

Research Article

Can allelopathy be used to efficiently resist the invasion of exotic plants in subtropical forests?

Jin Zheng¹, Qiao-Jing Ou¹, Tai-Jie Zhang², Wei-Jie Liang¹, Bo-Hui Li¹ and Chang-Lian Peng^{1*}

¹Guangdong Provincial Key Laboratory of Biotechnology for Plant Development, Guangzhou Key Laboratory of Subtropical Biodiversity and Biomonitoring, School of Life Sciences, South China Normal University, Guangzhou 510631, PR China

²Guangdong Provincial Key Laboratory of High Technology for Plant Protection, Institute of Plant Protection, Guangdong Academy of Agricultural Sciences, Guangzhou 510640, PR China

*Corresponding author

E-mail: pengchl@scib.ac.cn

Citation: Zheng J, Ou Q-J, Zhang T-J, Liang W-J, Li B-H, Peng C-L (2019) Can allelopathy be used to efficiently resist the invasion of exotic plants in subtropical forests? *BioInvasions Records* 8(3): 487–499, <https://doi.org/10.3391/bir.2019.8.3.03>

Received: 13 March 2019

Accepted: 3 July 2019

Published: 12 August 2019

Handling editor: Margarita Arianoutsou

Thematic editor: Stelios Katsanevakis

Copyright: © Zheng et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

Mature subtropical forests can resist the invasion of *Mikania micrantha*, a notorious exotic invasive plant, but the underlying mechanism for this resistance is still debated. In this study, we explored whether allelochemicals produced by the dominant species in a subtropical forest were sufficient to inhibit the invasion of *M. micrantha*. Allelopathic effects of three tree species (*Syzygium rehderianum*, *Cryptocarya concinna* and *C. chinensis*) on the germination and vegetative growth of *M. micrantha* were investigated. The results showed that aqueous extracts from the leaves of all tree species had allelopathic inhibitory effects on *M. micrantha* seed germination at a concentration of 5% aqueous extract. Variations were observed in the allelopathic effects of the tree species on germination rate (GR), germination energy (GE) and radicle length (RL), but all the tree species had the same synthetic allelopathic effect (SE). Reduced height, biomass, Chlorophyll (Chl a/b), Carotenoid/Chlorophyll (Car/Chl), antioxidant capacity, nonphotochemical quenching coefficient (NPQ) and increased specific leaf area (SLA) were observed in *M. micrantha* planted with the tree species. The allelopathic potential of the tree species on *M. micrantha* in a vegetative growth stage was weak. Our results indicated allelopathy alone was not sufficient to inhibit the invasion of exotic plants in subtropical forests, but the combination of allelopathy and shading may be sufficient.

Key words: Chlorophyll fluorescence, germination, inhibition, plant invasion, resistance

Introduction

It is well known that many mature forest ecosystems can resist invasions by alien plants. Several hypotheses have been proposed to explain this phenomenon. Early studies generally assumed that undisturbed, closed-canopy forests (especially late-successional forests) were resistant to exotic plant invaders due to shading (Von Holle et al. 2003). This was supported by the observation that disturbance facilitated exotic plant invasions in forest ecosystems (Lodge 1993). However, this hypothesis is focused on exotic species with early-successional life histories and based on an ideal environment (Rejmánek and Richardson 1996; Grotkopp et al. 2002),

neglecting the shade-tolerant exotic species. In fact, disturbance is ubiquitous in forests, providing many opportunities for invasions of exotic species with early-successional life histories. Furthermore, some closed-canopy forests in temperate and tropical regions were observed to be readily invaded by shade-tolerant exotic plants (Gilbert and Lechowicz 2005; Martin and Marks 2006). Another plausible hypothesis is allelopathy (Mitchell and Power 2003). The release of allelochemicals by invasive plants may have inhibitory effects on the growth of newly encountered native plants, thereby promoting their invasions (Callaway and Ridenour 2004). In contrast, allelopathy is an important strategy for native plant communities to strengthen their immunity to invasive species (Xie et al. 2017).

Mikania micrantha Kunth (Asteraceae), which is known as mile-a-minute weed, is one of the top ten invasive weeds in the world (Zhang et al. 2004). This perennial vine is native to tropical Central and South America and has spread rapidly to other tropical and subtropical climatic zones of the world since it was introduced in Indonesia as ornamental plant in the 1940s (Waterhouse 1994). In China, this notorious weed has widely invaded various ecosystems and caused extensive economic losses (Shen et al. 2015). At *Eucalyptus* plantations, *M. micrantha* can grow 6–8 m up tree trunks by twining. However, it is almost never seen in natural subtropical forests, particularly those at late-successional growth stages (He and Huang 2004).

Dinghushan biosphere reserve is a 1154 hm² area located in the middle of Guangdong Province, China, near the Tropic of Cancer. The vegetation type in the Dinghushan biosphere reserve is characterized as evergreen monsoon subtropical forests, which contain a complete natural successional series from early coniferous stage forest to regional climax broadleaf stage forest (Peng and Wang 1995; Zhou et al. 2007). Light is the main factor that drives plant succession in the Dinghushan forests. Therefore, the plant communities of early-, mid-, and late- successional stages have light-loving coniferous species (e.g., *Pinus massoniana* Lamb.), light-loving broadleaf species (e.g., *Schima superba* Gardn. et Champ., *Castanopsis chinensis* (Sprengel) Hance and *Castanopsis fissa* (Champ. ex Benth.) Rehd. et Wils.) and shade-tolerant broadleaf species (e.g., *Syzygium rehderianum* Merr. et Perry, *Cryptocarya concinna* Hance and *Cryptocarya chinensis* (Hance) Hemsl) as the main components (Zhang et al. 2015; Zhu et al. 2016). In this study, we explored whether allelopathy from the late-successional dominant species (*S. rehderianum*, *C. concinna* and *C. chinensis*) was sufficient to inhibit the invasion of the exotic plant, *M. micrantha*, in subtropical forests.

Materials and methods

Collection of M. micrantha seeds

In southern China, the rapid growing season of *M. micrantha* is from March to October, with flowering from October to December, and seed

production from November to December (Zhang et al. 2004). In December 2016, mature seeds of *M. micrantha* were collected in Huaguo Village, Xinxu Town, Huizhou, Guangdong, China. Dry inflorescences containing mature seeds were shaken by hand, allowing the seeds to fall into a paper bag. The seeds were taken to the lab for removal of impurities and then stored in a refrigerator at 4 °C until further use.

Culturing of tree species

Three dominant tree species from the late-successional stage forest, *Syzygium rehderianum*, *Cryptocarya concinna* and *C. chinensis*, were collected from the monsoon evergreen broad-leaf forests of Dinghushan biosphere reserve (23°09'21"–23°11'30"N; 112°30'39"–112°33'41"E) in January 2015. Tree saplings that were 40–50 cm tall were selected and grown in plastic pots (40 cm in diameter) containing a mixture of clay loam soil and peat soil (3:1, v/v) at the South China Normal University, Guangzhou, China. The plants were watered every day and fertilized with 1.5 g compound fertilizer (composed of nitrogen, phosphorus and potassium active ingredients at 15, 15 and 15%, respectively) twice a year. In 2017, the allelopathic potential of these tree species on *M. micrantha* seed germination was investigated.

Preparation of aqueous extract from leaves

Mature leaves of the tree species were detached from the potted-plants, washed with deionized water, air-dried in the shade and then ground to a powder. An aliquot of leaf powder (5 g) was soaked in 100 mL of deionized water at room temperature for 48 h with intermittent shaking for a period of one hour. Insoluble particles were removed by centrifugation at 2,500 g for 10 min and the supernatant was stored at 4 °C until further use.

Germination test

For each of the three tree species, two concentrations (0.5% and 5%) of leaf extract were used in the germination tests, and the lower concentration was diluted from the higher one. *M. micrantha* seeds were surface-sterilized for 15 min with 1% NaClO solution, rinsed three times with deionized water, and then germinated in Petri dishes (9 cm) containing two layers of filter paper with 5 mL of extract as a treatment or with 5 mL of distilled water as a control. Each treatment in the germination tests used 30 seeds in five replicates. The germination tests were conducted in a growth chamber (Model RXZ, Ningbo Jiangnan Instrument Factory, Ningbo, Zhejiang, China) at 28 °C (day, 14 h; 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation) and 25 °C (night, 10 h). The germination period was 7 days.

To prevent the Petri dishes from drying out, a moderate amount of leaf extract or deionized water (for the control group) was added to the filter

papers every day. The number of germinated seeds was recorded every day. A seed with 1-mm radicle emergence was considered to be germinated. At day 7, 10 seedlings in each treatment were randomly selected and the lengths of the radicles (RL) and plumules (PL) were measured through a stereomicroscope (M205FA, Leica, Germany). Germination rate (GR) and germination energy (GE) were calculated using the following formula (Ellis and Robert 1981; Ruan 2002):

$$GR = Nt/30 \quad (1),$$

$$GE = Nt'/30 \quad (2),$$

where Nt is the number of germinated seeds at day 7; Nt' is the number of germinated seeds at day 3; and the coefficient 30 is the total number of seeds.

Germination index (GI) was calculated according to Mukhtar (2008) by the following formula:

$$GI = \Sigma Gt/Dt \quad (3),$$

where Gt is the number of germinated seed and Dt represents the counted days.

The allelopathic effect index (RI) was calculated according to the formula described by Williamson and Richardson (1988):

$$RI = 1 - C/T \quad (T \geq C), \quad RI = T/C - 1 \quad (T < C) \quad (4),$$

where C indicates the value in the control group; T indicates the value in the treatment group, and a $RI > 0$ suggests a promotion effect, whereas a $RI < 0$ suggests an inhibitory effect. The absolute value of RI is consistent with the level of allelopathic effect. Synthetic allelopathic effect (SE) is the arithmetic mean of values calculated for RI, GR, GE, GI, and the lengths of the radicles and plumules.

Planting M. micrantha with the tree species

Effects of the tree species on *M. micrantha* growth were studied with pot experiments. Seedlings of *M. micrantha* were grown from seeds to the height of 15 cm in peat soil in July 2017 and transplanted into the pots with trees. Three seedlings were planted with one potted tree species, with five replications for each tree species. In the control group, intraspecific competition was used instead of interspecific competition, so six seedlings were grown in one pot without a tree. *M. micrantha* seedlings were grown with tree species under pot-culture conditions for three months, after which changes in photosynthetic pigments, specific leaf area, photosynthetic characteristics, antioxidant capacity and biomass were determined.

Determination of photosynthetic pigments

Mature leaf samples (0.05 g fresh weight [FW]) of *M. micrantha* were homogenized using a mortar and pestle in 4 mL of 80% acetone and

centrifuged at 4 °C at 8,000 g for 10 min. Next, the absorbance of the supernatant was detected at 663, 646 and 470 nm relative to an 80% acetone blank, and the contents of Chl a, Chl b and carotenoids (Car) were calculated according to Wellburn (1994).

Determination of specific leaf area

Twenty leaf discs (10 mm diameter) were cut from each *M. micrantha* plant, put into paper bags, dried to a constant weight at 80 °C, and then weighed. Specific leaf area (SLA) was calculated as the ratio of leaf area to leaf dry mass.

Determination of antioxidant capacity

Fresh leaf samples (0.025 g) of *M. micrantha* were cut into pieces and submerged in 1.5 ml of 95% methanol at 4 °C for 24 h. Leaf antioxidant capacity was determined by the 1,1-diphenyl-2-picrylhydrazyl (DPPH) test (Nguyen et al. 2010) and the Folin-Ciocalteu test (Everette et al. 2010). The DPPH test was carried out as follows: an aliquot of the extract (10 µL) was mixed with 3 mL of DPPH solution (freshly prepared in 95% methanol at 100 µM) and then the absorbance at 517 nm was measured. DPPH scavenging ability (DSA) was calculated using a calibration curve constructed with 20–100 µM DPPH. The Folin-Ciocalteu test was performed as follows: 0.5 mL of 20-fold diluted extract was mixed with 1 mL of 10% Folin-Ciocalteu reagent and 2 mL of 0.7 M Na₂CO₃ and absorbance was measured at 760 nm. The Folin-Ciocalteu test is often used to determine the total phenolic content (TPC), but Everette et al. (2010) showed that it is not specific for phenolic compounds and suggested using it to determine the total antioxidant capacity rather than phenolic content. In this study, gallic acid was used as the standard for the Folin-Ciocalteu test. So, besides DPPH scavenging ability, the antioxidant capacity is also expressed as the total phenolic content (TPC).

Determination of gas exchange

Gas exchange was measured in the morning (8:30–11:30 a.m.) of a sunny day using an LI-6400 photosynthesis system (LI-COR, Lincoln, NE, USA). During measurements, photosynthetic photon flux density (PPFD) in the leaf chamber provided by an LED light source was controlled at 800 µmol m⁻² s⁻¹, CO₂ concentration was maintained at 410 µmol mol⁻¹, the relative air humidity was 75–80% and leaf temperature was 26 °C. The gas exchange parameters, including net photosynthetic rate (Pn) and stomatal conductance (Gs), were recorded after the gas exchange of a leaf had reached a steady state in the leaf chamber.

Determination of chlorophyll fluorescence

Chlorophyll (Chl) fluorescence was measured using a Chl fluorescence imager (CF Imager, Technologica, Colchester, UK). Leaves were acclimated

Table 1. Effects of aqueous extracts from three tree species on seed germination of *Mikania micrantha*.

Treatment	GR	GE	GI	RL	PL
Control	0.87 ± 0.03 ^a	0.67 ± 0.03 ^a	21.66 ± 0.98 ^a	1.12 ± 0.09 ^a	0.48 ± 0.01 ^b
0.5%					
Sre	0.65 ± 0.03 ^{bc}	0.64 ± 0.03 ^a	19.99 ± 0.63 ^a	0.68 ± 0.05 ^b	0.46 ± 0.01 ^{bc}
Cco	0.55 ± 0.05 ^{cd}	0.67 ± 0.03 ^a	21.73 ± 0.81 ^a	0.50 ± 0.03 ^c	0.48 ± 0.02 ^b
Cch	0.51 ± 0.06 ^d	0.61 ± 0.03 ^a	20.88 ± 0.42 ^a	0.70 ± 0.04 ^b	0.54 ± 0.03 ^{ab}
5%					
Sre	0.45 ± 0.02 ^d	0.43 ± 0.06 ^b	17.02 ± 1.15 ^b	0.11 ± 0.01 ^e	0.38 ± 0.01 ^d
Cco	0.55 ± 0.02 ^{cd}	0.45 ± 0.04 ^b	16.14 ± 1.11 ^b	0.10 ± 0.01 ^e	0.42 ± 0.02 ^{cd}
Cch	0.49 ± 0.04 ^d	0.25 ± 0.02 ^c	14.73 ± 0.88 ^b	0.26 ± 0.02 ^d	0.42 ± 0.01 ^{cd}

Different lowercase letters within the same column indicate a significant difference ($P < 0.05$) according to the Duncan test. Abbreviations: Sre, *Syzygium rehderianum*; Cco, *Cryptocarya concinna*; Cch, *C. chinensis*. GR, germination rate; GE, germination energy; GI, germination index; RL, radicle length; PL, plumule length.

to the dark for 30 min and then placed in the measuring chamber immediately after they were detached. The minimum fluorescence yield (F_o) and the maximum fluorescence yield (F_m) were obtained under a mean light and a saturation pulse of $6000 \mu\text{mol m}^{-2} \text{s}^{-1}$, after which an actinic light ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$) was switched on. The steady fluorescence yield (F_s) and the maximum fluorescence yield (F_m') in the light-adapted state were measured after leaves were exposed to the actinic light for 4 min. The maximum photosystem II (PSII) quantum yield (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_o)/F_m$. The effective quantum yield of PSII ($\Delta F/F_m'$) was calculated as $(F_m' - F_s)/F_m'$ (Genty et al. 1989). The PSII efficiency factor reflects the capacity for photochemistry at PSII ($\Delta F/F_v'$) and was calculated as $(F_m' - F_s)/(F_m' - F_o')$, where F_o' was calculated according to Oxborough and Baker (1997). The nonphotochemical quenching (NPQ) was calculated as $(F_m - F_m')/F_m'$ (Bilger and Björkman 1990).

Statistics and analysis

Reported values were the mean and standard error (SE) of four to six parallel measurements made on different plants. One-way analysis of variance (ANOVA) was used to test for significant differences between different treatments using Statistics 18 (IBM SPSS, Chicago, USA). The Tukey test was used for post hoc analysis at the level $P = 0.05$. Data were checked for normality and homogeneity of variances prior to ANOVA and log-transformed if these conditions were not met.

Results

Allelopathic effects of the tree species on M. micrantha

Aqueous extracts from fresh leaves of the tree species inhibited seed germination of *M. micrantha* in a concentration-dependent manner (Table 1 and Figure 1). Compared with the control group, 0.5% aqueous extracts from

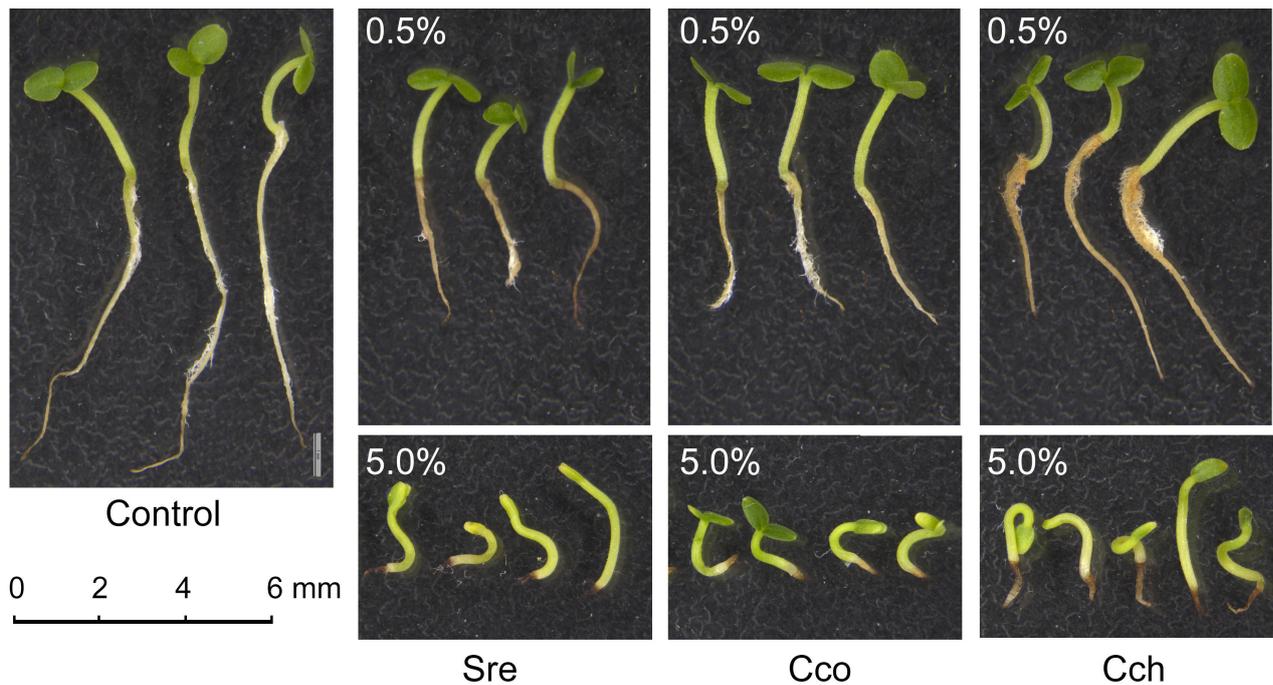


Figure 1. Effects of aqueous extracts from three tree species on seedling growth of *Mikania micrantha*. Abbreviations: Sre, *Syzygium rehderianum*; Cco, *Cryptocarya concinna*; Cch, *C. chinensis*. Photo by J. Zheng.

all the species significantly reduced GR and RL of *M. micrantha* ($P < 0.05$) but had no significant effect on GE, GI and PL. In contrast, 5% aqueous extracts from the tree species had a substantial impact on GR, GE, GI, RL and GL of the invasive species. Among the three tree species, the 5% aqueous extract from *Syzygium rehderianum* had the greatest inhibition on GR and PL, while *Cryptocarya chinensis* extract had the greatest inhibition on GE and GI (Table 1).

After the *M. micrantha* germination parameters (Table 1) were converted to relative inhibition rates, namely, allelopathic potentials (Figure 2), it can be seen that aqueous extracts from all tree species had allelopathic inhibitory effects on *M. micrantha* seed germination. At the concentration of 5% aqueous extract, the three tree species exhibited lower, intermediate and higher levels of allelopathic potentials on PL (−0.2 to −0.1), germination (including GR, GE and GI) (−0.7 to −0.2) and RL (−0.9 to −0.7), respectively. The three tree species, *S. rehderianum*, *C. concinna* and *C. chinensis*, had the greatest allelopathic effects on GR, RL and GE, respectively, and the lowest effects on GI, GR and PL, respectively. This resulted in all three tree species having the same SE on *M. micrantha*.

Changes in growth of M. micrantha planted with the tree species

Based on pot experiments, the average PPFD measured under the tree canopies of the three species was approximately one-quarter of the PPFD measured in open air, and the light interception of *S. rehderianum* was greater than that of the other two tree species (Figure 3). Lower height and yield were observed in *M. micrantha* when planted with the tree species.

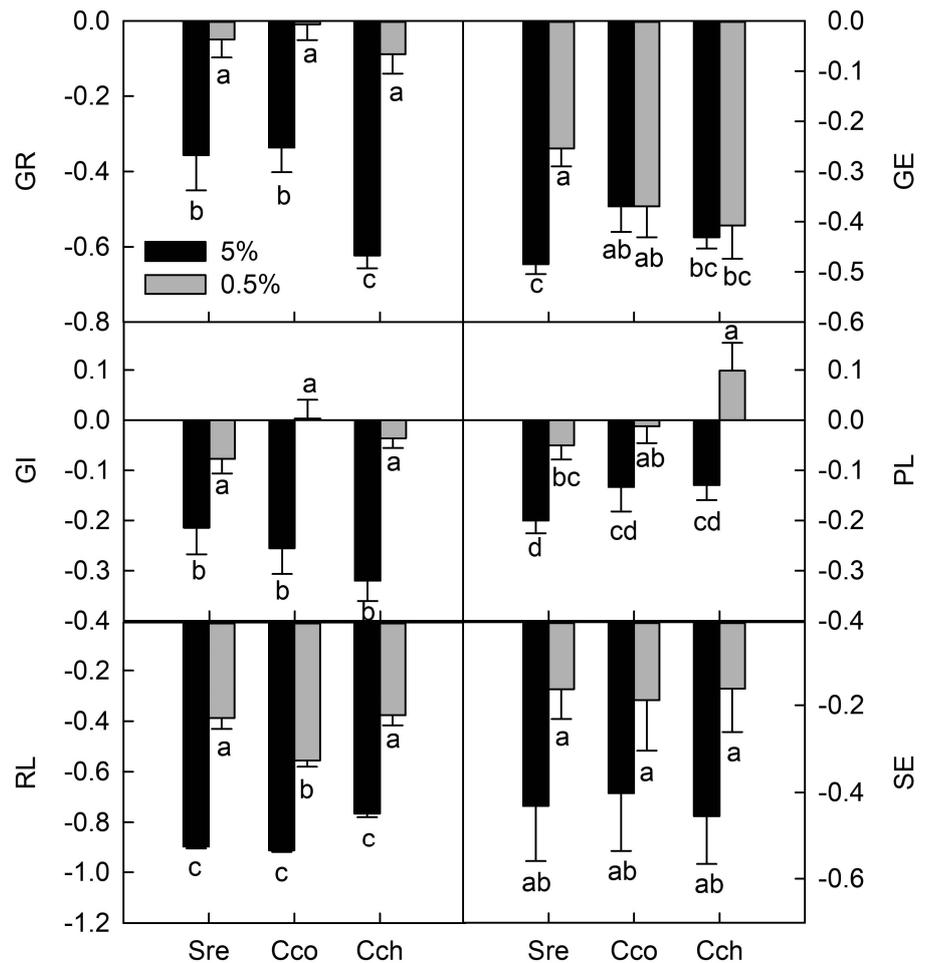


Figure 2. Allelopathic effects of three tree species on seed germination of *Mikania micrantha*. Different letters above the bars indicate statistical significance ($P < 0.05$). Abbreviations: Sre, *Syzygium rehderianum*; Cco, *Cryptocarya concinna*; Cch, *C. chinensis*; GR, germination rate; GE, germination energy; GI, germination index; RL, radicle length; PL, plumule length; SE, synthetic allelopathic effect.

The biomass of *M. micrantha* was positively related to PPFD levels under the tree species. Moreover, measurements of physiological traits showed that *M. micrantha* planted with the tree species had higher total Chl content and SLA and lower ratios of Chl a/b and Car/Chl, antioxidant capacity (expressed as either DSA or TPC), Pn, Cond, $\Delta F/Fv'$ and NPQ (Figures 4 and 5). By contrast, no changes were observed in Fv/Fm and $\Delta F/Fm'$ of *M. micrantha* planted with the tree species.

Discussion

Invasive species can utilize allelochemicals to facilitate invasions by suppressing the native species (Callaway and Aschehoug 2000; Callaway and Ridenour 2004). In contrast, many native plants can also release allelochemicals to resist alien invaders (Lodhi 1978; Souto et al. 1994). Our results showed that the dominant tree species in subtropical forests have allelopathic inhibition on the seed germination of *M. micrantha*, consistent with a previous study showing that the litter collected from subtropical forests

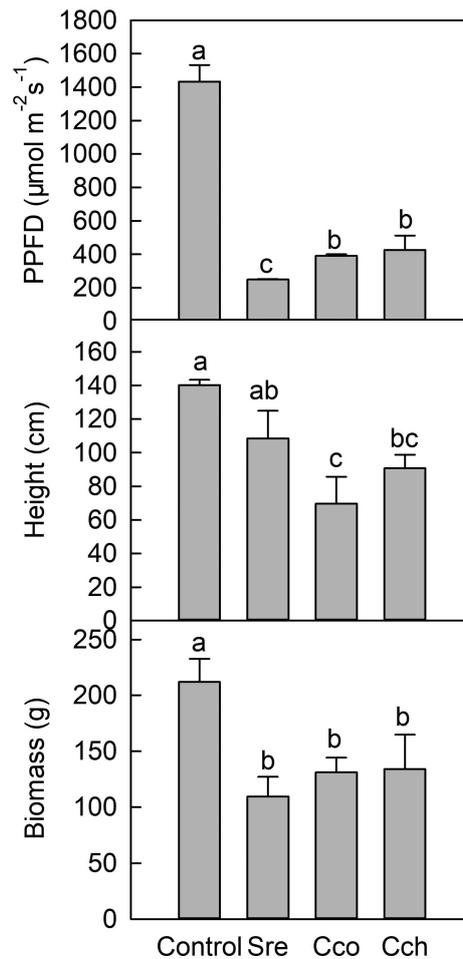


Figure 3. Changes in height and biomass of *Mikania micrantha* after growing under *Syzygium rehderianum* (Sre), *Cryptocarya concinna* (Cco) and *C. chinensis* (Cch) for three months. Different letters above the bars indicate statistical significance ($P < 0.05$). Photosynthetic photon flux density (PPFD) under the canopies of the tree species was measured at midday on a clear day.

has allelopathic potential against alien invasive species (Zhao et al. 2008). In addition to seed germination rate, seedling growth of *M. micrantha* was also affected by the aqueous extracts from tree species. Compared with plumule growth, the growth of the radicle was more sensitive to the aqueous extracts. This is in full agreement with previous studies (Wardle et al. 1991; Olson and Wallander 2002) and is likely due to greater allelochemical accumulation in radicles. This indicates that allelopathy of dominant tree species in subtropical forests can act as one of the defense mechanisms against alien plant invaders.

Reduction in height and biomass were observed in *M. micrantha* planted with the tree species. Since all the tree species have allelopathic potentials against *M. micrantha* and their canopy intercepts most of the incident light, the reduction in height and biomass of *M. micrantha* grown with the tree species is likely caused by the interaction of allelopathy and shading. However, the biomass of *M. micrantha* was positively related to PPF levels under the tree species suggesting that the impact of shading on the

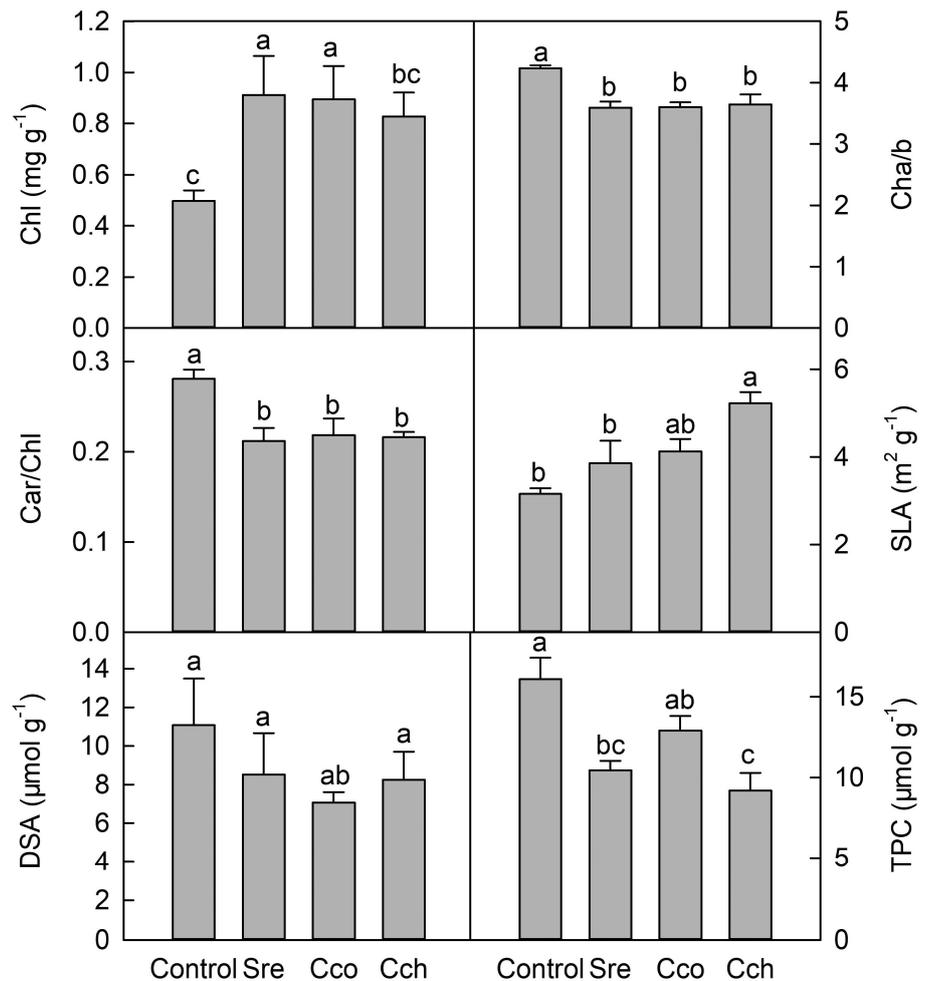


Figure 4. Changes in chlorophyll pigments, specific leaf area and antioxidant capacity in *Mikania micrantha* after growing under *Syzygium rehderianum* (Sre), *Cryptocarya concinna* (Cco) and *C. chinensis* (Cch) for three months. Different letters above the bars indicate statistical significance ($P < 0.05$). Abbreviations: Chl, the total chlorophyll; Chl a/b, the ratio of chlorophyll a to chlorophyll b; Car/Chl, Carotenoid/Chlorophyll; SLA, specific leaf area; DSA, DPPH scavenging ability; TPC, total phenolic content.

growth of *M. micrantha* is more important than allelopathy. Indeed, *M. micrantha* exhibited shade-induced characteristics after being planted with the tree species, such as reduced Chl a/b and increased SLA (Slot et al. 2018). Thus, the allelopathic potential of the tree species on *M. micrantha* vegetative growth was weak. Though plasticity in morphological and physiological traits due to light was observed in *M. micrantha*, it has been shown that *M. micrantha* is a shade-intolerant species (Zhang and Wen 2009) and would not survive in a forest understory with a 2% relative light intensity (Ipor and Tawan 1995). In the understory of a mature subtropical forest, the light is typically less than 10% of the open areas, which is insufficient for the normal growth of *M. micrantha*. However, the light conditions under the canopy of potted tree plants are close to those in the forest gaps, indicating that if there is an opportunity, *M. micrantha* is likely to occur in forest gaps, although there may be allelochemicals in the soil.

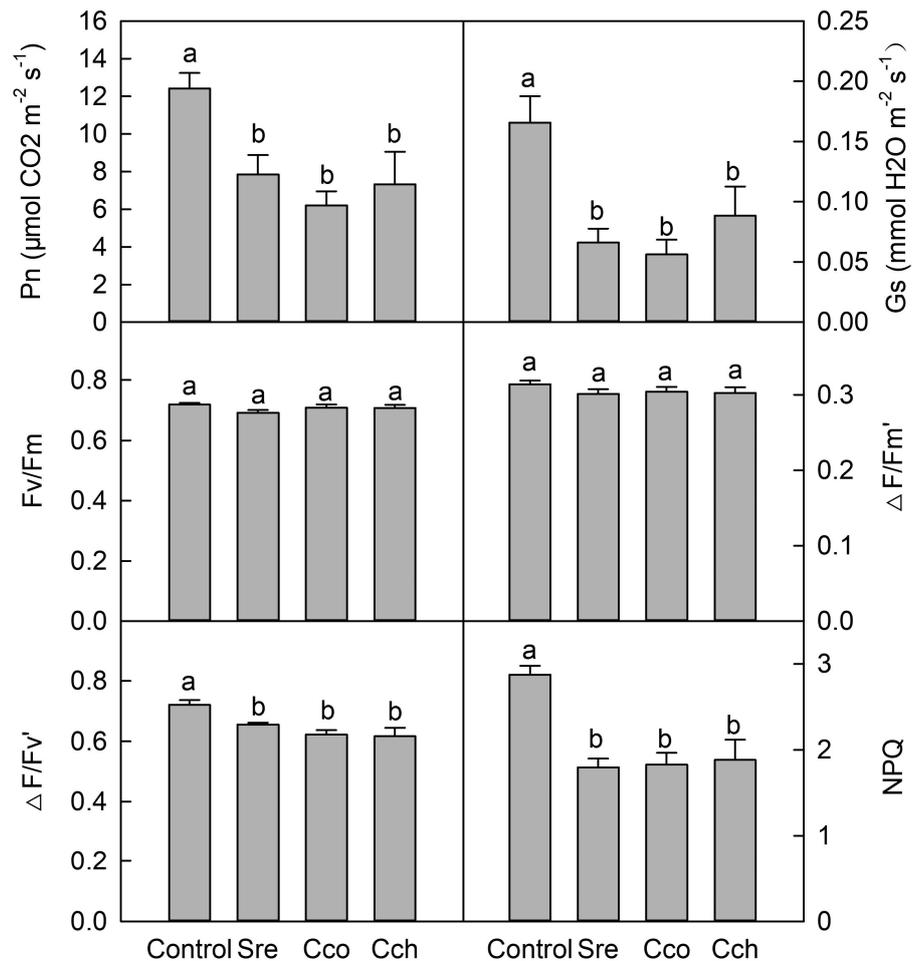


Figure 5. Changes in photosynthesis and Chl fluorescence in *Mikania micrantha* after growing under *Syzygium rehderianum* (Sre), *Cryptocarya concinna* (Cco) and *C. chinensis* (Cch) for three months. Different letters above the bars indicate statistical significance ($P < 0.05$).

Conclusions

Allelopathy of the tree species inhibits the germination of *M. micrantha*, while shading plays a more important role in inhibiting the vegetative growth of *M. micrantha*. Our results indicated that allelopathy is not sufficient to inhibit the invasion of exotic plants in subtropical forests, but that allelopathy combined with shading may be sufficient. It should be noted that *M. micrantha* can grow in the light conditions present in forest gaps.

Acknowledgements

This work was funded by the National Key R&D Program of China (2017YFC1200105) and the National Natural Science Foundation of China (31870374, 31570398). The study was also supported by the Guangdong Province Natural Science Foundation (2017A030313167) and Open Foundation of Guangdong Provincial Key Laboratory of Biotechnology for Plant Development, South China Normal University (2018KF0203). We would like to thank the anonymous reviewers for their valuable and detailed comments.

References

- Bilger W, Björkman O (1990) Role of the xanthophyll cycle in photoprotection elucidated by measurements of light-induced absorbance changes, fluorescence and photosynthesis in leaves of *Hedera canariensis*. *Photosynthesis Research* 25: 173–185, <https://doi.org/10.1007/BF00033159>

- Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290: 521–523, <https://doi.org/10.1126/science.290.5491.521>
- Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* 2: 436–443, [https://doi.org/10.1890/1540-9295\(2004\)002\[0436:NWISAT\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2)
- Ellis RH, Roberts EH (1981) The quantification of ageing and survival in orthodox seeds. *Seed Science and Technology (Netherlands)* 9: 373–409
- Everette JD, Bryant QM, Green AM, Abbey YA, Wangila GW, Walker RB (2010) Thorough study of reactivity of various compound classes toward the Folin–Ciocalteu reagent. *Journal of Agricultural and Food Chemistry* 58: 8139–8144, <https://doi.org/10.1021/jf1005935>
- Genty B, Briantais JM, Baker NR (1989) The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta (BBA)-General Subjects* 990: 87–92, [https://doi.org/10.1016/S0304-4165\(89\)80016-9](https://doi.org/10.1016/S0304-4165(89)80016-9)
- Gilbert B, Lechowic MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology* 86: 1848–1855, <https://doi.org/10.1890/04-09997>
- Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *The American Naturalist* 159: 396–419, <https://doi.org/10.1086/338995>
- He WQ, Huang ZL (2004) Dynamics and impacts of invasion by nonnative plant species to Dinghushan Nature Reserve. *Guangdong Forestry Science and Technology* 20: 42–45
- Ipor IB, Tawan CS (1995) The effect of shade on leaf characteristics of *Mikania micrantha* (Compositae) and their influence on retention of imazapyr. *Pertanika Journal of Tropical Agricultural Science* 18: 163–168
- Lodge DM (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133–137, [https://doi.org/10.1016/0169-5347\(93\)90025-K](https://doi.org/10.1016/0169-5347(93)90025-K)
- Lodhi MAK (1978) Allelopathic effects of decaying litter of dominant trees and their associated soil in a lowland forest community. *American Journal of Botany* 65: 340–344, <https://doi.org/10.1002/j.1537-2197.1978.tb06076.x>
- Martin PH, Marks PL (2006) Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). *Journal of Ecology* 94: 1070–1079, <https://doi.org/10.1111/j.1365-2745.2006.01159.x>
- Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421: 625–627, <https://doi.org/10.1038/nature01317>
- Mukhtar I (2008) Influence of *Trichoderma* species on seed germination in okra. *Mycopath* 6(1&2): 47–50
- Nguyen PM, Kwee EM, Niemeyer ED (2010) Potassium rate alters the antioxidant capacity and phenolic concentration of basil (*Ocimum basilicum* L.) leaves. *Food Chemistry* 123: 1235–1241, <https://doi.org/10.1016/j.foodchem.2010.05.092>
- Olson BE, Wallander RT (2002) Effects of invasive forb litter on seed germination, seedling growth and survival. *Basic and Applied Ecology* 3: 309–317, <https://doi.org/10.1078/1439-1791-00127>
- Oxborough K, Baker NR (1997) Resolving chlorophyll *a* fluorescence images of photosynthetic efficiency into photochemical and non-photochemical components - calculation of qP and Fv'/Fm'; without measuring Fo'. *Photosynthesis Research* 54: 135–142, <https://doi.org/10.1023/A:1005936823310>
- Peng S, Wang B (1995) Forest succession of Dinghushan, Guangdong, China. *Chinese Journal of Botany* 7(1): 75–80
- Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77: 1655–1661, <https://doi.org/10.2307/2265768>
- Ruan S (2002) Effects of seed priming on germination and health of rice (*Oryza sativa* L.) seeds. *Seed Science and Technology* 30: 451–458
- Shen S, Xu G, Clements DR, Jin G, Liu S, Zhang F, Yang Y, Chen A, Hisashi KN (2015) Effects of invasive plant *Mikania micrantha* on plant community and diversity in farming systems. *Asian Journal of Plant Sciences* 14: 27–33, <https://doi.org/10.3923/ajps.2015.27.33>
- Slot M, Krause GH, Krause B, Hernández GG, Winter K (2018) Photosynthetic heat tolerance of shade and sun leaves of three tropical tree species. *Photosynthesis Research* 141: 119–130, <https://doi.org/10.1007/s11120-018-0563-3>
- Souto XC, Gonzales L, Reigosa MJ (1994) Comparative analysis of allelopathic effects produced by four forestry species during decomposition process in their soils in Galicia (NW Spain). *Journal of Chemical Ecology* 20: 3005–3015, <https://doi.org/10.1007/BF02098405>
- Von Holle B, Delcourt HR, Simberloff D (2003) The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science* 14: 425–432, <https://doi.org/10.1111/j.1654-1103.2003.tb02168.x>
- Wardle DA, Ahmed M, Nicholson KS (1991) Allelopathic influence of nodding thistle (*Carduus nutans* L.) seeds on germination and radicle growth of pasture plants. *New Zealand Journal of Agricultural Research* 34: 185–191, <https://doi.org/10.1080/00288233.1991.10423358>

- Waterhouse DF (1994) Biological control of weeds: Southeast Asian prospects. ACIAR, Canberra, Australia, pp 126–137
- Wellburn AR (1994) The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *Journal of Plant Physiology* 144: 307–313, [https://doi.org/10.1016/S0176-1617\(11\)81192-2](https://doi.org/10.1016/S0176-1617(11)81192-2)
- Williamson GB, Richardson D (1988) Bioassays for allelopathy: measuring treatment responses with independent controls. *Journal of Chemical Ecology* 14: 181–187, <https://doi.org/10.1007/BF01022540>
- Xie WY, Hu NY, Yu YN, Niu ZJ, Li X (2017) Resistance of plant community to exotic invasive *Mikania micrantha* through allelopathy of multiple species. *Allelopathy Journal* 41: 239–248, <https://doi.org/10.26651/2017-41-2-1099>
- Zhang LL, Wen DZ (2009) Structural and physiological responses of two invasive weeds, *Mikania micrantha* and *Chromolaena odorata*, to contrasting light and soil water conditions. *Journal of Plant Research* 122: 69–79, <https://doi.org/10.1007/s10265-008-0197-1>
- Zhang LY, Ye WH, Cao HL, Feng HL (2004) *Mikania micrantha* HBK in China—an overview. *Weed Research* 44: 42–49, <https://doi.org/10.1111/j.1365-3180.2003.00371.x>
- Zhang Q, Zhang TJ, Chow WS, Xie X, Chen YJ, Peng CL (2015) Photosynthetic characteristics and light energy conversions under different light environments in five tree species occupying dominant status at different stages of subtropical forest succession. *Functional Plant Biology* 42: 609–619, <https://doi.org/10.1071/FP14355>
- Zhao H, Peng S, Wu J, Xiao H, Chen B (2008) Allelopathic potential of native plants on invasive plant *Mikania micrantha* HBK in South China. *Allelopathy Journal* 22(1): 189–196
- Zhou G, Guan L, Wei X, Zhang D, Zhang Q, Yan J, Wen D, Liu J, Liu S, Huang Z, Kong G, Mo J, Yu Q (2007) Litter fall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. *Plant Ecology* 188: 77–89, <https://doi.org/10.1007/s11258-006-9149-9>
- Zhu H, Zhang TJ, Zhang P, Peng CL (2016) Pigment patterns and photoprotection of anthocyanins in the young leaves of four dominant subtropical forest tree species in two successional stages under contrasting light conditions. *Tree Physiology* 36: 1092–1104, <https://doi.org/10.1093/treephys/tpw047>