Interactive Effect of Herbivory and Competition on the Invasive Plant *Mikania micrantha*

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Abstract

A considerable number of host-specific biological control agents fail to control invasive plants in the field, and exploring the mechanism underlying this phenomenon is important and helpful for the management of invasive plants. Herbivory and competition are two of the most common biotic stressors encountered by invasive plants in their recipient communities. We predicted that the antagonistic interactive effect between herbivory and competition would weaken the effect of *Mikania micrantha*. PLoS ONE 8(5):

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Introduction

Invasive plants pose severe threats to biological diversity and ecosystems [1], and many methods have been used to control invasive plants. Biological control, i.e., using natural enemies to control invasion success, has received much attention [2,3] and has been highly successfully used to control noxious weeds, such as *Senecio jacobaea* [4] and *Ageratina riparia* [5]. Biological control, being effective and having a low cost and relatively high environmental safety, has been widely accepted [6]. However, many natural enemies have recently been verified as being inefficient in biologically controlling invasive plants in the invaded communities [7,8], even though the host-specific agents were efficient in pot experiments. Thus, exploring the mechanism underlying this phenomenon would be important and useful in developing future biological controls of invasive species.

It has been noted that the failure of biocontrol might be due to the focus on simple predator-prey relationships and the disregard of more complex interactions in the invaded community [8]. In a natural ecosystem, herbivory and competition are two of the most common biotic stressors that plants encounter [9,10], and both play important roles in shaping the structure and dynamics of the community [11]; this is true for both the invasive plants and the invaded community [11]. It is well known that both herbivory and competition from native competitors in the invaded community can negatively affect invasive plants and reduce their growth and fitness [12,13]. Inter-specific competition and herbivory can have synergistic effects on the performance of the attacked invasive host plant [14–16] and, as a result, release native neighbours from competition [17], thus limiting invasive success in the invaded community and facilitating the restoration of the native community [18]. However, only few studies have revealed the independent [19] and antagonistic [10,20] interactive effects of herbivory and competition on invasive plants. We predicted that the antagonistic interactive effect between herbivory and competition could induce the compensatory growth of invasive plants and weaken the effect of herbivory on invasive plants, which would release invasive plants from the naeighbouring competitors and result in the failure of herbivory to control invasive plants. Obviously, an understanding of the interactive effect of herbivory and competition on the performance of invasive plants and the structure and dynamics of the invaded community is important to predict the effectiveness of biological agents on the invasive plants in an invaded community.

Mikania (Asteraceae) (hereafter referred to as *Mikania*), a perennial weed native to Central and South America, was introduced into China in ca. 1919 and subsequently became an invader. *Mikania* has caused serious and extensive damage to many Chinese ecosystems, particularly in recent decades [21]. *Mikania* rarely behaves as a weed in its native range because it encounters strong natural enemies in its habitats [22]. Since 1989, herbivores, such as *Liothrips mikaniae*, were introduced to Malaysia, India and China but failed in the biological control of *Mikania* [23]; however, the main reason for the failure is still unknown.

Coix lacryma-jobi (Poaceae) (hereafter referred to as *Coix*) is a native annual grass, commonly occurring in the communities that are subject to invasion by *Mikania*. We conducted an experiment in which invasive *Mikania* was growing with native *Coix* and was treated with defoliation-mimicking herbivory to examine the interactive effect between herbivory and competition on invasive *Mikania*. We predicted that an antagonistic interaction between herbivory and competition from native species would enhance the performance of the invasive *Mikania* and release it from competition. In particular, we addressed the following questions: 1) Can competition from the native neighbouring *Coix* affect the response of the invasive *Mikania* to defoliation? 2) Can defoliation affect the impact of competition on the invasive *Mikania* and subtropical evergreen broadleaved forest codominated by *Dactyloctenium aegyptium, Paederia scandens* and *Pharbitis nil. Mikania* began to invade this area in the early 1990 s and spread extensively in shrublands and old fields.

Experimental Design and Measurements

Invasive *Mikania* was collected from the fields surrounding Dengshuiling and then propagated using cuttings. The site is located in an open and abandoned field, and no specific permits were required for the described field studies. Native *Coix* was germinated from seeds that were purchased from Shandong Heze Chinese Medicine Institute. We filled our experimental pots (3 L) with field-collected red clay soil mixed with sand (3:1).

Artificial defoliation has been employed extensively as a method of simulating herbivore attack [12,28–30] and has recently been used to simulate biological agents to control invasive plants [20,31,32]. Although artificial defoliation does not always elicit the Foix

75% or 100%) and competition (with or without) were applied to treat invasive *Mikania*. A total of 10 treatments were used in this experiment, and 5 replicates were used for each treatment, amounting to 50 pots. For the experiment without competition, an individual *Mikania* plant was transplanted into each pot; for the competition treatment, an individual *Mikania* plant and one *Coix* plant of similar size were transplanted together into each pot with a distance of 15 cm between them. The pots were irrigated with tap water twice daily and fertilised with 50% Hoagland's nutrient solution once per week [33]. Bamboo sticks (1 m long) were inserted into the soil near *Mikania* to allow the plant to climb. Three weeks after transplantation, *Mikania* plants of similar size were chosen for defoliation. Herbivory by *A. thalia pyrrha* on *Mikania* herbivory do not interact and respond multiplicatively on a linear scale. If DR or CR = 1, there would be no effect of competition or herbivory on plant growth. If DR or CR <1, there would be a negative effect; If DR or CR>1, there would be a positive effect. We also calculated TR_{pred} (DR $\times$ CR) to indicate the simple multiplicative effects of competition and herbivory together on plant growth and TR_{true} (with defoliation and competition/ without defoliation and competition) to indicate the observed combined effect of both competition and herbivory [10]. If TR_{pred} $>$ TR_{true}, there would be a synergistic interaction between competition and herbivory; If TR_{pred}

conclusions, in this study, defoliation had a negative effect on the growth of invasive *Mikania* growing alone: growth declined with increasing defoliation intensities. However, the negative effect of defoliation may be modified by competition. The response values to different defoliation intensities tested on *Mikania* growing with native *Coix* were all significantly higher than those of *Mikania* growing alone, indicating a compensatory growth of *Mikania* induced by competition in response to defoliation, particularly at 75% defoliation. This result indicates that native *Coix* could help invasive *Mikania* be more vigorous after defoliation.

Although the mechanism underling the compensatory growth of *Mikania* that is induced by the competition is unknown, the underground network between the roots of invasive *Mikania* and native *Coix* mediated by mycorrhizae might be a possible mechanism. Although it is still unknown why defoliation can induce a potential transfer of nutrients between a plant and a neighbouring plant, evidence using stable isotopes verified that defoliation could change the underground nitrogen flow [41] and that carbon could be transferred via mycorrhizae from native neighbouring plants to the invasive plant [42]. Native *Coix* is a mycorrhizal plant [43], and the soil in the *Mikania* community is rich in fungi [44]. It has also been verified that native neighbours are capable of enhancing compensatory growth of invasive plants to defoliation in the presence of soil fungi [20,34]. Further atention should be paid to the underground mechanism.

The successfully invasive plants are always strong competitors of the native plant species, however, native plants has been verified as a major force in the resistance of exotic invasions [3,45]. In this study, competition from native *Coix* did significantly decrease the growth of invasive *Mikania* because of the limited resources. However, the negative effect of competition on the growth of *Mikania* may be modified by defoliation. The response values of *Mikania* to competition increased at each defoliation intensity, indicating a release from native competitor *Coix* induced by defoliation, particularly at 75% defoliation. The release of *Mikania* from competition that can be induced by defoliation could increase the number of invasive plants and allow the domination of niche spaces to the detriment of native species [46], perhaps facilitating the invasiveness of *Mikania* and helping to shape the structure and dynamics of the invaded communities.

Plants have the ability to (at least partially) compensate for herbivory only above a certain threshold level of damage [29], and this threshold can differ among plant species. Yu et al. found that invasive *Alternanthera philoxeroides* can only rapidly recover from 50% defoliation [47]. Similarly, in the present study, when the native *Coix* was present, 75% defoliation induced the compensatory growth of invasive *Mikania*. Many morphological and physiological mechanisms have been proposed to explain the compensatory growth that follows herbivory or defoliation [30], such as the increased allocation of substrates from the roots to shoots [48] and the increased photosynthetic rate of the regrowing tissue [49]. In our study, 75% defoliation decreased the root/shoot ratio and significantly increased net photosynthetic rate, light use efficiency and water use efficiency. The resources stored in the roots were shifted to the shoots, significantly reducing the root/shoot ratio [50]. Barton found that *Plantago lanceolata* (Plantaginaceae) seedlings were plastic in their resource allocation between the shoots and roots, resulting in compensatory growth [50]. This type of strong compensatory growth due to phenotypic plasticity and the physiological acclimation of invasive *Mikania* was maximised at 75% defoliation.

Although artificial defoliation has been widely used to mimic the effect of truly herbivory on plants [12,28–30,51], there are undeniably significant differences between defoliation and herbivory [52]. Artificial defoliation can only mimic the effect of the loss of leaf area which decreased the ability of plants to intercept light [53] but not the effect in responding to the physiological and chemical interactions (e.g., due to nutrient supply) between herbivores and plants. In spite of some pitfalls, artificial defoliation has been used more often in herbivory research than real herbivores for easily and precisely controlling, targeted effect and efficient experimental designs [53]. And there were only a few cases (as low as 3%) with the outcomes where artificial and natural damage had opposite effects on plants. The biological control agent of *Mikania* are found to consume all of the young leaves and stems of *Mikania* [26], so the defoliation can at least partially mimic the effect of the loss of leaf area caused by the biological control agent.

In conclusion, our results suggest that natural herbivory might not necessarily be safely used as a potential agent to control invasive *Mikania* in the field because of the induced compensatory growth of *Mikania* by native *Coix*. Further studies should consider the interactions at the intertrophic and multitrophic levels in invaded communities as well as among more factors including, e.g., nutrient supply which seems difficult to investigate with simulated herbivore, whereby the ecological risk of the releasing of the biological control agents can be comprehensively evaluated.

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Author Contributions

Conceived and designed the experiments: JL MD. Performed the experiments: JL. Analyzed the data: JL MD. Contributed reagents/materials/analysis tools: JL. Wrote the paper: JL MD.

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