Flooding with shallow water promotes the invasiveness of *Mikania micrantha*

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Abstract
The invasive ability of alien plants is not only affected by their biological characteristics but also by environmental factors. Therefore, investigating the relationship between plant growth and environmental factors is helpful for predicting the invasive potential of alien species. *Mikania micrantha* H.B.K. (a vine of Asteraceae) is one of the top 10 most invasive weeds worldwide and causes serious damage to agroforestry ecosystems. Water is an important environmental factor that affects plant growth; however, the relationship between water conditions and the rapid growth of *M. micrantha* is not clear. In this study, 162 *M. micrantha* population sizes were investigated in dry, wet and aquatic habitats in the Pearl River Delta region of Guangdong, China. In addition, the seed germination and seedling growth characteristics of *M. micrantha* were determined by submerging tests. The results showed that the population size of *M. micrantha* was the largest in aquatic habitats, and the soil moisture content was positively correlated to the population size in dry and wet habitats. Furthermore, *M. micrantha* seeds could germinate underwater and grow out of the water surface at a depth of 6 cm with a survival rate of 7.4%. Aquatic habitat promoted vine elongation, whereas dry habitats resulted in the reverse pattern. After 8 weeks of water treatments, the vine stem length was 2 and 3 times longer in the aquatic habitat than the wet and dry habitats, respectively. The total root length, root volume, and root tip number increased significantly in the aquatic habitat when compared to those in the wet habitat; however, these parameters exhibited the opposite pattern in the dry habitat. The results showed that flooding with shallow water is conducive to the invasiveness of *M. micrantha*, suggesting that water is the key determinant during the intrusion process of *M. micrantha* populations.

KEYWORDS
germination rate, invasive species, population size, seedling growth, water conditions

1 INTRODUCTION

Biological invasion represents the second most important threat to global biodiversity after land use change (Chytrý et al., 2012). The damage caused by invasive plants has increased annually and resulted in serious threats to human health, agricultural production, and biodiversity around the world (Ozaslan et al., 2016; Pejchar & Mooney, 2009). During the intrusion process of invasive plants,
environmental factors play an important role on the growth and distribution of invasive plants (Ensslin, Mollie, Hemp, & Fischer, 2018; Karkanis, Ntatsi, Alemardan, Petropoulos, & Bilalis, 2019). Therefore, investigating the relationship between plant growth and environment factors is helpful for predicting the invasive potential of alien species and establishing effective management strategies.

Soil moisture is a key environmental factor for plant growth and development. The effect of soil moisture on invasive plants has received widespread attention, especially in the context of global climate change (Awada et al., 2019; Saptiningsih, Dewi, Santosa, & Purwestri, 2018). Different invasive plants showed different responses to soil water conditions; for example, the invasive species *Centaurea diffusa* Lam. and *Poa pratensis* L. showed strong adaptability to drought, which leads them to form dominant populations in arid environments (Dong, Patton, Wang, Nyren, & Peterson, 2014; Turner, Nerkowski, & Rieseberg, 2017), whereas the invasive plants *Bidens pilosa* L. and *Alternanthera philoxeroides* (Mart.) Griseb. showed a stronger tolerance to waterlogging than natives, which benefits their invasion ability in waterlogged environments (Chen, Zhou, Yin, Liu, & Luo, 2013; Yue et al., 2019). Thus, the response of invasive plants to soil moisture will be helpful for determining the habitats that are more vulnerable to invasion.

*Mikania micrantha* H.B.K. (belonging to the family Asteraceae) is a fast-growing perennial herbaceous or slightly woody vine native to tropical America (Lowe, Browne, Boudjelans, & De Poorter, 2001) and has been listed as one of the top 10 most invasive weeds worldwide (Holm, Plucknett, Pancho, & Herberger, 1977). This species has rapidly expanded in tropical and subtropical parts of the Asia-Pacific region, which has resulted in serious damage to plantation crops and agroforestry ecosystems (Day et al., 2016). The vine stem grows rapidly and can increase by 20 cm in one night (Du, Yang, Li, & Yin, 2006); therefore, the plant has been nicknamed “mile-a-minute” weed (Waterhouse, 1994). Due to the rapid elongation of its vine stems, *M. micrantha* can climb over other plants and prevent them from receiving adequate sunshine, thereby hindering their growth and reproduction or eventually causing their death (Huang et al., 2000; Zhang, Ye, Cao, & Feng, 2004); however, little is known about how such rapid growth is maintained.

Although *M. micrantha* is found in various habitats, such as disturbed roadsides, wastelands, plantations and secondary forests in low-altitude valleys, barren farmlands, and orchards, as well as the sides of ditches and rivers (Zhang et al., 2004), some studies have shown that the species prefers humid environments (Murphy et al., 2013; Shen et al., 2015). However, the effect of soil moisture on its

**FIGURE 1** The locations of 162 *Mikania micrantha* populations in drylands (dry habitats; $n = 74$), on riverbanks (wet habitats; $n = 36$), and in wetlands with shallow water (aquatic habitats; $n = 52$) in the Pearl River Delta region of Guangdong, China
population size has rarely been addressed (Xu, Shen, Zhang, Li, & Zhang, 2013).

Here, we hypothesize that *M. micrantha* presents a number of biological characteristics to adapt to aquatic or wet habitats, thereby benefiting its population expansion. Firstly, we investigated the population size of the invasive species *M. micrantha* under three water conditions (dry habitats, wet habitats, and aquatic habitats). Second, the seed germination and seedling growth characteristics were determined by different submerging tests to further elucidate the specific effects of water conditions. Lastly, the survival rates of *M. micrantha* were examined at different water-drown depths to reveal the effects of flooding. Our aim is to provide a scientific basis for predicting the invisibility or susceptibility of ecosystem and setting up an effective management strategy for *M. micrantha* in the field.

2 | MATERIALS AND METHODS

2.1 | Population sizes of *M. micrantha*

The *M. micrantha* population sizes were randomly investigated in the field across agricultural systems in the Pearl River Delta in Guangdong, China in April 2015 (Figure 1). When a population appeared continuously in one habitat, it was treated as one population, and when the gap between populations was >300 m, it was considered two habitats. We investigated the *M. micrantha* population size in drylands, on riverbanks, and in wetlands by approximating their geometric shape using a measuring tape in the field. The soils of the *M. micrantha* populations in drylands and on riverbanks were brought back to the laboratory to determine their relative humidity (Moore, 2001). Soils with a relative humidity of <60% were considered to be from dry habitats, and those with a relative humidity of more than 80% but not covered by water were considered to be from wet habitats (Burns, 2004; Klemedtsson, Svensson, & Rosswall, 1988). The wetlands with a water depth of no more than 30 cm were regarded as aquatic habitats. The dry habitats included wastelands, roadsides, orchards, and secondary forests, and the wet habitats included both sides of river banks where water flow could be seen with the naked eye. The aquatic habitats included ditches, ponds, and depressions where the water was almost stationary. A total of 162 *M. micrantha* populations were investigated in three different habitats, including 74 populations in dry habitats, 36 in wet habitats, and 52 in aquatic habitats.

2.2 | Seed germination of *M. micrantha* under different water conditions

To study the effects of drought on the seed germination of *M. micrantha*, drought was imitated by a polyethylene glycol 6000 (PEG6000) solution, with 0, 85.4, 160.6, 212.6, 255.0, or 291.7 g of PEG6000 dissolved in 1 L of distilled water to obtain aqueous solutions with osmotic potentials of 0, −0.1, −0.3, −0.5, −0.7, or −0.9 MPa, respectively, according to Wei et al. (2009). Germination tests were conducted by placing 30 seeds in a 9-cm-diameter Petri dish containing two layers of filter paper, which were moistened with 8 ml of distilled water or PEG6000 solution. In addition, Petri dishes containing *M. micrantha* seeds were placed at the bottom of transparent plastic boxes with a water depth of 6 cm to test the effects of flooding on seed germination. All Petri dishes used in this experiment were placed in a growth chamber (RXZ-430c, Ningbo Southeast Instrument Co., Ltd) at 30/25°C (day/night) under a 12-hr photoperiod. Each treatment set consisted of eight replicates. Germinated seeds were counted after 14 days, and the seed germination rates under the different treatments were calculated (Wei et al., 2009).

2.3 | Growth of *M. micrantha* seedlings under different water-submerging test

The experiment was conducted in Guangzhou (E 113°21′, N 23°9′; elevation, 14 m), Guangdong Province, China from April to June 2016. Seedlings of similar sizes were transplanted to plastic pots with sandy soil (pH, 6.0; soil organic C, 9.50 g/kg; available N, 59.63 mg/kg; available P, 40.5 mg/kg; and available K, 44.5 mg/kg; the same soil was used in the subsequent experiment) at the 2-leaf stage. Water treatments were applied when the seedlings were at the 6-leaf stage. Three water treatments were established: soil with a 40% water-holding capacity as the dry habitat; soil with a 90% water-holding capacity as the wet habitat (Burns, 2004); and flooding with a water depth of 2 cm as the aquatic habitat. Each treatment set consisted of 8 replicates, and the plants subjected to three treatments were arrayed randomly. The initial dry biomasses of seedlings before treatments were determined on control groups (72°C, dry for 48 hr). After 8 weeks of water treatments, the total root length, root surface area, root volume, and root tip number were determined with the WinRHIZO Root Analysis System (Version 3.9, Regent Instruments Inc.). The total leaf area of *M. micrantha* plants was measured with a leaf area meter (Yaxin-1241, Yaxinliji Technology Co., Ltd). The roots, stems, and leaves of *M. micrantha* were dried (72°C, 48 hr), and their biomasses were determined. In addition, the relative growth rate (the averaged increase in dry matter per unit of dry mass per day over 56 days; Lombardi & Sebastiani, 2005), specific leaf area (leaf area per unit of leaf dry mass; Evans & Poorter, 2010), and root/shoot ratio of *M. micrantha* were calculated.

2.4 | Survival of *M. micrantha* at different water depths

The experiment was conducted in Guangzhou (E 113°21′, N 23°9′, elevation 14 m), Guangdong Province, China from April to May in 2016. Four seedlings at the 2-leaf stage were transplanted to one plastic pot with a diameter of 12 cm containing sandy soil. Flooding treatments were applied when the *M. micrantha* seedlings were at the 4-leaf stage with heights of ~6 cm. The tested flooding depths were 0, 2, 4, 6, and 8 cm. The *M. micrantha* seedlings were planted
in soil with a 90% water-holding capacity as the control treatment. To calculate the survival rate, each treatment had eight replicates, each with 32 plants. Seedlings that grew above the water surface were regarded as surviving plants (preliminary experiments showed that M. micrantha would survive as long as it grew above the water surface). When all the M. micrantha seedlings underwater had died (after 4 weeks), the experiment was terminated, and the survival rates of M. micrantha at different water depths were calculated.

2.5 | Statistical analysis

All statistical tests were performed using SPSS 16.0 (SPSS Inc.). The population size, germination rate, growth index, and root morphology of M. micrantha under different water conditions were compared using a one-way ANOVA followed by Tukey’s test at \( p < .05 \). All observations were independent of one another, and the scores in groups were normally distributed. A univariate F test for each variable was used to interpret the respective effects. The equality of error variances was tested by using Levene’s test, and the error variance of the dependent variable was considered to be equal across groups when \( p > .05 \). A linear regression analysis was used to assess the response of the population size of M. micrantha (as the dependent variable) to relative soil humidity (as the independent variable). Figure 1 was drawn using ArcGIS 10.2 software (ESRI) and Figures 2-4 were drawn using SigmaPlot 12.5 software (Systat Software Inc.).
3 | RESULTS

3.1 | *M. micrantha* population sizes in different habitats

The results showed that the *M. micrantha* population size in the aquatic habitat was the largest, followed by wet habitat, and the smallest one was found in dry habitat. The *M. micrantha* population size in the aquatic habitat was 3 and 38 times larger than that in the wet and dry habitats, respectively (Figure 2a). The population size in the dry and wet habitats depended on the soil moisture content (Table 1). The relative growth rate showed a similar trend (Table 1).

The root biomass in the aquatic habitat was similar to that in the wet habitat, and both were significantly higher than that in the dry habitat (*p < .05*). Compared with the wet habitat, the aquatic habitat significantly promoted the stem biomass of *M. micrantha* while the dry habitat significantly inhibited it (*p < .05*). The leaf biomass of *M. micrantha* in the aquatic and dry habitats was significantly lower than that in the wet habitat, while the leaf biomass in the aquatic habitat was significantly higher than that in the dry habitat (*p < .05*; Table 1).

The root/shoot ratio of *M. micrantha* in the dry habitat was the highest among the three treatments and was significantly higher than that in the wet and aquatic habitats (*p < .05*). The root/shoot ratio in the aquatic habitat was similar to that in the wet habitat. Compared with the wet habitat, the aquatic and dry habitats inhibited the leaf area of *M. micrantha* (*p < .05*), resulting in areas that were 51% and 65% smaller compared with the wet habitat, respectively. The specific leaf area and branch number of *M. micrantha* in the aquatic and dry habitats were less than those in the wet habitat (*p < .05*). Compared with the wet habitat, the aquatic habitat promoted the stem node length while the dry habitat inhibited it (*p < .05*; Table 1).

3.2 | Germination rate and seedling growth under different water conditions

In the seed germination test, the seeds of *M. micrantha* could germinate underwater (flooding). The germination rate was not significantly different between the flooding and the lower osmotic potential treatments (0 to −0.3 MPa). With an increase in the osmotic potential, the seed germination rate decreased significantly (Figure 3).

In the water-submerging test, the speed at which the main stem of *M. micrantha* extended varied significantly among the three water environments (Figure 4). *M. micrantha* stems extended most rapidly in the aquatic habitat (flooding with a water depth of 2 cm), most slowly in the dry habitat (soil with 40% water-holding capacity), and at an intermediate rate in the wet habitat (soil with 90% water-holding capacity). Eight weeks after the treatments, the main stem length in the aquatic habitat was 2 times longer than that in the wet habitat and 3 times longer than that in the dry habitat.

After 8 weeks of different water treatments, the total biomass of *M. micrantha* in the aquatic and wet habitats was much higher than that in the dry habitat (Table 1). The relative growth rate showed a similar trend (Table 1).

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3.3 | Survival rate of *M. micrantha* seedlings at different water depths

Almost all *M. micrantha* seedlings could survive at a water depth of 0 cm. The survival rate at a water depth of 0 cm was similar to that in the wet habitat (soil with 90% water-holding capacity). With an
increase in water depth, the survival rate decreased significantly ($p < .05$). When the water depth was 6 cm, the survival rate was only 7.4%. None of the *M. micrantha* plants survived at a water depth of 8 cm (Figure 5).

**TABLE 2** Root morphological changes in *Mikania micrantha* in a dry habitat (soil with a 40% water-holding capacity), wet habitat (soil with a 90% water-holding capacity), and aquatic habitat (flooding with a water depth of 2 cm; mean ± SD, $n = 8$)

| Treatment          | Total root length (cm) | Root surf. area (cm$^2$) | Root volume (cm$^3$) | Root tip number |
|--------------------|------------------------|--------------------------|----------------------|-----------------|
| Dry habitat        | 735.62 ± 17.18c         | 98.80 ± 17.09c           | 2.21 ± 0.12c         | 774.38 ± 25.12c |
| Wet habitat        | 1,877.06 ± 59.78b       | 450.35 ± 7.99b           | 8.55 ± 0.37b         | 1,274.13 ± 44.93b |
| Aquatic habitat    | 3,751.52 ± 78.94a       | 761.97 ± 16.79a          | 13.33 ± 0.45a        | 3,234.88 ± 101.17a |

Note: Data with different letters within the same column indicate significant differences at $p < .05$ according to the results of a post hoc Tukey’s test. Degrees of freedom ($df$) (between groups) = 2; $df$ (within groups) = 21; $df$ (total) = 23.

**4 DISCUSSION**

Water is an important environmental factor that dictates the growth and distribution of plants (Boyer, 1982; Kelly & Goulden, 2008). Therefore, the invasion process of exotic plants is partially dependent on the soil moisture (Kercher & Zedler, 2004; Sher, Marshall, & Gilbert, 2000). In this study, the largest population size of *M. micrantha* was found in the aquatic habitat in the field (Figure 2a), and the controlling experiment also showed that flooding could significantly promote the vine stem growth of *M. micrantha* (Figure 4). Our results were supported by previous studies that indicated that *M. micrantha* prefers wetlands and can even cover large areas of ponds (Zhang et al., 2004). Therefore, *M. micrantha* can survive in shallow water and the elongation of its vine stems can be stimulated by flooding. Similar studies elsewhere have found that other invasive species (e.g., *Bidens pilosa* and *Alternanthera philoxeroides*) are also very tolerant to waterlogging (Chen et al., 2013; Yue et al., 2019). In addition, the results of this study also indicated that the stem growth of *M. micrantha* was very sensitive to drought (Figure 4). Although studies have shown that *M. micrantha* exhibits broad niche breadth under drought stress (Shen et al., 2015; Zhou, Liu, Sun, Wu, & Hou, 2015), our results indicated that the growth of *M. micrantha* was significantly inhibited under drought conditions, presumably drought habitats is not susceptible to *M. micrantha* invasion. These findings suggest that flooding with shallow water would promote the invasiveness of *M. micrantha* while drought would be a limiting factor for its growth.

Since *M. micrantha* prefers aquatic habits, it will meet the demands of flooding in places where water is abundant and may therefore have gradually developed characteristics to adapt to flooded environments. Internode and stem elongation are related to the enhancement of oxygen transport and dispersal in plants (Fu, Xu, Ronald, & Bailey, 2006; Kawano, Ito, & Sakagami, 2008), and plants can accelerate the elongation of stems to quickly “escape” the adverse conditions of flooding (Groeneveld & Voesenek, 2003; Voesenek et al., 2004). The main stem length and stem node length of *M. micrantha* increased significantly in the aquatic habitat in this study (Table 1 and Figure 4). These morphological changes contribute to a better adaptation of *M. micrantha* to aquatic environments or flooding tolerance. Thus, the rapid growth of stems in shallow water might help *M. micrantha* to occupy the habitats and favor its invasion. In addition, we found that the total root length, root surface area, root volume, and root tip number of *M. micrantha* were all significantly increased in the aquatic habitat (Table 2). This observation may be related to flooding, which could induce the adventitious root primordia to form adventitious roots, while the ventilated tissue in the adventitious roots expanded the root porosity to increase the ability to obtain and transport oxygen (Drew, Jackson, & Giffard, 1979; Visser, Colmer, Blom, & Voesenek, 2000). Flood-tolerant plants are often able to form a large number of adventitious roots in the aquatic environments to adapt to hypoxic habitats (Ayi et al., 2016; Dawood et al., 2014). Therefore, for *M. micrantha*, the growth of a large number of adventitious roots is favorable for its adaptation to aquatic environments.

The *M. micrantha* population sizes on both sides of rivers did not represent the largest population among the three examined water conditions, although the soil water content was high at the riverbanks. This finding may be related to the inability of *M. micrantha* to survive in deep water. Our results showed that...
M. micrantha can grow at a water depth of 6 cm with a low survival rate but can’t survive at a water depth of 8 cm (Figure 5). Similarly, Xu et al. (2013) found that the nutritional propagation of M. micrantha could not continue at a water depth >6 cm. Precipitation is high in southern China (more than 1,000 mm) and concentrated from April to September (Yu, 1996); therefore, the water levels of the main rivers are often substantially increased in the rainy season. If the water levels rise too high and cover M. micrantha by more than 8 cm, it will be fatal to the plant. In South China, the rainy season often deepens the river, which is unfavorable for M. micrantha growing along the riverbank.

In the agroecosystem, the aquatic and wet habitats should be eliminated around the farmland and orchard sits since these two types of habitats are more conducive to the growth of M. micrantha. Because the vine stems of M. micrantha can grow infinitely as long as there is adequate water, we should prioritize the management of M. micrantha populations in aquatic and wet habitats with shallow water or riverbanks over those in terrestrial habitats.

In conclusion, M. micrantha prefers aquatic habitats and flooding with shallow water promoted its stem elongation, which makes M. micrantha form largest population size under waterlogging conditions. Thus, flooding with shallow water could be conducive to the invasiveness of M. micrantha, which implies that water is the key determinant during the intrusion process of M. micrantha populations. Future research is needed to do with regard to the ecological adaptability mechanism of M. micrantha to waterlogging.

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CONFLICTS OF INTEREST
None declared.

AUTHOR CONTRIBUTIONS
MY and XT designed the study; MY and WL wrote the manuscript; AY conducted most of the experimental work; HY and CY analyzed the data; and all co-authors contributed to writing the manuscript and discussions.

DATA ACCESSIBILITY
All the data used in this manuscript are available from https://osf.io/a5ymf/.

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