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# Host plant effects on generalist and specialist lepidopterous cabbage pests modulated by organic soil amendment

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ABSTRACT

An organic product of earthworm digestion upon organic matter (vermicompost) has been shown to increase plant growth, production, and resistance to a variety of pests. However, the mechanisms of resistance effective against different insect species still need to be fully characterized. Furthermore, host plant resistance to herbivory has been shown to affect natural enemies yet, this has not been investigated for vermicompost-mediated resistance. For these reasons, we tested the effects of plants grown in various vermicompost concentrations on the preference (antixenosis) and performance (antibiosis) of a generalist (*Helicoverpa zea* Boddie) and specialist (*Pieris rapae* L.) lepidopterous cabbage pests. We also tested the generalist parasitoid, *Cotesia marginiventris* Cresson responses to *H. zea* feeding on vermicompost grown plants. Insect preference was evaluated in leaf disc larval and whole plant oviposition choice assays. After 24 h of feeding, *H. zea* larvae showed no aversion for any vermicompost treatment or leaf age, and *P. rapae* larvae consumed more of younger leaves indiscriminate of vermicompost treatments. There was also no antixenosis effects against *P. rapae* adults, which oviposited significantly more on plants grown on 60% vermicompost. Potential detrimental effects on performance was also evaluated in no-choice larval development assays. No significant treatment effects were found for *H. zea* development; however, vermicompost treatments had a significant negative effect on *P. rapae* survival. Vermicompost treatments did not have an effect on attraction or development of the parasitoid *C. marginiventris.* Results from this study suggest that the mechanism of resistance mediated by vermicompost is antibiosis, which results in lower performance and death of the specialist, but not the generalist insects tested in this study. Furthermore, this resistance appears to be caused by factors other than nutrient levels in plant tissue.

## Introduction

Organic composts, such as vermicomposts (the product of earthworm digestion) are rich in available nutrients and therefore, provide viable alternatives to synthetic inputs for crop production. Vermicomposts also contain high microbial activity and nutritional content, which promote plant growth and health (Gajalakshmi and Abbasi 2002; Gutiérrez-Miceli et al. 2007; Zaller 2007). For example, potting soil amended with vermicompost significantly increased the leaf area, nutrient and mineral content of spinach, *Spinacia oleracea* L. (Peyvast et al. 2008). Pepper, *Capsicum annuum* L., tomato, *Lycopersicum esculentum* L., and strawberry, *Fragaria* × *ananassa* Duchesne yields were also increased by amending soil with vermicompost (Arancon et al. 2004a; Arancon et al. 2004b; Arancon et al. 2006; Gutiérrez-Miceli et al. 2007). In addition to increasing yield, this substrate can increase plant resistance to pests. Population growth and damage by arthropods such as spider mites, *Tetranychus urticae* (Trombidiformes: Tetranichidae) C.L. Koch, mealybugs, *Pseudococcus* sp. (Hemiptera: Pseudococcidae), and green peach aphids, *Myzus persicae* Sulzer (Hemiptera: Aphididae), have been linked to soil amended with vermicompost (Arancon et al. 2005; Arancon et al. 2007; Edwards et al. 2010). Feeding on vermicompost-grown plants also led to poor performance of a generalist caterpillar, *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) on *Arabidopsis thaliana* (Cardoza 2011).

Host plant resistance can affect insects by making plants less attractive or tasteful to insects (antxenosis) or by having toxic effects that negatively impact insect performance (antibiosis). Plant resistance may also be differentially elicited depending on the host range and feeding habits of attacking insects. For example, aphids feed by tapping into sieve tube elements in the vascular tissue of plants; whereas caterpillars consume the entire leaf tissue and different chemical factors confer host plant resistance against these two types of insect pests (Howe and Jander 2009). Also, plant defensive compounds are generally more effective against generalist insect herbivores than specialist species which have adaptive mechanisms to circumvent, detoxify or sequester these

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compounds from their host plant (Wittstock and Halkier 2002; Ratzka et al. 2002). However, in a recent study, vermicompost was found to cause antibiosis resistance effective against two phloem-sucking aphid pests of cole crops: the generalist *M. persicae* and the specialist cabbage aphid, *Brevicoryne brassicae* L. (Hemiptera: Aphididae) (Little et al. 2011). Vermicompost-mediated resistance mechanisms to specialist and generalist chewing insects on the same plant have not yet been evaluated.

Plant resistance can affect natural enemies and such effects can be either positive or negative (Braman et al. 2004; Francis et al. 2001; Sarfraz et al. 2009). Plant defenses against insect herbivores serving as cues to natural enemies have been documented in various plant systems (i.e., Turlings et al. 1991a; Turlings et al. 1991b; Cardoza et al. 2003). Induced defenses to herbivory can also negatively impact natural enemies: Thaler (2002) found that induced tomato plants (*Lycopersicon esculentum*) had fewer syrphid fly eggs and negatively affected parasitism rate by *Hyposoter exiguae* (Hymenoptera: Ichneumonidae). On the other hand, vermicompost is a rich nutrient source (Cardoza 2011) and nutrient availability to the plant may enhance parasitoid performance (Sarfraz et al. 2009; Moon et al. 2000). Plants may also emit volatile compounds in response to insect damage which attract predators and parasitoids (Van Poecke et al. 2001; Mattiacci et al. 1994). Therefore, it is possible for vermicompost to influence parasitoid response and performance by altering direct (non-volatile) and indirect (volatile) plant responses to caterpillar herbivory.

For all the above reasons, this study was undertaken to: (1) evaluate host plant resistance to chewing insect pests differing in their host range, (2) determine if this resistance is due to antixenosis (non-preference) and/or antibiosis (negative biological effects, (3) ascertain potential impacts of vermicompost-resistance on the searching behavior and performance of *Cotesia marginiventris* Cresson (Hymenoptera: Bracconidae), a parasitoid of caterpillars of the family Noctuidae, on plants damaged by *H. zea* larvae, and (4) evaluate potential role of nutritional composition of soil and plant tissue in these plant–insect interactions. To test for resistance mechanisms against the herbivores, we evaluated preference and performance of generalist (*H. zea*) and specialist (*P. rapae*) lepidopterous cabbage pests. In addition, effects of vermicompost-mediated resistance on parasitism rate, survival and development of the wasp on *H. zea* hosts fed on plants grown in control (no-vermicompost) and vermicompost-amended soil were evaluated. We hypothesized that vermicompost will positively affect the preference and performance of the specialist *P. rapae* and negatively affect the preference and performance of the generalist *H. zea*. We also expect that vermicompost treatment will affect searching behavior and performance of *C. marginiventris.* To test for antixenosis and antibiosis effects we evaluated direct plant resistance based on the feeding preference and performance of the aforementioned pests on vermicompost-grown plants. We also expect that increased nutrient availability afforded by vermicompost amendment will help explain any effects found in insect responses to the various treatments.

## Materials and methods

### *Plant and insect rearing*

Cabbage, *B. oleracea* var. *capitata* ‘Early Jersey’ seeds were planted in 6-in. pots in Sun-Gro Redi-Earth (Sun Gro Horticulture) potting mix amended with 0 (control), 20, 40 or 60% food based vermicompost (Oregon Soil Corporation, Portland, OR). Plants were grown in environmentally controlled chambers with a 10:14 h light:dark cycle and maintained at 22:20 °C, respectively. Plants where watered with 100 ml of deionized water every day; all plants received 100 ml of Hoagland’s nutrient solution instead of water once a week. Plants were used for the experiments when they reached their 8th or 10th true-leaf stage.

Corn earworms, *H. zea*, and imported cabbageworms, *P. rapae* were raised individually on artificial diet in an incubator maintained at 25 ± 2 °C and 10:14 h L:D until needed for the experiments at either their 3rd instar or adult stages.

The parasitoid wasps, *C. marginiventris*, were originally obtained from a colony maintained by Dr. John Ruberson’s laboratory (University of Georgia, Department of Entomology, Athens, GA) and were subsequently reared on *H. zea* larvae from the colony mentioned above. Adult wasps were supplied with 10% sugar water and deionized water. One hundred fifty 1st to 2nd instar larvae were placed on cabbage leaves inside each cage for the adult wasps to oviposit upon every 48 h. After 2 days larvae were taken out of the cage and placed on artificial diet (5 per cup). Cocoons produced from each batch were transferred from diet cups to a wasp emergence cage as they were formed. Wasps and parasitized caterpillars were kept in a room maintained at 25 ± 2 °C and 10:14 h L:D.

### *Larval feeding choice assays*

Immature feeding assays were performed to determine if vermicompost-mediated host plant resistance is due to antixenosis effects. Vermicompost treatments used for these experiments were 0 (control), 20, 40 and 60% vermicompost. Immature feeding preference for vermicompost treatment was evaluated using a four-choice leaf disc (2.5 cm diam.) assay. Plants used to obtain the discs were representative from each treatment and leaf discs were taken from either the second oldest (Old) or second youngest (Young) leaves from plants at the 8th true-leaf stage. Discs were weighed, and placed atop two layers of no. 1, 9 cm Whatman filter paper (Fisher Scientific, Pittsburgh, PA) moistened with 4 ml of deionized water in a plastic Petri dish (14 cm diam.). Four leaf discs, one from each of the treatments, were randomly placed in one of four positions, equidistant from each other and the center of the dish. Each plate arena received discs from either young or old leaves from all treatments. Two-third instar caterpillars (either *H. zea* or *P. rapae*) were placed in the center of the dish. The dish was covered and placed in the incubator where insects were reared. Larvae were allowed to feed freely on the discs for 24 h. Leaf discs were weighed before and after insect feeding to determine percent tissue consumed for each leaf disc. These experiments were set up using complete randomized block design containing four randomly spaced 4-way choice blocks (to control for any positional effects within the growth chamber) and were repeated over time (trial) using new sets of plants and insects to obtain a total of 24 replicates for each insect species. Each block was made up of a Petri dish containing four leaf discs, one replicate from each treatment.

### *Adult oviposition choice assays*

Adult oviposition assays were performed to determine if vermicompost-mediated host plant resistance is due to antixenosis effects against this insect stage. Two mated pairs of 2–3-day-old *H. zea* or *P. rapae* adults were released into a 1 m × 1 m × 1 m PVC-framed cage covered with a translucent mesh. Each cage contained one plant (10 true leaves) from each of the control (0), 20, 40 and 60% vermicompost treatments (4 plants total). Plants were randomly assigned to each corner of the cage. Four replicates were conducted in each of 3 trials (different dates) for a total of 12 replicates per insect species. The experiment was run under greenhouse conditions, 14:10 L:D and 25 ± 5 °C. Adults were allowed to oviposit for 48 h after which, plants were collected and the number of eggs