Invasive plant has higher resistance to native generalist herbivore than exotic non-invasive congener

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Abstract

Studies on the effects of invasive plants on native herbivores often only concern about short-term effects, and few studies have focused on the long-term effects of invasive plants on herbivores. We investigated the development of Spodoptera litura to the second generation on the invasive plant Phytolacca americana and the exotic non-invasive plant Phytolacca icosandra, meanwhile, we tested the impacts of the P. americana on the S. litura through laboratory bioassay, oviposition preference and detoxifying enzyme activity analysis. The results show that S. litura have feeding and oviposition preference to P. icosandra, the larval weight and oviposition preference index (OPI) of S. litura feeding on P. icosandra are higher. However, the developmental duration of S. litura on P. icosandra is shorter than that of P. americana; the activities of Acetyl cholinesterase (AchE) and Glutathione-S-transferase (GST) of S. litura feeding on the leaves of the P. americana were higher than those of feeding on artificial diet and P. icosandra. There is no significant difference of activities of AchE and GST between S. litura feeding on artificial diet and P. icosandra. These findings have important implications for the evaluation of the impacts of invasive plant P. americana on native herbivores in the local ecosystem and explain that invasive plant has higher resistance to herbivores and suffer less damage than exotic non-invasive plant in the invaded range.

Introduction

Invasive plants were more likely to have novel chemicals than native plants in introduction region (Lankau et al., 2004; Cappuccino & Arnason, 2006; Schaffner et al., 2011; Macel et al., 2014), these chemicals facilitate exotic plants successful invasion via higher resistance to herbivores and inhibiting native plant growth (Sedio et al., 2020). Many studies indicated that invasive plants suffer less herbivory than non-invasive plants, and the reason for this phenomenon is attributed to the invasive plants possess anti-herbivore chemicals (Cappuccino & Carpenter, 2005; Schaffner et al., 2011). However, invasive plants as a potential food resource (Schlaepfer et al., 2011) will increase the possibility of being feeding by herbivores as time of invasion increases (Dai et al., 2014). The low adaptability of native insects to invasive plants will form a trap that affects the reproduction and growth of native insects and even causes the extinction of some native insect populations, this phenomenon was reported as ecological trap (Mack et al., 2000; Schlaepfer et al., 2002; Battin, 2004; Sun et al., 2020). The fecundity and performance of insects will be affected by the quality of the host (Awmack & Leather 2002). Wang et al. (2006) indicated that female insects reared on the plant with higher nitrogen content have greater weight and higher oviposition rate. Rane et al. (2019) found that when Gypsy moths (*Lymantria dispar*) were fed on artificial diet that lacking protein, vitamins and minerals, the growth rate was slow, the pupae weight was small and the development period was prolonged . Besides, plant defensive chemicals can extend the developmental period of insects, increase their exposure to natural enemies, and increase mortality (Awmack & Leather, 2002). In the case of nutrition deficiency or presence of high amounts of defensive substances, insects would produce a large number of small eggs or a small number of eggs but a large volume, respectively (Leather & Burnand, 1987). Under extremely harsh conditions, female aphids invest in greater embryonic development or reabsorb embryos (Ward & Dixon, 1982; Xu et al., 2019), even if female insects have laid eggs, they will reabsorb the eggs and obtain nutrients to extend their life cycle until the next opportunity for oviposition (Leather, 1983; Sequeira & Dixon, 1996).

Plants are sessile organisms, to defend against herbivorous insects, a series of defense mechanisms are evolved, including long spines, poor palatability, and the production of toxic substances (Lindroth et al., 1990; Wittstock & Gershenzon, 2002; Schuman & Baldwin, 2016; Stahl et al., 2018). In order to survive, herbivore insects have also taken corresponding measures to solve this problem, including behavioral avoidance, excretion and detoxification mechanisms (Karban & Agrawal, 2002; Heckel, 2014; Erb & Robert, 2016; Stahl et al., 2018). The detoxification enzymes in the midgut of herbivores are effective against toxic substances produced by plants. Detoxification is aimed specifically at the toxic substances of plants (Yi et al., 2018). Common detoxification enzymes are Acetyl cholinesterase(AChE), Carboxylesterase(CarE) and Glutathione-S-transferase(GST) and so on, CarE mainly plays a role in the detoxification of organophosphorus compounds and is involved in the metabolism of foreign substances (Xu et al., 2006). AChE targets organophosphorus and carbamate compounds and GST can metabolize many compounds and directly affect the ability of insects to resist toxic compounds (Enayati et al., 2005). Furthermore, insects convert toxic substances taken into the intestinal tract into more easily absorbed substances by increasing the enzyme activity in the body and at the same time remove unusable substances from the body to reduce damage to themselves (Rane et al., 2019). The poisonous substances that plants produced sometimes are also benefit to herbivores. Several insects could use the poisonous substances of plants to protect themselves from natural enemies by eating plants carrying poisonous substances (Despres et al., 2007) and secrete toxic substances to prevent attacks from natural enemies (Heckel, 2014; Erb & Robert, 2016).

Most of the researches on the impacts of invasive plants on native herbivores use local plants for comparison to determine the extent of the impact of invasive plants on native herbivorous insects. In this process, the presence of exotic plants is often ignored. Dai et al. (2014) demonstrated that beetles oviposition preference older invader, the results show that the adaptation of native herbivores to exotic plants is related to the time dynamics. There for, comparing the effects of exotic plants on native herbivorous insects and the effects of invasive plants on native herbivorous insects can better reveal the impacts of invasive plants on herbivores. Huang et al. (2020) study found that invasive plants had lesser herbivory and structural defense and greater nutriment than non-invasive plants.

P. americana originated from North America and was introduced into China as an ornamental plant in 1935 (Xu et al., 2006). It has been spreading in several provinces and become an invasive plant in Southern China (Thompson, 1988; Dicke, 1999; Pearson, 2009). Researches on*P. americana* have focused on the accumulation of heavy metals and the medicinal value of secondary metabolites(Liu et al., 2011; Chaudhury et al., 2018). *P. americana* can be enriched in several heavy metals as Mn and Cd, which are stored in the cell wall and vacuole (Liu et al., 2010). The plants of *P. americana* have high concentration of saponin, which has medicinal value but toxic to herbivores (Wang et al., 2008). In medical science, it has been confirmed that the secondary metabolites in *P. americana* have antibacterial, antioxidant and anti-malignant cell proliferation effects (Patra et al., 2014; Boo et al., 2015). At the same time, some studies have shown that the content of secondary metabolites of *P. aericana* are higher than that of other *Phytolacca* members (Kim et al., 2005). *P. acinosa* is a native congener with *P. americana* in China. Although Huang et al. (2016) research indicated that the reason for the successful invasion of *P. americana* in China may be the reallocate resources for defense to growth and reproduction. Through our previous field observations, *P. americana* suffer less damage than *P. acinosa* when they grow in same sites (Liu et al., 2020). In the field and our common garden, *Spodoptera litura* Fabricius, which is a common native generalist in China and could damage more than 180 plant species from several families, was observed it's feeding on *P. americana* and *P. acinose* (personal observation).

In this study, we examined the effects of the invasive *P. americana* and exotic non-invasive *P. icosandra* on native herbivore *S. litura* through laboratory biological assays, oviposition preference and detoxification enzyme assay to reveal impacts of invasive plant *P. americana* on native herbivore in native ecosystems.

Materials and methods

Plants and insects

Berries of *P. americana* and *P. icosandra* were collected in June 2019 near the hospital of Yunnan University (24°83'N, 102deg85'E,) and Yunnan Agricultural University (25deg13'N, 102deg74'E,), respectively. After being mashed, the seeds were washed and then dried in a dry environment for subsequent experiments. Before germination, seeds were soaked with concentrated sulfuric acid for 10-15 minutes to break dormancy, and then were sterilized by75% ethanol. After washing3-5 times with purified water, the seeds were transferred to 1% agar medium and cultured in an incubator (26oC +- 1oC, 14L:10D). After two cotyledons were formed, the seedlings were transferred to a plug tray until at least three leaves were fully expanded, and then they were cultivated in flower pots (outer diameter x height = 17 cm x 14 cm) and watered every two days.

The eggs of *S. litura* were purchased from Yun Ke Biocontrol Company (Henan, China) and then were kept in an incubator (26.0oC +- 1, 14L:10D) until hatching. The larvae were reared with artificial diet (purchased from Yun Ke Biocontrol Company). All experiments were conducted with second-instar larvae.

Physiological impacts of invasive plants on native herbivorous insects: laboratory assay

A larva in a petri dish, 90 repeats per plant. A total of 180 *S. litura* of second-instar were placed on a 9-cm diameter disposable petri dish lined with moist filter paper and clean leaves of *P. americana* . Similarly, *S. litura* larvae were reared with the leaves of *P. icosandra* . All petri dishes were placed in a thermostat incubator (27 oC +- 1, 14L:10D). Petri dishes were refreshed daily with clean filter paper and fresh leaves. The weight of the larvae was recorded every three days. After pupation, the pupae were weighed individually, and then males and females were separated for subsequent mating. Upon eclosion, two pairs of one male and one female were put into a 0.6L plastic bottle with the bottom removed and sealed with gauze. Adults were provisioned with 1% honey water absorbed on cotton and egg laying of *S. litura* was observed. Then, the second generation experiment was carried out using the eggs of *S. litura* . The plant leaves that the larvae fed corresponded to the previous ones, and the experiment method was the same as the first generation. The duration of each development stage of the larvae was recorded. The experiments stopped until all *S.litura* died.

Oviposition preference of *S. litura*

To examine the oviposition preference of*S. litura,* the larvae were fed with artificial diet until pupae as described above. After pairing was placed in a separate container. Until the *S. litura* emerged, adult of *S. litura* were covered in a shroud, put three pairs in each cage, and at the same time, three*P. americana* and *P. icosandra* plants of the same size were placed along the diagonal in a cage (length x width xheight = 1m x 1m x 1m). The number of *S. litura* eggs on the plant leaves was observed and counted daily. Each cage was regarded as a replicate and thirteen replicates were performed for each test. The calculation method for the oviposition preference index is OPI = (the total number of eggs on plant A -the total number of eggs on plant B) / (the total number of eggs on plant A + the total number of eggs on plant B) .

Determination of detoxification enzyme activity

To test whether feeding on the invasive plant *P. americana* will effect the enzyme activity of *S. litura* , *P. americana*plants were put in the shroud and second-instar *S. litura* were placed on the leaves of the plant and allowed to feed until the fourth instar, three *P. americana* were placed in each cage(length x width x height = 0.75 m x 0.75 m x 0.75 m), four *S. litura* larvae were placed in each plant. In the same way, *P. icosandra* plants were placed in the cage for feeding *S. litura.* The preparation of the enzyme stock solution was based on the method of Chen et al. (2008). The activity of detoxifying enzymes, such as glutathione-S-transferase and acetylcholinesterase, were measured. The specific measurement method is based on the instructions of Glutathione S-transferdse (GSH-ST) assay kit (Colorimetric method) and Acetylcholinesterase assay kit Nanjing Jiancheng Bioengineering Research Institute.

Statistical analyses

Two-way analysis of variance (ANOVA) was used to test the effects on insect performance (i.e. larval weight) of each plant species. Others performance of *S. litura* pupal weight, egg numbers, development duration and OPI were compared by nonparametric t-test. Then, a one-way ANOVA was used, in which we analized intestinal detoxifying enzyme (i.e. AChE and GST) activity of*S. litura.* (SPSS 25.0, Armonk, NY, USA),.

Results

S. litura **prefers exotic non-invasive plant**

The *S. litura* larvae reared on the leaves of*P. americana* and *P. icosandra* had similar weights on day 12, 21 and 24 of larval development ($P > 0.05$), but the weight of *S. litura* bred on *P. icosandra* was higher than that of *P. americana* on the 15th and 18th days of larval development ($P < 0.005$) (Fig. 1). The development of the second-generation*S. litura* larvae ware similar to that of the first-generation larvae (Fig. 1). To sum up, the larvae reared on the leaves of *P. icosandra* weighed more than that of *P. americana* . The larvae of first and second generation all showed the same pattern. In addition, no matter which plant was used to feed the *S. litura*second-generation larvae weighed less than first-generation larvae (Fig. 1).

The pupal weight and egg number of *S. litura* reared with *P. americana* and *P. icosandra* were not significantly different in the laboratory ($P = 0.7861$) (Fig. 2A and B). There were significant differences between the developmental duration of *S. litura* feeding on isolated leaves of *P. americana* and *P. icosandra* , and the development period of *S. litura* reared on the leaves of *P. americana* was longer than that of *P. icosandra* (Fig. 2C, $P = 0.0147$).

Oviposition preference

In the choice test, although the number of eggs laid by *S. litura*on the *P. icosandra* and *P. americana* plants had no significant significance (Fig. 3A, $P = 0.1902$), *S. litura*females preferred to oviposit on *P. icosandra* can be find from oviposition preference index (OPI) (Fig. 3B, $P = 0.0103$). The environmental choice of female *S. litura* affects the survival rate of the next generation of larvae and the OPI can better reflect the preference of *S. litura* . Obviously, the OPI of *P. icosandra* is higher than that of *P. americana* (Fig. 3B), indicating that the female *S. litura* finds it more suitable for the development of larvae compared with *P. americana.*

Detoxification enzyme activity

The enzymes activity induced by the *P. americana* was higher than that of *P. icosandra* and artificial diet, but there was no significant in the enzyme activity of the latter two (Fig. 4A). GST activity was similar to the results of AChE activity test. Both had high activity when larvae were allowed to feed on *P. americana*. However, the activity of GST in the midgut of larvae fed artificial diets and *P. icosandra* in the determination of GST activity was small (Fig. 4B).**Discussion**The host plant quality has the impacts for insect's performance and preference (Awmack & Leather, 2002), larvae development was significant different between host plant species (Andrea et al., 2019). In addition, most invasive plants are phytochemically unique and suffer less herbivory than non-invasive plants (Cappuccino & Carpenter, 2005; cappuccino & Arnason, 2006). In this study, we investigated the larval performance of *S. litura*on *P. americana* and *P. icosandra,* the results show that the larval weight of *S. litura* was higher on *P. icosandra*than that on *P. americana* on days 15th and 18th of larval development (Fig. 1). On the whole, the larvae of *S. litura*develop better on *P. icosandra*, the development of the larvae from first and second generation showed the same results. This is consistent with most previous studies which have confirmed that phytophagous insects develop poorly on exotic invasive plants (Ditommaso et al., 2010; Dai et al., 2014). However, some results from other studies have found the opposite pattern, Fielding and Conn. (2011) demonstrate that native generalist herbivore *Melanoplus borealis*prefer to feed invasive weed *Crepis tectorum*. Possible explanation for these different results is due to species specific.*S. litura* could grow to the second generation when feeding on *P. americana* but its performance is worse, indicating that *p. americana* has a long-term effect on development of *S. litura.*There was no significant difference in the weight of the pupae of*S. litura* between the two plants, but *S. litura* that had fed on *P. icosandra* produced more eggs compared to *P. americana* (Fig. 2B). There may be because the nutrients provided by*P. americana* are not sufficient for the development of *S. litura* and there are many defensive substances in *P. americana*which have negative effects on *S. litura*. The types and quantities of nutrients and defensive substances can also affect the reproduction strategy of insects (Meghan et al., 2016), such as, the number and size of eggs and resource allocation (Awmack et al., 2002). The experiment of rearing *S. litura* larvae on the leaves of *P. americana* and *P. icosandra* was terminated in the second generation because of the death of the larvae and the larvae of third generation could not develop to pupae. In addition to the difference in the number of eggs laid by *S. litura*, the quality of the eggs should also be different, probably because the resources obtained by the eggs are relatively small and the later development is poor (Meghan et al., 2016), coupled with the influence of nutrients and defense substances, *S. litura* could maintain on *P. americana* just for two generations. In the future, we will monitor the population dynamics of *S. litura* on *P. americana* in the field with caged plants for several generations to confirm this conclusion. In the oviposition preference experiment, *S. litura* laid more eggs on *P. icosandra* plants compared with *P. americana*(Fig. 3A). This result was possibly influenced by the volatile organic compounds released by plants. Volatile organic compounds as an important source of information for insects and insects can judge the suitable of the host plants (i.e quality host) based on volatile organic compounds (Schoonhoven et al., 2005; Tasin et al., 2011) present. The *P. icosandra* and *P. americana* are similar in size, the seedlings used in this experiment were the same size. Therefore, it is unlikely that the oviposition location is selected based on the plant's sheltering function and may be because the two plants have different defense chemicals, *P. americana* contains more saponins (Yong et al., 2005), and subsequently less eggs were laid. According to the oviposition preference index of *S. litura*, it is considered that it prefers to lay eggs on the *P. icosandra* (Fig. 3B). It is more objective to judge the oviposition preference of insects based on the egg-laying quantity of insects only, as some insects will lay greater numbers of eggs on plants in order to improve their own fitness, even if this plant is not conducive to the survival of offspring (Mayhew, 2001). Therefore, when measuring the insect's oviposition preference, the egg production of the insect should be combined with the survival rate of the offspring (Despres et al., 2007). In this experiment, *S. litura* laid a large number of eggs on *P. icosandra* and during the development of the second generation of larvae, larvae of *S. litura* that fed on the *P. icosandra* showed higher performance, so the *S. litura* laid eggs more preferentially on *P. icosandra* compared to *P. americana*.

Detoxification enzymes are an effective strategy for insects responding to plant defense substances (Heckel, 2014). Insects convert toxic substances taken into the intestinal tract into more easily absorbed substances by increasing the enzyme activity in the body and at the same time remove unusable substances from the body to reduce damage to themselves (Xu et al., 2006). The detoxification enzymes of *S. litura* , which had been fed with *P. icosandra* , *P. americana* , and artificial diet were measured. The activity of AChE and GST of *S. litura*after feeding *P. americana* leaves was relatively higher. This demonstrated that the quantity of defensive chemicals in *P. americana* was higher than *P. icosandra* . Francis et al. (2005) tested the GST activity induced by*Myzus persicae* on secondary metabolites of Brassica plants, and the results showed that the higher GST activity of *Myzus persicae*may be for better adaptation to plant secondary metabolites such as glucosinolates and isothiocyanates (Wang et al., 2008). However, in this experiment, during the second generation of *S. litura* larvae, the larval detoxification enzymes were not measured due to the high larval mortality. The specific mechanism of long-term effects on *S. litura* was investigated by examining multiple generations. If the detoxification enzyme activity of the second generation of *S. litura* was different from that of the first generation, on the one hand, it can reflect the mechanism of the influence of *P. americana* , while on the other hand, it can also reflect the adaptation mechanism of *S. litura* on *P. americana* .

In summary, we found that native generalist *S. litura* prefer exotic no-invasive *P. icosandra* to invasive *P. americana*and its performance is poorly on *P. americana*. These results showed that the invasive plant *P. americana* has higher negative effect on the native herbivore *S. litura*. These findings have important implications for the evaluation of the impact of invasive plant *P. americana* on native herbivores in the local ecosystem.

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CONFLICT OF INTEREST

The authors have no competing interests.

AUTHOR CONTRIBUTION

LC: planed and designed the research(equal); performed experiments(equal); analyzed data and wrote the paper(equal).**ZL:** assisted to conduct the experiment(equal). **CC:**assisted to conduct the experiment (equal). **DFL:** planed and designed the research(equal); assisted to conduct the experiment(equal); revised the manuscript(equal). **YW:** planed and designed the research(equal); revised the manuscript(equal).

DATA AVAILABILITY STATEMENT

The all relevant data for this project may be found at*https://doi.org/10.6084/m9.figshare.13076882.v1* .

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