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Effect of tomato leaf traits on the potato tuber moth and its predominant larval parasitoid: A mechanism for enemy-free space

Bayeh Mulatu [a], Shalom W. Applebaum [b], Moshe Coll [b,*]

[a] *Ethiopian Agricultural Research Organization, P.O. Box 2003, Addis Ababa, Ethiopia*
[b] *Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot 76100, Israel*

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Abstract

Tomato plants are thought to provide the potato tuber moth (PTM), *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), with enemy-free space. The present study was aimed at assessing the role of plant surface factors in lowering enemy activity or efficiency on tomato plants. Specifically, we tested: (i) the compatibility of plant resistance traits and parasitoid activity in tomato; (ii) whether tomato leaf surface factors affect the main parasitoid species of PTM larvae to a larger extent than they would the host; and (iii) whether plant traits act on the parasitoid directly or indirectly, through the host. Results indicate that the settling response of PTM neonates on tomato leaves was not affected by trichome density and was similar on the three tested tomato cultivars. The parasitoid *Diadegma pulchripes*, however, failed to parasitize PTM larvae actively feeding in tomato leaves, whereas it successfully parasitized 46% of larvae feeding in potato leaves. Yet the parasitoid was not affected by the plants indirectly, through the hosts; both tomato- and potato-fed larvae were equally accepted by and suitable for the parasitoid when offered in the absence of the host plants. It can be concluded that factors associated with tomato leaves, such as glandular trichomes, have no effect on the larval establishment of PTM on the plant, but they do have a direct adverse effect on *D. pulchripes*, the primary PTM biological control agent in the system. In cultivated tomato, therefore, leaf traits which may confer resistance to generalist herbivores but not to the oligophagous PTM may not be compatible with natural enemies of these pests.

Keywords: *Diadegma pulchripes*; *Phthorimaea operculella*; Glandular trichome; Tomato; Enemy-free space; Host plant resistance; Biological control

1. Introduction

Pest species are often found to exploit plants or plant parts on which their performance is sub-optimal (review by Thompson, 1988). This could be, in part, to escape from competitors, predators, or parasitoids (Bernays and Graham, 1988). A plant is said to supply "enemy-free space" (EFS) to an insect if it provides a higher degree of protection against natural enemies than does an alternative host plant (Jeffries and Lawton, 1984). Results of a recent study strongly suggest that tomato plants provide the potato tuber moth (PTM), *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae), with enemy-free space (Mulatu et al., 2004). It appears that the pest has only recently included tomato into its host range (Mulatu et al., 2004), and that neither the pest nor its natural enemies have had sufficient time to adapt to tomato. It is not clear, however, which plant factors negatively affect PTM enemies, providing refuge for the pest in tomato. Such plant factors are expected to have a stronger effect on the natural enemies than on their PTM host. The present study was aimed at testing the role of some tomato traits in these interactions.

Leaf trichomes are one of the most important morphological defense traits in plants (Smith et al., 1994; Valverde et al., 2001 and references therein). Foliage of wild and cultivated tomato genotypes is covered with both glandular

* Corresponding author. Fax: +972 8 946 6768.
E-mail address: coll@agri.huji.ac.il (M. Coll).

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and non-glandular trichomes. In wild tomato, trichomes contain toxic chemicals and exude chemical mixtures, gummy or sticky substances, that impede the ability of insects to feed, move, and survive on the plants (review by Duffey, 1986 and Kennedy, 2003). For example, foliar trichomes on the wild tomato *Lycopersicon hirsutum f. glabratum* C.H. Mull possess antixenosis and antibiosis resistance against a number of tomato pests, including the tobacco flea beetle and greenhouse whiteflies (Gentile and Stoner, 1968a,b); spider mites (Aina et al., 1972); the Solanaceae-specific *Manduca sexta* (L.); the polyphagous *Heliothis zea* (Boddie) (Kennedy and Yamamoto, 1979; Farrar and Kennedy, 1987a,b) and *Helicoverpa armigera* (Hubner) (Rath and Nath, 1995; Sivaprakasam, 1996); the pink potato aphid, *Macrosiphon euphorbiae* (Musetti and Neal, 1997); and the potato tuber moth, *P. operculella* (Zeller) (Gurr and McGrath, 2001).

Host plant resistance to insects and mites has been attributed primarily to Luckwill's (1943) type VI glandular trichome (Snyder and Carter, 1984); both the quantity and chemical characteristics of these structures have been found to be important. Type VI glandular trichomes are the most abundant type in both wild and cultivated tomato species (Duffey, 1986; Farrar and Kennedy, 1987a). In the wild tomato *L. hirsutum f. glabratum*, this trichome type has been confirmed to contain methyl ketones 2-tridecanone (Williams et al., 1980) and 2-undecanone (Farrar and Kennedy, 1987b; Farrar et al., 1994), and the low molecular weight phenolics rutin and chlorogenic acid (Duffey, 1986) all of which are allelochemicals adversely affecting herbivorous insects. No appreciable levels of the two methyl ketones were found in type VI glandular trichomes of the cultivated tomato, cv. Better boy (Barbour et al., 1993; Dimock and Kennedy, 1983).

Type VI glandular trichomes in wild tomato have an adverse effect on natural enemies (Kashyap et al., 1991; Farrar et al., 1992, 1994). For example, parasitism of *Heliothis* spp. egg by *Trichogramma* spp. was significantly lower on wild than cultivated plants (Kauffman and Kennedy, 1989). Some evidence suggests similar adverse effects of leaf trichomes on natural enemies on cultivated tomato plants. Baggen and Gurr (1995) compared the adverse effect of foliar pubescence of different solanaceous species on *Copidosoma koehleri*, an egg-larval parasitoid of PTM. They observed trichome-related wasp entrapment on the leaves of tomato, *Lycopersicon esculentum*, compared to the other tested plant species.

The objective of the present study was, therefore, to test the possible effects of leaf traits on PTM and its predominant hymenopteran parasitoid, *D. pulchripes* (Kokujev) (Hymenoptera: Ichneumonidae) on three cultivated tomato genotypes characterized with different trichome densities. Specifically, we tested: (i) the compatibility of plant resistance traits and parasitoid activity in tomato; (ii) whether tomato leaf surface factors affect the main parasitoid species of PTM larvae to a larger extent than they would the host; and (iii) whether plant traits act directly on the parasitoid, or indirectly through the host.

2. Materials and methods

2.1. Insects and plants

Cherry, processing and fresh market tomatoes (Ceres, Serio and Marglobe cultivars, respectively) were transplanted into experimental plots (10×30 m) at the Melkassa experimental station in Ethiopia (39°21′E 8°26′N). For the laboratory experiments, foliage was collected when the plants were at the pre-blossom and blossom (at ca. 50% flowering) stages (95 and 121-day-old tomato plants, respectively).

A culture of *P. operculella* was established from ca. 300 field-collected larvae and maintained in a walk-in rearing room at 24 ± 1 °C, 14:10 L:D, following the protocol of Platner and Oatman (1968). Larvae developed in potato tubers and adults were fed a 10% sucrose solution from cotton wicks. A *D. pulchripes* culture was started with ca. 50 wasps reared from field-collected PTM larvae. The wasps were offered PTM larvae in potato tubers and kept at 24 ± 1 °C and 14L:10D. Voucher specimens of the pest and parasitoid were deposited in the Department of Entomology, the Hebrew University of Jerusalem, Rehovot, Israel.

2.2. Effect of tomato leaf trichomes on settling of PTM neonates

A pair of fully expanded leaves was cut from ten randomly selected plants from each of the three tomato cultivars. One leaf from each pair was used to determine trichome density and the second for assaying the ability of neonate larvae to settle on leaves with intact trichomes. To determine trichome density, we cut five leaf discs (10 mm ∅) out of each test leaf, at random locations. The number of non-glandular and type VI glandular-head trichomes on the abaxial and adaxial surfaces were determined under a stereomicroscope. This procedure was repeated for leaves collected from plants at the pre-blossom and blossom stages.

To determine the ability of PTM neonates to settle on tomato leaves, we conducted a non-choice test using two sets of leaflets. The first set of leaflets was kept intact, whereas the second set was washed with 0.1% Triton X-100 solution (Sigma), a non-phytotoxic detergent that removes trichomes and their contents as well as all other leaf-surface-linked chemicals. The leaflets were placed individually in Petri dishes lined with moist filter papers and were supplied with water in cotton wick. Five naïve PTM neonates (i.e., not previously exposed to plants) were placed on each leaflet. Four hours later, the settling behavior of the neonates was assessed under a stereomicroscope. A larva was considered fully settled when observed feeding while its entire body was concealed under the leaf sheath. The experiment was replicated ten times for each leaf surface (abaxial