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Native Expanding *Merremia boisiana* Is Not More Allelopathic than Its Non-Expanding Congener *M. vitifolia* in the Expanded Range in Hainan*

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ABSTRACT

Exotic invaders may possess novel biochemical weapons that native plants do not have, and these novel biochemical weapons may be more allelopathic than those from native plants to other native competitors. During range expansion, native species also encounter many new plant competitors. Thus, allelochemicals from native expanding species may also be more novel and allelopathic than those from non-expanding species to other plant competitors in the expanded range. We test this hypothesis using the native expanding *Merremia boisiana* and its non-expanding congener *M. vitifolia* in year 2012 in the expanded range in Hainan. In petridish bioassays, we found that aqueous extracts of *M. boisiana* leaves were often less inhibitory or more stimulatory to seed germination and seedling growth of five vegetable species than those of *M. vitifolia* leaves. In pot culture, we also found that aqueous leaf extracts of the two congeners could both inhibit the growth of a naturally co-occurring plant *Paederia scanden*, but their effects did not differ from each other. These results indicate that while allelopathy may contribute to the competitive ability of *M. boisiana*, it may not act as a novel weapon explaining its success in the expanded range in Hainan.

Keywords: Allelopathy; Expansion; Invasion; *Merremia boisiana*; Native Expanding Species; Novel Weapons Hypothesis; Vine

1. Introduction

Determining the mechanisms that facilitate species invasions is a fundamental objective for invasion ecology. The Novel Weapons Hypothesis (NWH) proposes that some exotic invaders possess novel biochemical weapons that are more allelopathic to newly encountered plants in the exotic range than to their old neighbors in the original range [1], probably because their old neighbors have adapted to these biochemical weapons after a long time of interaction. Support for this hypothesis has frequently been found in the literature. For example, in North America, highly invasive exotic species are more likely to have unique phytochemicals that native plants do not have than less invasive exotic species [2]. Levels of the allelochemicals were lower in *Solidago canadensis* s.l. populations from the invasive range than in populations from the native range, probably because of a higher susceptibility of plant competitors in the invasive range to these allelopathic compounds [3]. Highly noxious plant invaders in China were also reported more likely to exert strong allelopathic effects on native plants than less noxious plant invaders [4].

For the NWH to hold, exotic invaders and natives should grow and evolve independently, such that the allelochemicals from exotic plants could be novel to native plants. Therefore, the NWH may be more likely to apply in situations where the original and new ranges of exotic species are far from each other and separated by natural barriers (e.g. oceans). In line with this, many exotic invaders in China from America were reported to have strong allelopathic effects, but no such exotic invaders from Eurasia were reported to have allelopathic effects [5]. Exotic invaders from America are also more noxious than those from Eurasia [5]. Inferring from the NWH, exotic species should also be more allelopathic than related native species to other co-occurring native plants,

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because the biochemical weapons from exotic species are more novel to native competitors than those from related native species [6].

In recent decades, probably because of global climate change and human disturbance, some native species can also become invasive [7]. For example, native *Lactuca serriola* L. has been rapidly expanding its geographical range in Europe [8], and native *Dennstaedtia punctilobula* (Michx.) Moore behaves as an exotic invader in disturbed habitats in North America [9]. *Merremia boisiana* (Gagnep.) Oostr. (Convolvulaceae), a perennial evergreen woody vine originated from North Vietnam and South Yunnan of China, could be recognized as a native species in South Asia that is rapidly expanding its geographical range [10]. In the expanded range in the Hainan island and Guangdong province of China, the vine behaves like *Mikania micrantha* H. B. K., one of the most damaging exotic invaders in China [11,12]. The first discovery of the vine in the Hainan island was in the Chengmai County in year 1882 and in the Danzhou city in year 1922 [10]. In 1940s it was recorded in more counties such as Yazhou, Lingshui, Wanning, Ledong, and Baisha, and it has been widely distributed across the island after year 1990 [10]. The first discovery of the vine in Guangdong province was in year 1994 in Guangzhou [13], and now it has infested multiple areas in Guangzhou and also Luofu Mountain in Huizhou [10]. The vine typically invades secondary forests, shrub lands and open woodlands. It establishes from seeds in a new place, but can form a blanket through stolon growth and ramification that covers the whole habitat from a single individual after several years later [14,15]. Once established, the vine twists and overtops other plants nearby, smothering them to death. In several mountains in Hainan, the vine has formed a continuous canopy reaching 10 hectares [15]. In Taihezhang Mountain in Guangzhou in year 2004, the vine was found to severely infest and harm more than 300 hectares of forest [10].

During range expansion, *M. boisiana* encounters many new plant competitors, and thus the allelopathic substances released from *M. boisiana* may be novel to the new plant competitors. Also, many of the most noxious exotic plant invaders in China have strong allelopathic effects [4], and *M. boisiana* is not less noxious than them. In this paper, we examine if allelopathic effects contribute to the explosion of *M. boisiana* in its expanded range in Hainan. Specifically, we test if *M. boisiana* is more allelopathic than its native non-expanding congener, *M. vitifolia* (Burm. f.) Hall. f.

2. Materials and Methods

2.1. Aqueous Extracts Preparation

A previous study indicated that aqueous extracts of *M. boisiana* leaves were more allelopathic than those of stems or roots [16]. Therefore, we chose aqueous extracts of leaves to do the comparison. Leaves of *M. boisiana* and *M. vitifolia* were collected in Danzhou City and Baisha County in Hainan. Fresh leaf samples of the two species were soaked separately in distilled water for 48 hours at room temperature in dark and filtered through gauze. The obtained extracts were diluted with distilled water to prepare 0.1, 0.25, 0.5 g/ml concentrations for vegetable bioassays, and 0.15, 0.3 g/ml for bioassays with *Paederia scandens* (Lour.) Merr. The extracts were either assayed immediately or stored at 4˚C. Because a large volume of aqueous extracts was used during a two-month period for the bioassay with *P. scandens*, they were prepared once in half a month.

2.2. Petridish Bioassay Using Vegetable Seeds

Seeds [Purchased from seed company, Danzhou] of *Brassica oleracea var. capitata* Linnaeus, *Raphanus sativus* Linnaeus, *Lactuca sativa* L. *var. ramosa* Hort, *Capsella bursa-pastoris* (Linnaeus) Medikus, and *Lactuca sativa* Linnaeus were used to determine the influence of test spp. leaf extracts on their germination and seedling growth in petridish bioassays in a growth chamber. Thirty seeds of a species were placed on filter paper in a Petri dish (9 cm in diameter) and 5.0 ml aqueous extracts of either of the two test species (*M. boisiana* and *M. vitifolia*) were added to the Petri dish as per treatment. There were three replicates for each treatment. Aqueous extracts of *M. boisiana* and *M. vitifolia* leaves each had three concentrations: 0.1, 0.25, and 0.5 g/ml. The control Petri dishes received 5 ml distilled water. The Petri dishes were kept in growth chamber at an alternating cycle of 28˚C/light (12 h) and 25˚C/dark (12 h). A seed was considered germinated when radicle protrusion was 1 mm or more. The germinated seeds were counted after five days of incubation, and shoot and root lengths of germinated seedlings were recorded.

2.3. Pot Culture Growth Bioassay Using a Naturally Co-Occurring Plant Species

The choice of target species may be important for bioassays in allelopathy. The high sensitivity of vegetable seedlings to plant extracts, limits its wider use as indicator spp. for allelopathic potential. The use of wild plants co-occurring with the invasive species could be more informative [6,17]. Hence, we choose *P. scanden*, a native perennial vine naturally co-occurring with *M. boisiana* and *M. vitifolia* in the field, to compare the allelopathic effects of *M. boisiana* and its related congener, *M. vitifolia*.

P. scandens were propagated through vegetative cuttings. We collected the cuttings of the species in the campus of Hainan University in Danzhou city in March 2012. The cuttings were similar in length (10 cm) and diameter (4 mm). Every cutting had two nodes and buds at each end. Then, we planted the cuttings in nursery pots filled with field-collected latosol soil that was typical in Hainan.

After two weeks, uniform seedlings were selected for transplant. Three seedlings were transplanted into one pot (diameter, 20 cm; height, 15 cm) with a small hole at the bottom. The pots were filled with the same soil as in the nursery pots. Each pot was irrigated with 200 ml aqueous extracts of either of *M. boisiana* and *M. vitifolia* leaves at one time. There were two concentrations for aqueous extracts: 0.15 g/ml and 0.3 g/ml. Each control pot was irrigated with 200 ml distilled water at one time. There were four pots for each treatment. Therefore, there were a total of 20 pots (five treatments, four replications) containing 60 individual plants. The irrigations were typically done every other day, but more often when soil was dry. The pots were placed in greenhouse at air temperature, and the plants were grown for two months. Thereafter, shoot length and root length were recorded, and aboveground biomass and belowground biomass were determined after drying at 60˚C to constant weight.

2.4. Statistical Analysis

Analysis of variance was used to determine the effects of aqueous extracts of *M. boisiana* and *M. vitifolia* leaves at different concentrations on the growth variables of the five vegetables and *P. scandens*. Germination rate was calculated as under:

$$\mathrm{GR}(\%) = \mathrm{N_g}/\mathrm{N_t}$$

where, GR: Germination rate; N_g: Numbers of germinated seeds, N_t: Numbers of total sowing seeds.

A one-way analysis of variance (ANOVA) was performed on the data in one treatment factor (the two comparative species with different extract concentrations) to reveal differences in means. Significant differences among the means were determined by Student-Newman-Keuls tests.

3. Results and Discussion

3.1. Petridish Bioassay Using Vegetable Seeds

Aqueous extracts of *M. boisiana* and *M. vitifolia* leaves at 0.1 g/ml concentration either had no effect or stimulated the germination rate of vegetable seeds and shoot and root growth of vegetable seedlings compared to the control, while those at 0.5 g/ml concentration inhibited the germination rate and shoot and root growth (**Table 1**). At the concentration of 0.25 g/ml, effects of aqueous extracts of *M. boisiana* and *M. vitifolia* leaves could be neutral, stimulatory, or inhibitory (**Table 1**). In most cases where there were differences in effects between aqueous extracts, extracts of *M. vitifolia* leaves had either stronger inhibitory effects or less stimulatory effects than extracts of *M. boisiana* leaves, except for extracts at the 0.1 g/ml concentration on the shoot growth of *L. sativa var. ramosa* Hort. (**Table 1**). These results suggested that although *M. boisiana* may have allelopathic effects, its effects were not stronger than its non-expanding native congener, *M. vitifolia*. For example, compared to aqueous extracts of *M. vitifolia* leaves at the concentration of 0.25 g/ml, extracts of *M. boisiana* leaves at the same concentration inhibited less of the seed germination, stimulated more of shoot growth, and inhibited less of root growth of *B. oleracea var. capitata* (**Table 1**).

3.2. Pot Culture Growth Bioassay Using a Naturally Co-Occurring Plant Species

Aqueous extracts of *M. boisiana* and *M. vitifolia* leaves at 0.15 g/ml concentration did not inhibit the growth of *P. scandens* as compared to the control, but they inhibited the shoot weight, shoot length, and root length of *P. scandens* at 0.3 g/ml concentration (**Table 2**). Effects of aqueous extracts at the same concentration did not differ between *M. boisiana* and *M. vitifolia* (**Table 2**). These results suggested that *M. boisiana* may inhibit the growth of co-occurring plant species through allelopathy, but the inhibitory effects were not stronger than its non-expanding native congener, *M. vitifolia*, indicating that allelopathy may increase the competitive ability, but may not act as a novel weapon explaining the explosion of *M. boisiana* in its expanded range in the Hainan island.

The results from bioassay with vegetables and bioassay with a naturally co-occurring species were consistent, indicating the result that invasive *M. boisiana* was not more allelopathic than its non-expanding native congener *M. vitifolia* was robust.

Many studies on allelopathy of exotic species in China found that the NWH may apply to the most noxious exotic plant invaders [4,5]. Our results on a native expanding species that has become no less noxious than the most damaging exotic invaders indicate that while allelopathy may contribute to the competitive ability of *M. boisiana*, it may not act as a novel weapon explaining its explosion in the expanded range in Hainan. Unlike many other noxious invasive plant species that originated from America, *M. boisiana* originated from North Vietnam and South Yunnan province of China, and is now expanding its geographical range in Hainan and Guangdong provinces of China. The original and expanded ranges of *M. boisiana* are quite near and there are no strong natural barriers as compared to that between China and America,

Table 1. Effects of *Merremia boisiana* and *M. vitifolia* leaf aqueous extracts on seed germination and shoot and root length of five vegetables. Controls were treated with distilled water. Data are average ± SE. Significant differences (P < 0.05) among measure indicated by a, b, c and d.

Concentration (g/ml)	Germination rate (%)		Shoot length (cm)		Root length (cm)	
	M. boisiana	*M. vitifolia*	*M. boisiana*	*M. vitifolia*	*M. boisiana*	*M. vitifolia*
			Brassica oleracea var. capitata Linnaeus			
Control	91.1 ± 4.8^a		1.23 ± 0.06^a		4.98 ± 0.17^a	
0.1	92.2 ± 2.9^a	97.8 ± 1.1^a	3.2 ± 0.08^b	3.0 ± 0.06^b	4.7 ± 0.24^a	3.8 ± 0.17^b
0.25	90.1 ± 1.1^a	56.7 ± 1.9^b	3.1 ± 0.1^b	2.7 ± 0.13^c	3.9 ± 0.19^b	2.9 ± 0.15^c
0.5	1.1 ± 1.1^c	1.1 ± 1.1^c	0.6	2.5	1.5	1
			Raphanus sativus Linnaeus			
Control	75.6 ± 1.1^{ab}		4.42 ± 0.14^a		7.97 ± 0.54^a	
0.1	70.0 ± 3.3^{ab}	61.1 ± 4.4^b	5.33 ± 0.22^b	5.76 ± 0.2^b	12.18 ± 0.82^b	7.13 ± 0.46^a
0.25	80.0 ± 1.9^a	52.2 ± 11.8^b	5.29 ± 0.19^b	4.35 ± 0.18^a	7.21 ± 0.56^a	4.5 ± 0.37^c
0.5	27.8 ± 6.2^c	16.7 ± 10^c	2.71 ± 0.2^c	2.03 ± 0.35^c	1.6 ± 0.14^d	1.9 ± 0.19^d
			Lactuca sativa L. *var. ramosa* Hort			
Control	90.0 ± 3.9^a		1.75 ± 0.04^a		3.62 ± 0.12^a	
0.1	96.7 ± 1.9^a	78.9 ± 8^a	2.5 ± 0.06^b	2.69 ± 0.07^c	4.29 ± 0.17^b	4.01 ± 0.12^b
0.25	38.9 ± 21.3^a	73.3 ± 5.8^a	2.85 ± 0.09^c	2.85 ± 0.04^c	1.95 ± 0.13^c	1.53 ± 0.07^d
0.5	0^b	0^b	0	0	0	0
			Capsella bursa-pastoris (Linnaeus) Medikus			
Control	87.8 ± 2.2^a		1.6 ± 0.07^a		1.82 ± 0.07a	
0.1	87.8 ± 1.1^a	87.8 ± 2.9^a	2.98 ± 0.07^b	2.88 ± 0.06^b	4.28 ± 0.16^b	3.01 ± 0.11^c
0.25	60.0 ± 12.6^a	8.9 ± 4^b	3.05 ± 0.08^b	2.19 ± 0.19^c	2.54 ± 0.15^d	1.94 ± 0.26^{ad}
0.5	0^c	0^c	0	0	0	0
			Lactuca sativa Linnaeus			
Control	83.3 ± 3.3^a		1.6 ± 0.06^a		3.5 ± 0.14^a	
0.1	85.6 ± 2.2^a	88.9 ± 4.8^a	2.79 ± 0.07^b	2.27 ± 0.04^c	3.02 ± 0.08^b	2.53 ± 0.07^c
0.25	73.3 ± 12^a	34.4 ± 5.9^b	2.16 ± 0.06^{cd}	1.95 ± 0.11^d	1.79 ± 0.07^d	1.15 ± 0.04^e
0.5	0^c	0^c	0	0	0	0

Table 2. Effects of aqueous extracts of *Merremia boisiana* and *M. vitifolia* leaves at different concentrations on the growth of *Paederia scandens*. High concentration is 0.3 g/ml, and low concentration is 0.15 g/ml. Data are average ± SE. Significant differences (P < 0.05) among measure indicated by a, b and c.

	Low concentration		High concentration		Water
	M. boisiana	*M. vitifolia*	*M. boisiana*	*M. vitifolia*	
Aboveground biomass (g)	2.383 ± 0.279^{bc}	2.675 ± 0.328^c	1.392 ± 0.217^a	1.792 ± 0.243^{ab}	3 ± 0.196^c
Belowground biomass (g)	0.528 ± 0.059^b	0.421 ± 0.055^{ab}	0.325 ± 0.104^{ab}	0.34 ± 0.062^a	0.485 ± 0.027^{ab}
Shoot length (m)	1.56 ± 0.184^{bc}	1.575 ± 0.142^{bc}	1.068 ± 0.104^a	1.193 ± 0.149^{ab}	1.903 ± 0.116^c
Root length (m)	0.154 ± 0.01^b	0.154 ± 0.009^b	0.116 ± 0.008^a	0.116 ± 0.01^a	0.151 ± 0.006^b

and plants in the two ranges may have already pre-adapted to each other. Similarly, two recent studies found that allelopathy from some native plants in natural forests could inhibit the growth of exotic invasive *M. micrantha* that originated from South America [18], but did not inhibit the growth of *M. boisiana* [19]. Our results indicate that the mechanisms underlying the explosion of *M. boisiana* in the expanded range might not be due to its higher allelopathic effects as compared to non-expanding native congeneric species, although the weed does have allelopathic effects.

4. Conclusion

Aqueous extracts of *M. boisiana* and *M. vitifolia* leaves inhibited the seed germination and shoot and root elongation of five vegetable species at the concentration of 0.5 g/ml, and inhibited the shoot weight, shoot length, and root length of co-occurring *P. scandens* at the concentration of 0.3 g/ml. Unlike the novel biochemical weapons from many exotic invasive plants that have stronger inhibitory effects on newly encountered plants in the new range than those from native plants, *M. boisiana* does not have stronger allelopathic effects in its expanded range than its native noninvasive congener, *M. vitifolia*. This may indicate that while allelopathy contributes to the competitive ability of *M. boisiana*, it may not act as a novel weapon explaining its invasion success. However, we suggest that future studies that identify and isolate allelochemicals from *M. boisiana* are still needed to verify this conclusion. Furthermore, our results also indicate that the NWH may more likely to apply in situations where the original and new ranges of invasive species are far from each other and separated by natural barriers, such that the allelochemicals from invasive plants are more likely to be novel to native plants.

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