

RAPID COMMUNICATION

METHYL JASMONATE APPLICATION INDUCES
INCREASED DENSITIES OF GLANDULAR
TRICHOMES ON TOMATO,
Lycopersicon esculentum

ANTHONY J. BOUGHTON,* KELLI HOOVER, and GARY W. FELTON

Department of Entomology, Pennsylvania State University, University Park,
PA 16802, USA

(Received March 21, 2005; revised May 31, 2005; accepted June 2, 2005)

Published Online July 5, 2005

Abstract—This study was designed to address whether applications of methyl jasmonate (MJ) or Benzothiadiazole (BTH) to cultivated tomato, *Lycopersicon esculentum*, induced elevated densities of defense-related glandular trichomes on new leaves. Four-leaf tomato plants were sprayed with MJ, BTH, or control solutions, and the density of type VI glandular trichomes on new leaves was subsequently determined at 3, 7, 14, 21, and 28 d. At 7, 14, and 21 d, the density of type VI glandular trichomes on new leaves was significantly higher on MJ-treated plants than on BTH- or control-treated plants. At 7 and 14 d after treatment, the mean density of glandular trichomes on new leaves of MJ-treated plants was ninefold higher than on leaves of control-treated plants. We observed entrapment of immature western flower thrips in trichomes on MJ-treated plants at higher rates than on BTH or control plants. Studies to evaluate potential trade-offs between reductions in pest populations by increased trichome density and possible negative impacts of trichome induction on biological control agents are needed.

Key Words—*Lycopersicon esculentum*, tomato, methyl jasmonate, induced resistance, glandular trichomes.

* To whom correspondence should be addressed. E-mail: ajb25@psu.edu

INTRODUCTION

Plants have evolved numerous defensive strategies to reduce herbivory or its effects on plant fitness (Karban and Baldwin, 1997). These defenses may be constitutively expressed or may be induced following attack by herbivorous arthropods. Induced responses to herbivory have been widely documented and may involve changes in plant secondary chemistry, reductions in plant nutritional quality, emission of volatiles that attract predators and parasitoids of herbivores (Kessler and Baldwin, 2002), or increases in trichome density (Traw and Dawson, 2002). Responses to herbivores may be mediated by the jasmonic acid (JA) or salicylic acid (SA) signaling pathways (Kessler and Baldwin, 2002).

Trichomes occur on the surfaces of many plants and can make a contribution to plant resistance against herbivores (Simmons and Gurr, 2004). Trichomes play important roles in arthropod resistance within the plant family Solanaceae and particularly within the genus *Lycopersicon* (Kennedy, 2003). Seven types of trichomes occur on *Lycopersicon* spp., including glandular trichomes (types I, IV, VI, and VII) and nonglandular trichomes (types II, III, and V) (Luckwill, 1943). Glandular trichomes have heads containing various sticky and/or toxic exudates that may be secreted onto the plant surface or may rupture on contact with herbivores, causing irritation, entrapment, or death (Simmons and Gurr, 2004). Nonglandular trichomes do not have heads and affect herbivores by mechanically obstructing their movement across the plant surface (Simmons and Gurr, 2004). Four-lobed type VI glandular trichomes are associated with high levels of arthropod resistance in *L. esculentum* (Kennedy, 2003).

Recent studies of the tomato mutant *jasmonic acid insensitive 1* [*jai1*], which is defective in JA-based signaling, revealed several defense-related phenotypes, including abnormal glandular trichome production, suggesting a role for JA in glandular trichome-based defenses (Li et al., 2004). JA was recently shown to induce trichomes in *Arabidopsis* (Traw and Bergelson, 2003).

To our knowledge, jasmonates have not previously been demonstrated to induce elevated trichome densities in tomato. In preliminary studies, we found applications of methyl jasmonate (MJ) and BTH (Actigard™) to tomato reduced populations of *Myzus persicae* (Sulzer) (Homoptera: Aphididae) in the greenhouse (Boughton et al., unpublished data). Here, we present evidence showing that exogenous application of methyl jasmonate, but not BTH, induced dramatic increases in densities of type VI glandular trichomes on new leaves of *L. esculentum*. We suggest that resistance to herbivores induced by these elicitors probably operate by different mechanisms.

METHODS AND MATERIALS

Plants. Tomato plants (*L. esculentum* c.v. Trust) (DeRuiter Seeds) were grown in 4-in. plastic pots in sterile soil mix (peat-perlite-vermiculite, 55–20–25; Penn State Seed, Dallas, PA, USA). Plants were grown in the greenhouse under natural lighting with day and night temperatures varying between 21 and 33°C. Plants were irrigated daily with fertilizer solution (N–P–K, 4–18–38, Chem-Gro Tomato Formula; Hydro-Gardens Inc., Colorado Springs, CO, USA) containing supplemental magnesium sulphate and calcium nitrate.

Effect of Elicitors on Induction of Glandular Trichomes. Fourth-leaf tomato plants (45 per treatment) selected at random were treated with (1) 7.5 mM MJ (Bedoukian Research, Danbury, CT, USA), or (2) 0.1 mM BTH (Actigard®-Syngenta, Greensboro, NC, USA) (both in 0.8% ethanol and water), or (3) control solution (0.8% ethanol and water). Elicitor concentrations were within the range used in other studies and were selected in dose response trials as the lowest concentrations that induced resistance. Plants receiving different treatments were moved to opposite sides of the greenhouse and sprayed until leaves were saturated. After 24 hr, plants were arranged on three benches according to a randomized block design. At 3, 7, 14, 21, and 28 days post-treatment (DPT), three plants from each treatment were selected at random on each of the three benches, and the youngest terminal leaflet at least 5 cm in length on each plant was removed for sampling. This leaf selection process yielded terminal leaflets of similar sizes, which ranged from 5.8 to 8.0 cm in length, and 11.7 to 21.8 cm² in area. Two leaf disks (0.6 cm diam.) were punched midway between the leaf tip and leaf base, one on either side of the midrib, taking care to preserve trichomes on the upper leaf surface. Numbers of

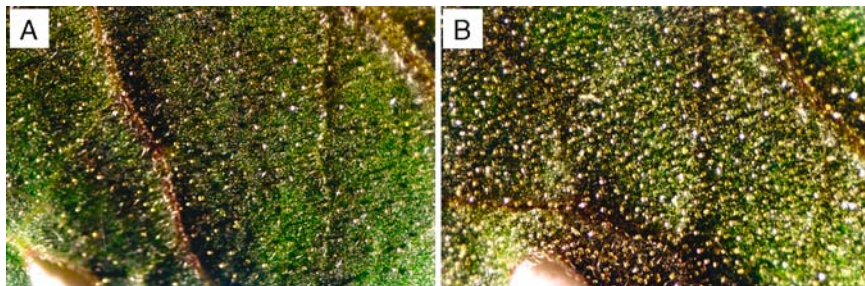


FIG. 1. Type VI glandular trichomes on upper surface of leaves from (A) control or (B) MJ-treated tomato plant at 12 DPT. Photographs show same field of view at 15× magnification.

TABLE 1. EFFECT OF ELICITOR TREATMENT ON GLANDULAR TRICHOME DENSITY ON NEW TOMATO LEAVES

Time point ^b (DPT)	Mean trichome density ^a (no./mm ² ± SE)			<i>P</i> value ^c
	Control-treated	BTH-treated	MJ-treated	
3	0.7 ± 0.1 a	0.8 ± 0.1 a	0.9 ± 0.1 a	0.105
7	1.1 ± 0.2 a	1.5 ± 0.3 a	9.4 ± 0.9 b	<0.001
14	2.1 ± 0.2 a	2.2 ± 0.4 a	17.9 ± 1.8 b	<0.001
21	3.1 ± 0.4 a	3.7 ± 0.4 a	12.5 ± 1.0 b	<0.001
28	5.3 ± 0.7 ab	4.7 ± 0.6 a	7.2 ± 0.5 b	0.027

MJ = Methyl jasmonate, BTH = Benzothiadiazole.

^a Mean density of type VI glandular trichomes on upper surface of new leaves. *N* = 9 plants per treatment. One leaf examined per plant. Plants sampled only once. Densities calculated from counts of trichomes on two leaf disks per leaf. Means within the same row followed by different letters are significantly different by Tukey's test (*P* < 0.05).

^b Days post-treatment (DPT).

^c One-way ANOVA evaluating effect of treatment on trichome density.

type VI trichomes were determined by using a dissecting scope. Preliminary observations had suggested MJ treatments increase type VI trichome density. Other trichome types were not examined in this study. Plants were sampled only once. Trichome density data were evaluated with one-way ANOVA.

RESULTS

Results showed that application of MJ to tomato plants induced increased densities of type VI glandular trichomes on new leaves expanding after treatment (Figure 1). BTH treatment had no effect on trichome densities (Table 1). Highest densities of trichomes were present on leaves produced 14 d after MJ treatment. At 7 and 14 DPT, trichome densities were ninefold higher on MJ- than control-treated plants. Trichome densities were significantly higher (Tukey's test, *P* < 0.05) on MJ plants than on BTH or control plants at 7, 14 and 21 DPT. MJ-treated plants were observed to entrap higher numbers of immature western flower thrips than BTH- or control-treated plants (Boughton et al., unpublished data).

DISCUSSION

Increasing interest has focused on the use of elicitors of natural plant defensive responses, such as JA and MJ, to induce resistance to herbivores and

plant pathogens (Thaler, 1999). In tomato, jasmonate-induced resistance to herbivores has been documented in several field studies and has frequently been attributed to the action of defensive proteins such as polyphenol oxidase and proteinase inhibitors (Thaler, 1999). These proteins are induced within 24 hr of elicitor treatment, before any changes in type VI trichome density are detectable. However, over subsequent weeks it seems likely that a component of jasmonate-induced resistance may be a result of increased densities of type VI glandular trichomes, contributing to elevated polyphenol oxidase levels and increased repellency, entrapment, or mortality of arthropod herbivores. We suggest that elevated trichome densities were likely responsible for increased thrips entrapment observed in our studies.

Although it is likely that jasmonate-induced resistance in crop plants will have direct negative impacts on arthropod pests, which may be beneficial from a pest management perspective, it is also possible that induced plant defenses may have indirect effects on natural enemies, such as insect parasitoids and predators, which contribute to the regulation of pest populations (Thaler, 1999; Simmons and Gurr, 2004). Trichomes, for example, may have differing impacts on natural enemies ranging from positive effects, such as increased searching efficiency, to negative effects, such as hindered movement, irritation by trichome exudates, and entrapment (Obrycki, 1986).

The use of jasmonates to induce plant resistance to arthropod pests as a management tactic will require careful evaluation to ensure that benefits arising from negative impacts on pest fitness are not outweighed by adverse effects that might reduce the efficacy of biological control.

Acknowledgments—This research was funded by Pennsylvania Department of Agriculture (Contract ME 442289).

REFERENCES

- KARBAN, R. and BALDWIN, I. T. 1997. Induced Responses to Herbivory. University of Chicago Press, Chicago.
- KENNEDY, G. G. 2003. Tomato, pests, parasitoids, and predators: Tritrophic interactions involving the genus *Lycopersicon*. *Annu. Rev. Entomol.* 48:51–72.
- KESSLER, A. and BALDWIN, I. T. 2002. Plant responses to insect herbivory: The emerging molecular analysis. *Annu. Rev. Plant Biol.* 53:299–328.
- LI, L., ZHAO, Y., MCCAIG, B. C., WINGERD, B. A., WANG, J., WHALON, M. E., PICHESKY, E., and HOWE, G. A. 2004. The tomato homolog of CORONATINE-INSENSITIVE1 is required for the maternal control of seed maturation, jasmonate-signaled defense responses, and glandular trichome development. *Plant Cell.* 16:126–143.
- LUCKWILL, L. C. 1943. The genus *Lycopersicon*: A historical, biological and taxonomic survey of the wild and cultivated tomato. *Aberd. Univ. Stud.* 120:1–44.

- OBRYCKI, J. J. 1986. The influence of foliar pubescence on entomophagous species, pp. 61–83, in D. J. Boethel and R. D. Eikenberry (eds.). *Interactions of Plant Resistance and Parasitoids and Predators of Insects*. Ellis Horwood, Chichester.
- SIMMONS, A. T. and GURR, G. M. 2004. Trichome-based host plant resistance of *Lycopersicon* species and the biocontrol agent *Mallada signata*: are they compatible? *Entomol. Exp. Appl.* 113:95–101.
- THALER, J. S. 1999. Jasmonate-inducible plant defences cause increased parasitism of herbivores. *Nature* 399:686–688.
- TRAW, M. B. and BERGELSON, J. 2003. Interactive effects of jasmonic acid, salicylic acid, and gibberellin on induction of trichomes in *Arabidopsis*. *Plant Physiol.* 133:1367–1375.
- TRAW, M. B. and DAWSON, T. E. 2002. Reduced performance of two specialist herbivores (Lepidoptera: Pieridae, Coleoptera: Chrysomelidae) on new leaves of damaged black mustard plants. *Environ. Entomol.* 31:714–722.