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Constitutive and induced resistance in soybean interact to affect the performance of a herbivore and its parasitoid

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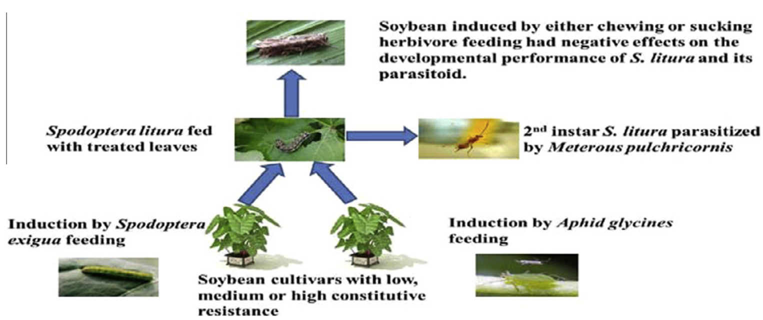
HIGHLIGHTS

- Herbivore-induced responses in soybean impair host and parasitoid development.
- Effects varied with level of constitutive resistance and herbivore feeding mode.
- The chewing herbivore had stronger inductive effects than the sucking herbivore.
- Herbivore treatments differed with low constitutive resistance, but similar with high.

GRAPHICAL ABSTRACT



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ABSTRACT

This study examined how the induced defenses of soybean cultivars that vary in levels of constitutive resistance affect the developmental performance of the tobacco cutworm, *Spodoptera litura*, and its parasitoid, *Meteorus pulchricornis*. Both soybean cultivars were injured to induce defenses by either the beet armyworm, *Spodoptera exigua*, or by the aphid *Aphis glycines*. Both types of feeding on soybean plants had a negative effect on *S. litura* development, extending development time, reducing larva-to-pupa survival and decreasing adult body size. The impact of induction treatments increased linearly with increasing levels of constitutive resistance. Induction by the chewing herbivore was stronger than induction by the sucking herbivore in negatively affecting developmental parameters at both low and medium levels of soybean constitutive resistance, but had similar impacts on *S. litura* survival and adult body weight at the high level of constitutive resistance. Induction by both chewing and sucking herbivores extended parasitoid development time and decreased survival and fecundity, with effects on both development time and fecundity increasing linearly with levels of constitutive resistance, but without any effect on offspring survival. Thus, induction by the two herbivore types differed in impact on parasitoid performance depending on the level of constitutive resistance expressed in the soybean cultivar. The chewing herbivore was more effective than the sucking herbivore at low and medium levels of constitutive resistance, but there were no differences in parasitoid performance at the high level of constitutive resistance. Overall, whereas both chewing and sucking herbivores had negative effects on the development of *S. litura* and its parasitoid, the chewing herbivore was more effective than the sucking herbivore at low and medium levels of constitutive resistance, but similar to it at the high level.

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1. Introduction

Plants have evolved a variety of resistance strategies and defensive mechanisms to protect themselves from damage by herbivores. Plants use both constitutive and induced defenses to influence herbivore settling, feeding, oviposition, development and reproduction. Constitutive defenses are physical and chemical traits that plants express regardless of the presence of herbivores, whereas induced defenses are expressed only following attacks by herbivores (Karban and Baldwin, 1997; Koricheva, 2002; Morris et al., 2006; Johnson, 2011). Both constitutive and induced defenses are costly, because nutrient resources are diverted from vegetative and reproductive functions to protective mechanisms (Baldwin and Preston, 1999). Therefore, plants must balance the need to survive immediate and subsequent feeding injury with the need to preserve plant vitality and reproductive success. A combination of constitutive and induced defenses can provide plants with some flexibility in this regard (Karban and Baldwin, 1997; Walling, 2000; Herms and Mattson, 1992). Many empirical studies have examined correlations between constitutive and induced defenses and demonstrated associations with other plant life-history traits (Kempel et al., 2011; Moreira et al., 2014).

Induced plant defenses are complex and can vary according to the feeding mode of the herbivore (Walling, 2000; Bidart-Bouzat and Kliebenstein, 2011; Ali and Agrawal, 2012). The genes activated upon herbivore attack are strongly correlated with the mode of herbivore feeding and the degree of tissue injury at the feeding site. While chewing insects such as caterpillars cause extensive tissue injury and predominantly activate the jasmonic acid (JA)-mediated signaling pathway, phloem-feeding insects such as aphids cause little injury to plant foliage and activate both the JA and the salicylic acid (SA)-dependent pathways (De Vos et al., 2005; Kessler and Baldwin, 2002). It has been suggested that some phloem-feeders can suppress the activation of plant defenses, given evidence that phloem-feeders suppress more genes than chewing herbivores (Sutter and Müller, 2011; Heidel and Baldwin, 2004; De Vos et al., 2005; Ali and Agrawal, 2012). When plants are sequentially attacked by herbivores from different feeding guilds, initial feeding by a sucking herbivore may make the plant more susceptible to subsequent feeding by a chewing herbivore. For example, when tomato, *Solanum lycopersicum* L., is attacked by the potato aphid, *Macrosiphum euphorbiae* (Thomas), and then fed to the beet armyworm, *Spodoptera exigua* (Hübner), the resulting caterpillars were heavier and had better survival when compared with controls (Rodriguez-Saona et al., 2010). It is therefore of interest to know if this induced susceptibility will vary in accordance with levels of constitutive resistance in the plant.

Parasitoid fitness is often tightly constrained by the quality of its host, which can affect parasitoid growth, survival and body size (Mackauer et al., 1997). Host quality is, in turn, closely correlated with the food quality of the host plant, which will vary with levels of constitutive resistance as well as plant responses induced by herbivore feeding. The resulting variation in plant quality may have tri-trophic impacts on herbivore-parasitoid interactions. Constitutively expressed plant secondary compounds are sometimes detrimental to the developmental performance of parasitoids due to the negative impacts of these chemicals on host quality (Hare, 2002; Ode, 2006) and the same is true for induced plant defenses (Havill and Raffa, 2000; Thaler, 1999, 2002). However, few studies have addressed the combined effects of constitutive and induced plant resistance on herbivore-parasitoid interactions (but see Bukovinszky et al., 2012), and scant attention has been given to how herbivores of different feeding guilds might modify interactions between constitutive and induced plant responses.

In this study, we investigated the combined effects of soybean constitutive resistance and herbivore-induced responses on interactions between a caterpillar host and its parasitoid. Three soybean cultivars expressing different levels of constitutive resistance were exposed to feeding by either beet armyworm, *S. exigua*, a generalist lepidopteran herbivore, or the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae). Following these treatments, soybean plants were supplied as food to a second herbivore, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) and these larvae were then parasitized by the solitary parasitoid *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae). *Spodoptera exigua* is a polyphagous leaf-chewing insect pest that has been shown to induce a jasmonate-regulated systemic response in tomato plants that increases the activity of several enzymes, including protease inhibitors (Fidantsef et al., 1999). *Aphis glycines* is an oligophagous phloem-feeding pest of soybean. It is native to Asia (Miao et al., 2005) and has caused severe injury to soybean following its North American invasion (Ragsdale et al., 2011). Aphid feeding often induces expression of pathogen-related proteins in plants (Walling, 2000). In eastern China, *A. glycines* infests soybean plants mostly during the summer, while *S. exigua* mainly colonizes plants in the fall, such that these pests almost never occur together (Cui et al., 1997; Li et al., 2000). The tobacco cutworm, *S. litura*, is a polyphagous herbivore that is one of the most economically important insect pests in Asia, feeding on 150 plant species, and it can inflict severe injury to soybean plants in summer and fall (Rao et al., 1993; Zhan and Gai, 2000). *Meteorus pulchricornis*, a thelytokous solitary endoparasitoid, attacks free-living lepidopteran larvae exposed on plant foliage (Maeto, 1989). Here, we observed the developmental performance of both the host and its parasitoid to answer the following question: Do soybean responses induced by either the chewing or the sucking herbivore vary depending on the level of constitutive resistance in the plant, with consequences for the herbivore-parasitoid interaction?

2. Materials and methods

2.1. Plants and insects

We obtained three soybean cultivars ("Lamar", "NN1138-2" and "JLNMH") from the National Soybean Germplasm Collection in Nanjing Agricultural University. These cultivars differ in the magnitude of constitutive resistance expressed to *S. litura* feeding, ranging from low (JLNMH), medium (NN1138-2), to high (Lamar), while being similar in other vegetative characters (Zhan and Gai, 2000; Wu et al., 2006). Soybean plants were grown in pots (20 cm in diameter × 18 cm in depth) in peat provided with compound fertilizer (Zhenjiang Xing Nong Organic Fertilizer Co., Ltd.) The pots were covered with gauze netting to prevent infestation by other organisms and maintained in the field. Soybean seeds were sown in sequential batches every five days from May 15 to June 24, 2012. To ensure enough food plants, each batch of each kind of soybean was grown in a dozen pots. Plants were used in experiments after reaching the V6–V7 growth stage, with each treatment equally represented in each batch.

Laboratory colonies of *S. litura* and *S. exigua* were established from collections made in the fall of the previous year in soybean fields from the suburb of Nanjing city (32.0°N and 118.7°E). Larvae were reared on artificial diets (Shen and Wu, 1995) in incubators at 25 °C ± 1, 60 ± 10% RH, and 14:10 (L:D) photoperiod. Adult moths were supplied with 10% honey solution on a cotton ball, refreshed daily, and provided paper strips as a substrate for oviposition. *Aphis glycines* was collected in soybean fields from the suburb of Nanjing city (32.0°N and 118.7°E) in 2011 and maintained thereafter on