replicates. Significant differences ($P < 0.05$ using Duncan's multiple range test) among all treatments are indicated by different letters above bars.

We observed from field investigations that *M. micrantha* has become more prevalent in the forests in south China (30). Although, there are many environmental factors affecting the invasiveness of alien plants, invasions of alien plants could adapt themselves to different environment by higher phenotypic plasticity and higher adaptability (30). Our results suggested that severe water stress may enhance the biosynthesis of allelochemicals in *M. micrantha*, which in turn might enhance its inhibitory allelopathic effects on the neighbouring native plants. Overall, this study provides a framework for better prediction of the future distribution of alien invasive plants from the point view of allelopathy under soil water stress.

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