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Original article

Tolerance and resistance of invasive and native *Eupatorium* species to generalist herbivore insects

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A B S T R A C T

Invasive plants are exotic species that escape control by native specialist enemies. However, exotic plants may still be attacked by locally occurring generalist enemies, which can influence the dynamics of biological invasions. If invasive plants have greater defensive (resistance and tolerance) capabilities than indigenous plants, they may experience less damage from native herbivores. In the present study, we tested this prediction using the invasive plant *Eupatorium adenophorum* and two native congeners under simulated defoliation and generalist herbivore insect (*Helicoverpa armigera* and *Spodoptera litura*) treatments. *E. adenophorum* was less susceptible and compensated more quickly to damages in biomass production from both treatments compared to its two congeners, exhibiting greater herbivore tolerance. This strong tolerance to damage was associated with greater resource allocation to aboveground structures, leading to a higher leaf area ratio and a lower root: crown mass ratio than those of its native congeners. *E. adenophorum* also displayed a higher resistance index (which integrates acid detergent fiber, nitrogen content, carbon/nitrogen ratio, leaf mass per area, toughness, and trichome density) than its two congeners. Thus, *H. armigera and S. litura* performed poorly on *E. adenophorum*, with less leaf damage, a lengthened insect developmental duration, and decreased pupating: molting ratios compared to those of the native congeners. Strong tolerance and resistance traits may facilitate the successful invasion of *E. adenophorum* in China and may decrease the efficacy of leaf-feeding biocontrol agents. Our results highlight both the need for further research on defensive traits and their role in the invasiveness and biological control of exotic plants, and suggest that biocontrol of *E. adenophorum* in China would require damage to the plant far in excess of current levels.

1. Introduction

The enemy release hypothesis (ERH) is a commonly accepted explanation for the success of invasive species, which assumes that exotic species become invasive because they are no longer controlled by predators in their new ranges (Keane and Crawley, 2002). This hypothesis has received support from many biogeographical studies that compare herbivore and parasite pressure on plants and show a reduction in the number and impact of herbivore and parasite consumers in the introduced range compared to the native range (Cripps et al., 2010; Meijer et al., 2015; Mitchell and Power, 2003). However, demographic benefits may not translate into a competitive advantage in the new habitat (Chun et al., 2010; Harvey et al., 2015; Van Kleunen and Fischer, 2009). Therefore, the different pressures on invasive and native species are more important than simple biogeographical comparisons between populations as these pressures are directly responsible for invasiveness (Prior et al., 2015).

Native herbivores and parasites prefer native plants for several reasons. For example, leaves of the exotic plants may be undesirable due to leaf nutrient contents or exotic plants may actually be a viable food source that native herbivores fail to recognize (Behavioral Constraint Hypothesis, Lankau et al., 2004). Alternately, exotic plants may have defenses that native herbivores have never encountered and thus cannot overcome, as is proposed in the Novel Weapons Hypothesis (Callaway and Ridenour, 2004). The lack of specialists for the exotic plant and the tendency of generalists to

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stick with native plants may give exotics an advantage over native plants (Keane and Crawley, 2002; Liu and Stiling, 2006). However, recent studies have found that reduced damage to exotic plants from native herbivores is by no means universal (Harvey et al., 2013, 2015; Rogers and Siemann, 2002). Generalist herbivores may actually play an important role in providing resistance to invasion (Parker et al., 2013; Weed and Schwarzländer, 2014).

Many plant species have evolved defensive capabilities against native herbivores and parasites in the form of tolerance, resistance, or both. Tolerance reflects the ability of a plant to regrow and reproduce after damage, which can minimize the loss of biomass (Strauss and Agrawal, 1999), whereas resistance is a plant trait that deters enemy attack or reduces the performance of herbivores (Strauss et al., 2002). However, most studies have only focused on either tolerance (Beckmann et al., 2016; Dawson et al., 2014; MacDonald and Kotanen, 2010; Rogers and Siemann, 2002; Schierenbeck et al., 1994) or resistance (Alba et al., 2013; Funk and Throop, 2010; Harvey et al., 2013, 2015; Meijer et al., 2015), not both. Recently, there has been increased recognition that both types of defense may need to be examined simultaneously to advance our understanding of plant invasion biology (Lieurance and Cipollini, 2013).

Plants with high tolerance can compensate for damage inflicted by a wide variety of herbivores and parasites because tolerance is a non-specific type of defense (Rogers and Siemann, 2002). Tolerance can be achieved by increasing photosynthetic rates after damage, increasing branching, increasing growth rates, and shifting biomass allocation (Day et al., 2015; Strauss and Agrawal, 1999). Some studies have indicated that invasive plants tend to have high tolerance to native generalist herbivores (Lu et al., 2014; Schierenbeck et al., 1994) and simulated insect herbivores in experiments where leaves were clipped (Ashton and Lerdau, 2008; MacDonald and Kotanen, 2010; Raghu et al., 2006).

In systems where generalist herbivore pressure on exotic plants is intense, the occurrence of highly resistant plants is higher than weakly resistant plants because this trait is required to successfully establish a population (Caño et al., 2009; Henriksson et al., 2016; Ridenour et al., 2008). In those cases, plants may depend on resistance from pre-adapted traits or post-introduction changes specific to the new generalist enemies (Colautti et al., 2004). Some phytochemical and mechanical forms of resistance may affect generalist enemies in invaded ecosystems (Keeler and Chew, 2008) by impeding any one of the inset's developmental stages (such as egg, larva, pupa, and molting as an adult). Recent studies on rearing generalists and examining putative defensive chemicals, have confirmed that some plant invaders may be more resistant to herbivores in their new ranges than in their native habitat (Alba et al., 2013; Cripps et al., 2010; Hull-Sanders et al., 2007; Joshi and Vrieling, 2005). However, field surveys or common garden experiments measuring visible damages among indigenous and exotic plants (Ashton and Lerdau, 2008; Cincotta et al., 2009; Dawson et al., 2014; Hill and Kotanen, 2010; Harvey et al., 2015; Meijer et al., 2015; Vasquez and Meyer, 2011), rearing generalist herbivores (Caño et al., 2009; Harvey et al., 2010), and examining single resistance chemicals (Alba et al., 2013; Funk and Throop, 2010) have produced mixed results. Several factors may contribute to these inconsistencies. For example, the observed damages may not be related to fitness, different species may employ different defensive strategies, or complementary resistance traits may occur together. To date, studies integrating visible damage measurements, rearing generalists, and examining putative resistance traits to compare resistance between exotics and indigenous plant species have not been performed.

Eupatorium adenophorum Sprengel (also known as *Ageratina adenophora* (Sprengel) R. M. King and H. Robinson), is an evergreen-perennial plant native to Central America that has invaded China. Previous studies have focused on the physiological characteristics of *E. adenophorum* (Feng et al., 2007; Feng, 2008a, 2008b), although a few studies have been conducted on its defensive traits in invaded areas. In its native range, there are more than 30 phytophagous insect species and numerous pathogens that attack *E. adenophorum*. However, *E. adenophorum* is sustained a monoculture in China and biocontrol has been effective in some invaded ecosystems, suggesting that tolerance and enemy release may play a role in its successful invasion (Bess and Haramoto, 1959). Yang et al. (2006) and Yan (2006) found several allelochemicals in the leaf and roots of *E. adenophorum* that have lethal effects on Aphidoidea and Bruchidae insects, indicating that this invader may possess high resistance capabilities. However, Zheng et al. (2012) suggested that *E. adenophorum* might be a good food source for native generalist herbivores. Ecophysiological comparisons between exotic and indigenous species are more informative if the pairs are sympatric and close phylogenetically (Garcia-Serrano et al., 2007; Liu and Stiling, 2006).

The main aims of this study were to determine (1) whether *E. adenophorum* experiences lower rates of damage from native generalists relative to its native congeners *E. japonicum* and *E. heterophyllum,* as predicted by ERH, and (2) the mechanism underlying the defensive traits (tolerance and resistance) of the three *Eupatorium* plants with regard to generalist herbivores.

2. Materials and methods

2.1. Study site and plant material

This study was carried out at Qujing Normal University, Qujing (25°31′N, 103°45′E), Yunnan Province, southwest China, between April 2010 and December 2010.

Eupatorium adenophorum spread into Yunnan Province from Burma (now Myanmar) in the 1940s and has invaded six provinces in southwestern China to date. It replaces the native species and forms a dense monoculture in many habitats. *E. japonicum* and *E. heterophyllum*, which have extensive native ranges in China, can be out-competed by *E. adenophorum*. All three of the *Eupatorium* plants are perennial forbs. Seeds from all three species were collected in 2009 from Qujing on Apr 4, Oct 21, and Nov 9. The seeds were dried for seven days at room temperature (20 ± 5 °C) and then stored in paper bags at room temperature until the experiment started.

2.2. Herbivore assays

Plants are rarely attacked by a single insect species in isolation, so it is necessary to assess the impact of an assembly of herbivores rather than individual species. There have been no comprehensive studies of the natural enemies of *E. adenophorum* in China. Therefore, two generalist herbivore moths (*Helicoverpa armigera* Hübner and *Spodoptera litura* Fabricius) were combined in this study. We selected these two species for several reasons. First, they are known to feed on plants in over 20 families and are the most common herbivore in the selected study site. Second, Zheng et al. (2012) observed that *H. armigera* and *S. litura* consume leaves of the plant species of interest at the study site. Third, the two insects have similar developmental processes, namely that the larvae pupate after completing approximately 5–6 instars. Finally, the insects are commercially available, reared on an artificial diet that can minimize or correct extraneous differences resulting from the larval developmental stages. We studied the larvae between the third and fifth instars, when they are most sensitive to external treatments.

Seeds were sown in April 2010 in planting trays with a 1: 1