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New Evidence for the Hypothesis of Reducing Natural Enemy Pressure of *Eupatorium adenophorum*: *Solenopsis invicta* Competing with *Doxrylus orientalis* to Feed on *E. adenophorum*

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Abstract

Natural enemy insects are important factors in regulating plant invasion. The interactions between multiple insect species resulting from invasive plants remain poorly understood despite their potential. We observed notorious invasive plants *Eupatorium adenophorum* Sprengel were competedly fed by *Solenopsis invicta* Buren (Hymenoptera: Formicidae) and *Dorylus orientalis* Westwood (Hymenoptera: Formicidae) beside the scientific research base of Kunming University. It was first observed that *D. orientalis* was eating the epidermis, cortex, phloem and other root and stem tissues of *E. adenophorum* in soil. Two months later, it was observed that *S. invicta* ate the epidermis, cortex, phloem and other aboveground stem tissues of *E. adenophorum*. *S. invicta* attacked *D. orientalis* and displaced their living space by causing the later dead, injured, or even disabled. This phenomenon suggested that local herbivorous insects have adapted to *E. adenophorum* well, which will intensify the naturalization process of *E. adenophorum* in local habitats. In a homogeneous garden planting experiment of *E. adenophorum* conducted at the experimental base of Kunming University, the biomass of the introduced (China) populations of *E. adenophorum* was lower than that of the native (Mexico) populations, although there was no statistically significant difference. These results indicate a possible positive correlation between the in-

crease in natural enemy pressure and the decrease in fitness of *E. adenophorum.*

Keywords

Eupatorium adenophorum Sprengel, *Solenopsis invicta* Buren, *Dorylus orientalis* Westwood, Natural Enemy

1. Introduction

Eupatorium adenophorum Sprengel (Asteraceae; hereafter *Eupatorium*) is a composite broad-leaved weed native to Central America, which has invaded more than 30 countries and regions with subtropical climates [1]. *Eupatorium* inhibits local plant growth with a great competitive advantage in the invaded area, causing significant damage to the local ecological and economic environment [2] [3] [4]. Increasing evidence shows that *Eupatorium* population faces an increasing pressure of natural enemies in the invaded habitats [2] [5] [6] [7] [8], and a decreasing trend of invasiveness [7].

The successful parasitism of the specific natural enemies *Procecidochares utilis* [9] [10] [11] reduced the reproductive capacity of *Eupatorium* and weakened its invasiveness to some extent. So far, the confirmed natural enemies of *Eupatorium* include *Dorylus orientalis* Westwood (Hymenoptera: Formicidae; hereafter *Dorylus*) [7], and *Orthezia quadrua* (Homoptera: Ortheziidae) [8]. Niu Yanfen and her colleagues found that *Acrydium japonicum* Bolivar (Orthoptera: Tettigidae), larvae of *Calimorpha albipuncta* Wileman (Lepidoptera: Arctidae), *Agriolimax* sp *(Stylommatophore: Agriolimacidae)]* and one larvae each of *Lepidoptera* and *Lepidop-tera, Lepidoptera,* also ate *Eupatorium [7]*. This indicated that *Eupatorium* in Yunnan habitats had already faced great pressure from natural enemies. This study supports the hypothesis of reduced pressure on natural enemies of *Eupatorium* by reporting the phenomenon that *Solenopsis invicta* Buren (Membranoptera Formicidae; hereafter *Solenopsis*) competed fiercely with *Dorylus* for *Eupatorium* and the biomass of invasive *Eupatorium* populations was lower than those of the original populations in a homogeneous garden.

Solenopsis, also known as the red imported fire ant, is the most destructive and aggressive worldwide invasive ant [12] [13]. It is a social insect commonly creating colonies in the soil [14]. It is native to central South America and has invaded many countries, including the United States, Mexico, Australia, New Zealand, China, Malaysia, Singapore, and the West Indies [15]. Under current climatic conditions, in China, Hainan, Guangdong, Guangxi, Fujian, Zhejiang, Jiangsu, Anhui, Hubei, Hunan, Jiangxi, Guizhou, Yunnan, Chongqing, Sichuan, Henan, and Taiwan are potentially suitable areas [12]. In the invaded areas, it had a very negative effect on biological diversity, public safety, agriculture, and economics [14] [15] [16]. However, it competed with the deadly natural enemy of *Eupatorium*, *Dorylus*, to feed on *Eupatorium*, which shows that this species

has a certain weakening effect on the invasion of *Eupatorium.*

2. Materials and Methods

2.1. Plant Materials

In cultivation experiment, seeds of *Eupatorium* were originally collected from their original (Mexico) and invasive (China) areas (Table 1) and planted for a generation at Qujing Normal University, Qujing City, Yunnan Province, Southwest China, and stored in 4˚C until used. On 10 August 2012, seeds from each population were sown in seedbeds. On 14 October 2012, when the seedlings were approximately 10 cm tall, vigorous seedlings with similar size were transplanted singly in soil in a common garden in Kunming University, Kunming City, Yunnan Province, Southwest China, where the mean annual temperature is 16.5˚C and the mean annual precipitation is 1450 mm, the frost free period is 278 d.

2.2. Experimental Design

In cultivation experiment, 10 populations of *Eupatorium* were cultivated. All plants were cultivated separately. 10 plants were used for each population, resulting in a total of 100 plants. Plants were watered via a trickle irrigation system every week. Populations were arranged in a completely randomized designed. Every two plants are spaced 40 cm apart in a community, and every two populations are spaced 60 cm apart. The roots of each plant are separated by plastic tubes (35 cm in width and 25 cm in depth) to prevent tangle. Hand weeding was

Table 1. Background information on each site where the seeds of the crofton weed were collected in the native and invasive ranges.

Sites	Latitude	Longitude	Elevation (m)	MAT (˚C)	MAP (mm)	Habitat
Native range Mexico						
Pinal de Amoles, Querétaro	N20˚35'	W100˚23'	1830	18.8	549.0	Pine, oak, prickly thicket
San Miguel de Allende, Guanajuato	N20˚55'	W100˚45'	1900	19.0	740.0	Prickly thicket
Acebuche, Tarimoro, Jalisco	N20˚25'	W102˚10'	2250	17.0	1000.0	Evergreen forest
Quérendaro, Michoacán	N19˚52'	W100˚54'	2300	18.0	700.0	Pine, holm oak
Umécuaro, Morelia, Michoacán	N19˚42'	W101˚11'	2700	17.7	764.0	Evergreen forest
Invasive range China						
Menglun, Mengla, Yunnan	N21˚58'	E101˚13'	640	21.0	1557	Crop fields
Taizhong, Jingdong, Yunnan	N24˚28'	E100˚55'	1610	16.3	1550.0	Evergreen forest
Taizhong, Jingdong, Yunnan	N24˚29'	E100˚59'	1950	14.5	1800.0	Evergreen forest
Kunming, Yunnan	N25˚06'	E102˚50'	2200	14.9	1000.5	Secondary forest
Xujiaba, Jingdong, Yunnan	N24˚31'	E101˚00'	2310	11.0	1931.1	Evergreen forest

MAT, mean annual temperature; MAP, mean annual precipitation.

performed when necessary.

On 20 March 2013, 156 days after being transplanted, plants were harvested and the total dry biomass was recorded for 7 plants of each population. Supporting organs (including stems, branches, and petioles) were severed at the soil surface, belowground tissue was harvested by washing soil off roots/rhizomes with water. Each plant parts were dried for 48 h at 60˚C until constant mass was achieved, and biomass determined by weighing to nearest 0.01 g. Total biomass was determined.

2.3. Observation of Natural Insect Enemy and Result

On March 3, 2015, it was observed that *Dorylus* attacking the wild population of *Eupatorium* on the outskirts of experimental base in Kunming University. Considering that was a familiar phenomenon, it attracted no extra attention. Two months later, researchers observed that there were many broken or complete bodies or dying *Dorylus* around *Eupatorium* which were once eaten by *Dorylus* (**Figure 1**), and a large number of *Solenopsis* were eating the epidermis and cortical stem tissue of *Eupatorium* (**Figure 1**). *Solenopsis* moved to another feeding position after eating up about 1 - 2 cm^2 of non-lignified tissue of stems of *Eupatorium*. The width of each destroyed point did not exceed half of the perimeter of the stem (**Figure 1**). *Solenopsis* generally ate from the lower part of the stem of *Eupatorium*, moving upwards, thus leaving many mottled damage symptoms on the stem of *Eupatorium*. Each patch measured 3 - 5 cm in length and about 1 cm in width (**Figure 1**).

During the observation period, the diseased bodies or remains of *Dorylus* were moved out by *Solenopsis* from the caves under *Eupatorium* from time to

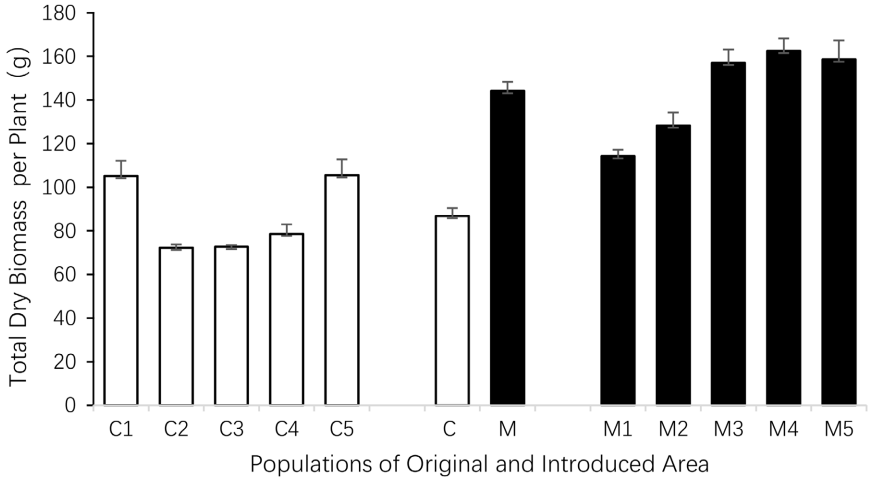

Figure 1. Differences in total biomass of *Eupatorium adenophorum* Sprengel from native (Mexico, filled bars) and introduced (China, open bars) populations. Open bars and filled bars depict means and SE for introduced population of introduced and native population, respectively. C1, C2, C3, C4, and C5 represent the five populations in the introduced area; M1, M2, M3, M4, and M5 represent the five populations in the introduced area; C and M bar depict means and SE across populations within each region.

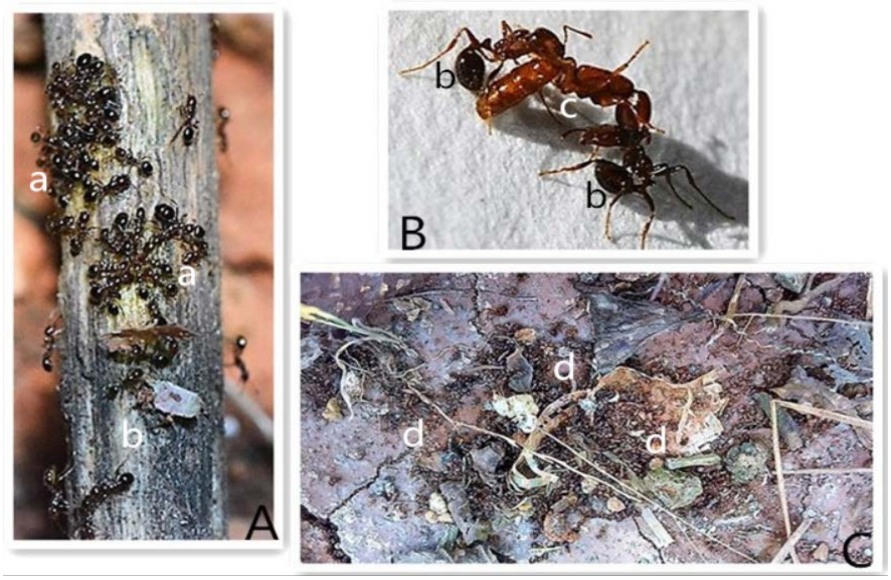

Figure 2. *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae) eating living roots, stems, leaves of *Eupatorium adenophorum* Sprengel and driving away *Dorylus orientalis* Westwood. Aa, *S. invicta* attacking epidermis and cortex tissue of stems of *E. adenophorum*; (B) *S. invicta* (a) and *D. orientalis* (c) engaged in a fight; Cd, corpses of *D. orientalis* were moved out by *S. invicta* and put on the ground around *E. adenophorum*; Ab, imprints on the stems of *A. adenophora* eaten by *S. invicta.*

time and stacked on the soil surface within 40 cm around *Eupatorium*. To confirm whether the two kinds of ants attack each other, the researchers put two comparable-sized ants into a Petri dish and observed that the ants attacked each other violently, the fight ending with the failure of *Dorylus*, without exception. If the number of *Solenopsis* was increased, even if *Solenopsis* were smaller, *Dorylus* rarely won (**Figure 2B**). *Solenopsis* attacked all parts of *Dorylus*, and even bit the ventral handle of *Dorylus* until it died. In field investigations it was found that the place formerly occupied by *Dorylus* had been displaced by *Solenopsis*. The most typical example could be found around the roots of *Conyza canadensis* (L.) Cronq, *Galinosoga parviflora* Cav., Bidens pilosa L, and *Eupatorium*, which had been occupied by *Dorylus*. These phenomena not only showed that *Solenopsis* was an important natural enemy of *Eupatorium*, but also the fierce survival competition for eating *Eupatorium* between *Dorylus and Solenopsi*.

3. Statistical Analysis

Two-way nested ANOVA was used to test the biomass difference in *Eupatorium* from native and introduced ranges. Population origin (native vs introduced) was used as fixed factors; population is nested within origin as a random factor. These data were tested for normality and homogeneity of variance before analysis. To meet test assumptions, total biomass was lg10 transformed. Biomass date analyses were performed using the statistical software package SPSS22.0 (SPSS Inc, Chicago, IL).

A significant difference in variables between origins in common garden envi-

ronments suggests genetically based changes in *Eupatorium* plants; compared with the original populations, the decrease in biomass in invasive populations indicates a decline in invasiveness of *Eupatorium*.

4. Results and Analysis

In cultivation experiment, there was no statistically significant differences in total biomass in *Eupatorium* from native (Mexico) and introduced (China) populations (**Figure 1**) in common garden. There was little evidence that invasive (China) populations had higher growth ability than native (Mexico) populations. On the contrary, the biomass of the invasive population of *Eupatorium* tends to be lower, although there was no statistically significant difference. In observation experiment, the competitive feeding behavior of *Solenopsis* and *Dorylus* on *Eupatorium* not only indicates that the red fire ant is a new natural enemy of *Eupatorium*, but also reveals complex interactions within the local herbivore community.

5. Discussion and Conclusion

The feeding of native enemies in Yunnan on *Eupatorium* may result from the adaptive evolution of this alien species. The unique geological history, geographical location, topography, and unique climate conditions make Yunnan rich in biodiversity [17]. High insect diversity may be the main reason for the increasing pressure of natural enemies of *Eupatorium* in Yunnan.

Local herbivorous insects can adapt to foreign plants and undergo adaptive evolution in behavior, physiology, and biochemistry, thereby increasing the feeding pressure on exotic plants [18] [19]. For example, *Uroleucan ambrosiae* only feeds on *Ambrosia trifida* L. in eastern North America, in order to adapt to the dispersion and unpredictability of the distribution of *A. trifida* in extreme arid regions, where it evolved into an oligophagous insect in western North America, feeding on several composite weeds [20]. In northern Argentina, the stem borer *Apagomerella versicolor* (Coleoptera: Cerambycidae, subribe Aerini) only feeds on *Pluchea sagittalis* Cabr, but in the central and southern regions, it feeds on seven species of composite plants, including Cerambycidae [21].

Wang *et al.* (2009) [22] conducted research in Liangshan Prefecture, Sichuan Province, China, and found that the number of species and individuals of Arthropod (especially herbivorous insects) in *Eupatorium* community on abandoned land (equivalent to heavily invaded habitats) was more than those in forest area (equivalent to uninvaded habitats) and agroforestry ecotone (equivalent to moderately invaded habitats). Jiang *et al* (2017) [23] investigated the Qilin Mountain and its surrounding areas (24˚42'N, 102˚52'E, 1957 - 2015 m above sea level) of Chengjiang County, Yunnan Province, and found that the diversity of natural enemies in the heavily invaded communities by *Eupatorium* was higher than those in the moderately invaded and uninvaded communities. These phenomena indicated that the feeding habits of local natural enemies to *Eupatorium*

are related to the degree of invasion. As the invasion time prolongs, the behavioral limitations of insects are broken and their physiological and biochemical adaptation to *Eupatorium* strengthen [18]. In this study, the strong competition of *Dorylus* and *Solenopsis* for eating *Eupatorium* showed that local omnivorous insects have established a stable feeding relationship to *Eupatorium*. With the strengthening of the feeding relationship of local insects to *Eupatorium*, the invasiveness of *Eupatorium* will gradually weaken, eventually leading to its naturalization as one of the common populations.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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