Tomato, Pests, Parasitoids, and Predators: Tritrophic Interactions Involving the Genus *Lycopersicon*

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■ **Abstract**   Insect-plant interactions involving the cultivated tomato and its rela-
tives in the genus *Lycopersicon* have been intensively studied for several decades,
resulting in one of the best documented and in-depth examples of the mechanistic
complexities of insect-plant interactions, which encompass both herbivores and their
natural enemies. Trichome-mediated defenses are particularly significant in *L. hirsutum
f. glabratum* and have been extensively implicated in negative tritrophic effects medi-
ated by direct contact of parasitoids and predators with trichomes, as well as indirect
effects mediated through their hosts or prey. Both constitutive and inducible defense
traits of *L. esculentum* exert effects on selected parasitoids and predators. The effects
of any particular plant defense trait on parasitoids and predators depend on the specific
attributes of the plant trait and the details of the physical, biochemical, and behavioral
interaction between the natural enemy, its host (prey), and the plant.

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INTRODUCTION

The cultivated tomato, *Lycopersicon esculentum*, is attacked by a number of seri-
ous arthropod pests (81). During the past 25 years, considerable research has been
directed toward identifying and developing a mechanistic understanding of traits

that confer pest resistance within the genus *Lycopersicon*. That body of research reveals a level of detail and complexity in plant-herbivore-natural enemy interactions that is unique among well-studied systems involving crop plants and their close relatives. This review focuses primarily on defensive traits in *L. esculentum* and *L. hirsutum f. glabratum* and their interactions with several pests of tomato and some of the parasitoids and predators that attack them. General reviews of relevant aspects of tritrophic interactions are presented in (9b, 121a). Farrar & Kennedy (32) provide a more complete overview of resistance traits in *Lycopersicon*. For information on genetics, breeding, biology, and production of tomato and its relatives see (65, 89).

The genus *Lycopersicon* is characterized by great diversity within and among its nine species (65, 87). Arthropod resistance has been studied most intensively in *L. esculentum*, *L. hirsutum*, and *L. pennellii*. Of these, the highest levels of resistance to the greatest number of arthropod species are found in *L. hirsutum f. typicum* (= *hirsutum*) and *L. hirsutum f. glabratum* (32). There is extensive variation in the spectrum and level of arthropod resistance among accessions of these species. Arthropod resistance has been associated with a diverse array of traits, including the physical and chemical properties of glandular trichomes, and constitutively expressed and wound-induced chemical defenses associated with the leaf lamella (33, 39, 113). Resistance traits in each of these categories exert effects on the third trophic level. Although the genetics and mechanisms of arthropod resistance in *L. pennellii* and *L. hirsutum f. typicum* have been studied extensively, tritrophic effects of resistance traits in these species have received little attention. Hence, neither species is treated in detail in this review. It must be pointed out, however, that the potential exists for effects such as those described below for *L. hirsutum f. glabratum* to occur in other highly defended *Lycopersicon* species.

TRICHOMES AND DEFENSE IN *LYCOPERSICON*

Trichomes, both glandular and nonglandular, are prominent features of the foliage and stems of *Lycopersicon* spp. Four types of glandular trichomes occur most commonly (85). Of these, type IV and type VI trichomes have been associated with high levels of arthropod resistance. Type IV trichomes have a short, multicellular stalk on a monocellular base and produce a droplet of exudate at their tip. High densities of type IV glandular trichomes and the presence of high levels of toxic acylsugars in their exudate play a major role in the resistance of *L. pennellii* to a number of arthropods, including aphids (*Macrosiphum euphorbiae* and *Myzus persicae*), whiteflies (*Bemisia argentifolii*, *Trialeurodes vaporariorum*), tomato fruitworm (*Helicoverpa zea*), beet armyworm (*Spodoptera exigua*), and the agromyzid leafminer *Liriomyza trifolii* (8, 41–43, 47–50, 61, 82, 94, 99). Genes from *L. pennellii* conferring resistance to arthropods can be introgressed into *L. esculentum* for the development of resistant cultivars. However, glandular trichome-mediated whitefly resistance is not considered suitable for use in tomato cultivars for greenhouse production because the sticky trichomes entrap *Encarsia*

formosa wasps used in the biological control of whitefly (99). High densities of type IV trichomes have been implicated in resistance of *L. hirsutum* f. *typicum* to two-spotted spider mite (*Tetranychus urticae*) (15a, 15b, 123).

Type VI trichomes, which have a four-celled glandular head on a short multicellular stalk and a monocellular base (85), have been implicated in resistance of several *Lycopersicon* species to a number of arthropod pests. Type VI trichomes have been specifically implicated in the entrapment of aphids and other small arthropods (20, 86). They correspond to the well-studied type A trichomes of the wild potato species *Solanum berthaultii*, which play an important role in resistance to aphids by fouling their legs and mouthparts and entangling them in exudate (44). The chemical mechanisms responsible for entanglement are the same in *Lycopersicon* and *S. berthaultii*. The trichome tips contain several phenolics [primarily rutin (80%–90%)] but also chlorogenic acid and conjugates of caffeic acid and polyphenol oxidase and peroxidase. When an insect discharges the trichome tip, the contents are mixed. The ensuing enzymatic reaction results in oxidation of the phenolic substrates to quinones, which polymerize (browning reaction) or react with proteins, reducing or eliminating their nutritive value. In addition, the quinones may be directly toxic to the insect. The product of the browning reaction collects on and entangles appendages and mouthparts of small arthropods (20, 23, 44).

There is extensive variation both within and among *Lycopersicon* species in the level of browning reaction associated with type VI trichomes, which reflects differences in polyphenol oxidase/peroxidase activity as well as density of type VI trichomes (20). Even in the absence of a significant browning reaction, the phenolics contained in the trichome tips of some *Lycopersicon* species may alkylate plant proteins, thereby reducing their nutritional value to leaf-chewing insects (20, 37, 57). Type VI trichomes contain only about 15% of the total foliar catecholic phenolics. The remainder is contained within the leaf lamella where it contributes to plant defense. The glandular tips of type VI trichomes of *L. hirsutum f. typicum* contain several sequiterpenes, including zingiberene γ-elemene, δ-elemene, α-curcumene, and α-humulene, which are acutely toxic to *Spodoptera exigua*. As a group, these compounds do not fully account for the toxicity of the crude trichome tip content, indicating the presence of additional, unidentified toxins (24, 24a). Zingiberene, the predominant sesquiterpene in the tips of type VI trichomes of at least some accessions, is also toxic to Colorado potato beetle larvae and has been implicated in resistance to that important pest (14, 15).

Trichome-Mediated Effects in *Lycopersicon hirsutum f. glabratum*

The effects of glandular and nonglandular trichomes on parasitoids and predators attacking phytophagous insects have been extensively investigated in a number of plant systems (95). Nonglandular trichomes may impede searching behavior of parasitoids and predators (54, 80, 95, 100, 102, 103). Glandular trichomes entrap small hymenopterous parasitoids in sticky exudates (66, 96, 97, 101) and reduce

predator mobility. In addition, exudates of glandular trichomes can be directly toxic to natural enemies of pests (69, 70). Virtually all of these effects have been documented in *L. hirsutum f. glabratum*.

BASIS OF RESISTANCE   *L. hirsutum f. glabratum* expresses traits conferring resistance to at least 19 arthropod pest species of tomato (32, 83, 88). Glandular trichomes have been implicated in the resistance to most species, although factors not associated with trichomes contribute to the overall resistance to at least some species. One accession of *L. hirsutum f. glabratum*, PI134417, has been investigated extensively and possesses multiple defenses against a number of phytophagous arthropods. Foliage of PI134417 is lethal to a number of phytophagous species because of the presence of toxic methyl ketones, 2-tridecanone and 2-undecanone, in the tips of the type VI glandular trichomes, which abound on the foliage and stems (32, 125). These ketones comprise 90% of the tip contents of type VI trichomes of PI134417, but only trace amounts are present in the type VI trichomes of *L. esculentum* (19, 84). 2-tridecanone is acutely toxic to a number of phytophagous species when assayed in contact bioassays (19, 76, 84, 125). For example, in bioassays involving neonates confined on treated filter paper, LC_{50} values of 2-tridecanone for *Manduca sexta*, *Helicoverpa* ($=$ *Heliothis*) *zea*, and *Leptinotarsa decemlineata* are 17.0, 17.1, and 26.5 ug/cm^2 treated surface (19, 72). Published concentrations of 2-tridecanone associated with PI134417 foliage range from 6.3 ng to 146 ng per trichome tip (72, 84). Because 2-tridecanone is contained in the trichome tips, the amount per cm^2 of leaflet surface is determined by both the amount produced per trichome tip and by the number of type VI trichomes per cm^2. These traits vary independently with plant age and with leaf age and position on the plant. Consequently, there is substantial variation in resistance expression and in the potential for tritrophic level effects among plants and among leaves on individual plants (84, 105). 2-tridecanone concentration averaged 44.6 μg/cm^2 of leaflet surface on young fully expanded foliage of PI134417 (72).

Both 2-tridecanone level and type VI trichome density are under separate genetic control but there are epistatic effects (38, 90). Expression of both traits is highly influenced by environmental conditions, including day length, light intensity, and plant nutrient status (2, 78, 104, 123). High levels of 2-tridecanone and resistance to *M. sexta* and *L. decemlineata* are conditioned by at least three major genes inherited in a recessive manner (38, 106). Restriction fragment length polymorphism (RFLP) analyses of quantitative trait loci (QTLs) associated with 2-tridecanone levels in F_2 progeny of crosses between *L. esculentum* and PI134417 identified three different linkage groups associated with the expression of 2-tridecanone. One of the RFLP loci having the highest correlation with 2-tridecanone levels is primarily associated with expression of type VI trichome density (75, 90).

2-undecanone, a second ketone, in the tips of type VI trichomes of PI134417 is less abundant than 2-tridecanone [range 1.1 to 47 ng per tip and less acutely toxic to *H. zea* in contact bioassays (73, 84)]. In contrast, 2-undecanone and 2-tridecanone do not differ in acute contact toxicity to *Keiferia lycopersicella* and

to *S. exigua* (84). At the ratio that occurs in type VI trichome tips, 2-undecanone synergizes the toxicity of 2-tridecanone to neonate *H. zea*, *K. lycopersicella*, and *S. exigua* (28, 84). At levels present in foliage, 2-undecanone has no effect on survival, growth, or development of *M. sexta* (28).

Resistance of PI134417 to *M. sexta* and *L. decemlineata* results from exposure of neonates to lethal concentrations of 2-tridecanone, although other factors associated with the leaf lamella contribute to resistance to *L. decemlineata* (38, 72, 77). Despite the presence of 2-tridecanone at levels potentially lethal to *K. lycopersicella* and *H. zea*, on plants both species avoid significant mortality from exposure to the ketone. *K. lycopersicella* larvae avoid lethal exposure because they are leafminers (84). The situation is more complex with *H. zea* (19, 28–30, 33, 36, 71, 74). Sublethal exposure of eggs and neonates on the foliage of PI134417 to 2-tridecanone vapors from type VI trichomes induces elevated levels of detoxifying enzymes (cytochrome P-450 isozymes) in neonates. Induced *H. zea* larvae tolerate subsequent exposure to 2-tridecanone with no apparent effects; they are also more tolerant to the insecticide carbaryl, which is metabolized by inducible P-450 isozymes. Approximately 15% of *H. zea* neonates are killed by their initial exposure to 2-tridecanone. The remaining larvae quickly recover and begin to feed on the foliage. Most are subsequently killed prior to pupation by resistance factors contained in the leaf lamellae. Unlike 2-tridecanone/trichome-mediated resistance, which is inherited in a recessive fashion, the lamella-based resistance is inherited as a dominant trait. The few *H. zea* that complete larval development on the foliage ingest 2-undecanone during the last instar and die in the pupal stage. 2-undecanone ingested during the last larval instar appears to interfere with lipid metabolism essential for successful pupation and pupal survival.

A series of laboratory and field experiments, involving F_1 and F_1 backcross progeny from crosses between *L. esculentum* and PI134417, which expressed a range of densities of type VI trichomes and methyl ketone levels, demonstrated that glandular trichomes of PI134417 exert dramatic effects on egg and larval parasitoids and predators of *H. zea* and *M. sexta*. F_1 plants express intermediate densities of type VI trichomes but only trace amounts of the methyl ketones; backcross plants are intermediate between F_1 hybrids and PI134417 in both type VI density and methyl ketone levels (27, 69).

EFFECTS ON EGG PARASITOIDS   *Trichogramma* spp. are a major source of mortality of *H. zea* eggs on tomato (27, 69). Parasitism rates of *H. zea* eggs by *Trichogramma* (primarily *T. pretiosum* and *T. exiguum*) over a four-year period averaged 43% on *L. esculentum*, 14% on F_1 hybrids, and <2% on a backcross line and PI134417. The latter two plant lines expressed comparable, high trichome densities and methyl ketone levels (27). Because plant lines with the highest trichome densities also had the highest concentrations of 2-tridecanone, it was not possible to separate effects of trichome density from those of 2-tridecanone (69). Similar reductions in parasitism of *Manduca* eggs were observed on *L. esculentum*, F_1, and PI134417 plants by *Trichogramma* and by the somewhat larger *Telenomus sphingis* (27).

Both physical effects of elevated trichome densities and toxic effects of the methyl ketones contribute to the near elimination of egg parasitism on PI134417. Walking speed of adult *T. pretiosum* was reduced on foliage having high type VI trichome densities and moderate-to-high levels of 2-tridecanone (67, 68). *T. pretiosum* adults contacting PI134417 foliage or exposed to the 2-tridecanone-rich volatiles produced by the foliage also suffered higher mortality (36% and 10%) within 4 h than adults exposed to foliage or volatiles from *L. esculentum* (5% mortality for both). In addition, emergence of adult *T. pretiosum* from parasitized *H. zea* eggs was lower when eggs were incubated on PI134417 foliage than when incubated on *L. esculentum* foliage (emergence 42%–56% and 80%–86%). Mortality of *T. pretiosum* within host eggs is apparently due to exposure of the developing parasitoid to 2-undecanone. Exposure within the egg to 2-tridecanone has no effect on adult emergence.

Telenomus sphingis, which parasitizes *Manduca* eggs, is larger than *T. pretiosum* (adult lengths about 2.0 and 0.5 mm). Although both species are adversely affected by the trichome/methyl ketone-mediated defenses of *L. hirsutum f. glabratum*, the interactions that result in those effects are different (31, 67). Parasitism of host eggs by *T. sphingis* in the field is significantly reduced on PI134417 and F_1 plants compared to *L. esculentum* (parasitism rates 6, 6, and 23%). Fewer adults land on PI134417 than on *L. esculentum* or F_1 foliage because they are repelled by the 2-tridecanone vapors produced by PI134417 foliage. In addition, searching efficiency by adult *T. sphingis* is greatly reduced on both PI134417 and F_1 foliage. Adults placed on *L. esculentum* foliage spent 78% of their time searching (walking). In contrast, adults on PI134417 and F_1 foliage spent 57% and 41% of the time grooming or resting. Excessive grooming, which occurs on PI134417 and F_1 foliage, cannot be attributed to the methyl ketones because they are not produced by F_1 foliage. Although parasitism is greatly reduced on PI134417 plants, it is not completely prevented. Unlike *T. pretiosum*, *T. sphingis* larvae and pupae within eggs incubated on PI134417 foliage develop normally, unaffected by either 2-tridecanone or 2-undecanone. *T. sphingis* is not entrapped and killed by the glandular trichomes of *L. hirsutum f. glabratum*, an observation consistent with findings in other systems in which large-bodied parasitoid species were less affected by glandular trichomes than were small-bodied parasitoids (7, 96). However, despite its larger size, *T. sphingis* does not effectively utilize host eggs on PI134417 or F_1 plants because the trichome constituents elicit behavioral responses that severely impede effective searching for host eggs.

EFFECTS ON LARVAL PARASITOIDS OF *H. zea*   Larval parasitoids interact with their host and the food plant of their host in a variety of ways depending on their specific biological attributes and host-finding behaviors. The details of the interactions between parasitoids and plant defensive traits are important determinants of the type and magnitude of potential tritrophic effects. A comparison of the tritrophic interactions involving PI134417, *H. zea*, and three species of larval parasitoids illustrates this point and some of the subtleties involved.

In the field, larval parasitism of *H. zea* and *Heliothis virescens* by *Campoletis sonorensis* is lower on PI134417 than *L. esculentum* and F_1 (27). Adult *C. sonorensis* are less efficient at locating host larvae on PI134417 plants, although the specific behavioral causes are not known (69). However, the effects of PI134417 on *C. sonorensis* extend beyond behavioral modification. *C. sonorensis* oviposits in second and early-third instar hosts. The parasitoid larvae kill their host when it is in the late-third or early-fourth instar. They then emerge from the dead host onto their host's food plant, where they spin a cocoon and pupate. On PI134417, this cocoon-spinning behavior results in disruption of glandular trichomes and direct contact with the methyl ketones contained in their tips. Both in the field and in the laboratory, mortality of *C. sonorensis* larvae during cocoon spinning is high on PI134417 (90% versus 10% on *L. esculentum*). 2-tridecanone is lethal to *C. sonorensis* larvae at the concentrations expressed on PI134417 foliage, and mortality of *C. sonorensis* larvae on foliage from parental and backcross plant lines expressing different levels of 2-tridecanone is directly related to the 2-tridecanone concentration of the foliage (69, 70). Although 2-tridecanone is similarly toxic to both *C. sonorensis* and *H. zea*, the parasitoid is much more affected by PI134417 foliage than its host is. *C. sonorensis* larvae are killed because they experience a massive dose of the toxin as they spin their cocoons. In contrast, neonate *H. zea* rarely discharge trichome tips before exposure to 2-tridecanone vapors induces elevated levels of cytochrome P-450, which then allow the larvae to tolerate subsequent exposures to 2-tridecanone (70, 74).

The tachinids *Archytas marmoratus* and *Eucelatoria bryani* both parasitize *H. zea* but interact with the food plants of their host in distinctly different ways. The methyl ketone/glandular trichome-based resistance of PI134417 differentially affects both *A. marmoratus* and *E. bryani*. At least a portion of the difference between the two species can be attributed to differences in their interactions with the host plant (34, 35). *A. marmoratus* larviposits minute planidia on its host's food plant. The planidia attach to passing hosts and penetrate the cuticle. The parasitoid undergoes limited development within its host until the host pupates. It then develops rapidly and emerges from the host pupa as an adult (53). In contrast, *E. bryani* larviposits directly into larvae of its host. The parasitoid larvae develop rapidly and kill the host within a few days. Mature larvae emerge from the dead host larva and pupate. A single host often yields several parasitoids (12, 59). Because the parasitized host typically drops to the ground before it is killed by the parasitoid, *E. bryani*, unlike *A. marmoratus*, has minimal direct contact with its host food plant.

In field cage studies, parasitism of *H. zea* larvae by *E. bryani* was not affected by plant line. In contrast, parasitism by *A. marmoratus* was lower on PI134417 and on a backcross line expressing high levels of 2-tridecanone and high trichome densities (mean parasitism about 55%) than on *L. esculentum* and F_1 lines (mean parasitism 74% on both). More detailed studies revealed that the difference in parasitism was due to elevated mortality of *A. marmoratus* planidia on PI134417 and backcross plants due to a combination of toxic effects of 2-tridecanone and physical effects

of high trichome densities (34, 35). In addition, there is a host-mediated effect of 2-undecanone but not 2-tridecanone on survival of *A. marmoratus* within parasitized *H. zea* pupae. 2-undecanone ingested during the last larval instar causes premature death of *H. zea* pupae. At high RH, this does not prevent parasitoid larvae from completing development; but at low RH, host pupae desiccate, killing the parasitoid larvae before they complete development. 2-undecanone in the diet of *H. zea* does not affect *E. bryani*, but 2-tridecanone in the host diet reduces by about 45% the number of *E. bryani* puparia produced per host. It is not known if this effect is due to reduced larviposition by *E. bryani* in hosts reared on a diet containing 2-tridecanone or to mortality of parasitoid larvae within their host.

FIELD OBSERVATIONS   In a four-year field study, both egg and larval parasitism of *Manduca* spp. were lower on PI134417 plants (27). Egg parasitism of *M. sexta* and *M. quinquemaculata* by *T. sphingis* and *T. pretiosum* was significantly lower on PI134417 and F_1 than on *L. esculentum* plants. In addition, larval parasitism of *Manduca* spp. by *Cotesia congregata* was consistently lower on PI134417 than on *L. esculentum*. However, because *M. quinquemaculata* larvae are less affected than *M. sexta* by the resistance and because *C. congregata* prefers *M. sexta* to *M. quinquemaculata*, reduced larval parasitism on PI134417 could reflect the greater relative abundance of *M. quinquemaculata* on PI134417 in this study rather than an effect of PI134417 on the parasitoid.

Egg populations of *H. zea* and *H. virescens* on PI134417 averaged 3.2 and 16 times greater than on *L. esculentum* over a three-year period. Oviposition was also higher on F_1 plants than on *L. esculentum*. This difference is likely due to the presence of high levels of an oviposition stimulant associated with the foliage of PI134417 (60). Egg parasitism by *Trichogramma* on *L. esculentum*, F_1, and PI134417 averaged 43, 14, and 1% over four years. *H. zea* larvae were parasitized by *Campoletis sonorensis* and *Cotesia marginiventris*. *H. virescens* larvae were parasitized by *C. sonorensis*, *C. marginiventris*, and *Cardiochiles nigriceps*. The incidence of parasitism in both *H. zea* and *H. virescens* by *C. sonorensis* was lower on PI134417 than on *L. esculentum* and F_1. Parasitism by *C. marginiventris* was low and variable, revealing no consistent differences among plant lines. No differences in parasitism rates of *H. virescens* by *C. nigriceps* were observed among plant lines. Given that parasitism rates by *C. nigriceps* on PI134417 plants exceeded 75% in each of two years, it is unlikely that *C. nigriceps* is adversely affected by high densities of methyl ketone-rich, glandular trichomes on the foliage of its host's food plants.

Despite higher egg densities and greatly reduced levels of egg parasitism by *Trichogramma* spp. on PI134417 and F_1, and a 70% lower incidence of larval parasitism by *C. sonorensis* on PI134417 than on *L. esculentum*, densities of large *H. zea* larvae were similar on each of the plant lines. Overall, for *H. zea* higher oviposition and reduced parasitism and predation rates (3) on PI134417 were offset by higher larval mortality owing to the combined effects of trichome- and nontrichome-mediated resistance traits. For *H. virescens*, which is less affected by

the resistance traits, the combined effects of trichome- and nontrichome-mediated resistance traits did not compensate for the higher oviposition and lower parasitism and predation rates. As a result, populations of large *H. virescens* larvae tended to be higher on PI134417 than on *L. esculentum*.

NONTRICHOME DEFENSES IN *LYCOPERSICON*

Constitutive and induced defenses other than those associated with glandular trichomes have been well documented in *Lycopersicon* spp. However, only the glycoalkaloid α-tomatine, the growth-inhibiting phenolics rutin and chlorogenic acid, and the jasmonic acid-inducible defenses have been studied from the perspective of tritrophic level effects.

Constitutive Defenses

α-tomatine has been hypothesized as a possible contributor to the lamella-based resistance of *Lycopersicon* spp. to *H. zea* and *S. exigua*. It is present in both tomato foliage and unripe fruit, but not in ripe fruits or in the tips of type VI trichomes (23). Foliar α-tomatine levels vary both within and among *Lycopersicon* species, with the highest levels occurring in *L. esculentum* var. *cerasiforme* and *L. pimpinellifolium* (64). Variation in α-tomatine levels among progeny of crosses between high- (*L. esculentum* var. *cerasiforme* and *L. pimpinellifolium*) and low- (*L. esculentum*) expressing plants is controlled by segregation of two codominant alleles at a single locus (62). α-tomatine content of tomato fruit was positively correlated with development time and mortality of *H. zea* larvae fed fruit of different ages, and it was negatively correlated with larval growth rate and adult weight. In contrast, there were no correlations between α-tomatine content of fruit and growth or survival of *S. exigua* (63). When incorporated into artificial diets at concentrations representative of those found in commercial tomato varieties, α-tomatine is a potent growth inhibitor of both *H. zea* and *S. exigua* (9, 20, 25). However, the toxic effects of α-tomatine are dependent on concentrations of 3-beta-hydroxy-sterols present in the diet. In the presence of equimolar concentrations of dietary sterols, α-tomatine is nontoxic to *H. zea* and only minimally toxic to young *S. exigua* larvae. In addition, the sensitivity of *S. exigua* but not *H. zea* larvae to α-tomatine declines with age to the point that later stage *S. exigua* larvae are insensitive to its effects (9).

Hyposoter exiguae, a larval parasitoid of *H. zea* and *S. exigua*, is adversely affected when its hosts feed on diet containing α-tomatine (13). The toxicity of α-tomatine is mediated through the host larva and is manifested as prolonged larval development, disruption or prevention of pupal eclosion, deformation of antennal, abdominal and genital structures, and a reduction in adult weight and longevity. *H. exiguae* is affected by α-tomatine in its host diet at lower concentrations when parasitizing *S. exigua* than when parasitizing *H. zea*. α-tomatine in the host's diet at a concentration of 0.9 μmol/g.fr.wt. is lethal to *H. exiguae* when parasitizing

S. exigua, but it merely slows larval and pupal development and reduces adult longevity when parasitizing *H. zea* (21). As with *H. zea* and *S. exigua*, the toxic effects of α-tomatine on *H. exiguae* are eliminated by the presence of equimolar concentrations of sterols in the host diet (13a). The occurrence of adverse effects of α-tomatine in *Lycopersicon* foliage on *H. exiguae* or other parasitoids has not been documented.

The actual significance of α-tomatine as a mechanism of resistance in *Lycopersicon* to *H. zea* and *S. exigua* is not clear, nor is the occurrence, in the field, of α-tomatine-mediated tritrophic effects. Many *L. esculentum* cultivars contain levels of phytosterols sufficient to negate the toxic effects of α-tomatine, but the levels of antidotal phytosterols and α-tomatine in tomato foliage are not correlated (13a, 21, 22). The presence of high levels of phytosterols in the foliage may be related to the role of α-tomatine as a defense against fungi, which requires high levels of phytosterols (22). There is some evidence that α-tomatine in *Lycopersicon* foliage could inhibit infection of phytophagous insects by the entomopathogenic fungi *Beauveria bassiana* and *Nomuraea rileyi* (18, 40, 46). In addition, there is some evidence that α-tomatine may influence predation on *M. sexta* larvae by *Podisus maculiventris* (120). *P. maculiventris*, which had previously preyed upon tomatine-fed larvae, subsequently rejected *M. sexta* larvae as prey whether or not the larvae had fed upon a diet containing tomatine.

Phenolics have been implicated as possible factors in the growth-inhibitory effects of tomato foliage on *H. zea* and *S. exigua* larvae. The catecholic phenols rutin and chlorogenic acid in the leaf lamella and the tips of type VI trichomes account for over 60% of the total phenolic content of *L. esculentum* foliage (57, 58). These compounds are common in green plants (45, 79). When incorporated into artificial diet they act in an additive fashion to produce a dose-dependent growth inhibition of *H. zea* and *S. exigua* larvae (21, 25, 57, 58). However, the growth-inhibitory effects are dependent on the type and level of protein in the diet (21). Levels of both phenolics and proteins in tomato foliage are influenced by nitrogen fertilization, water stress, and light intensity (26, 116, 124). They also vary widely and independently both within and among plants of the same and different *L. esculentum* cultivars, although the concentrations of soluble phenolics are consistently higher in young than mature foliage (110). The interaction between phenolics and protein may explain a lack of correlation between total foliar phenolic content and growth of *H. zea* larvae on different *L. esculentum* cultivars, when phenolic levels in the foliage are within a range that retards larvae growth on artificial diet (57).

In artificial diet studies, rutin exerts mild effects on a parasitoid and a predator of *M. sexta*. Dietary rutin prolongs development of *M. sexta* larvae at cool but not at warm temperatures (52, 107–110, 122). This effect involves more than a reduction in availability of dietary protein; it includes interference with physiological processes relating to the initiation of molting. Development time of the parasitoid *C. congregata* is also increased when the host larvae are raised on artificial diet containing rutin at concentrations found in plants. Because *C. congregata* does not develop beyond the first instar until *M. sexta* reaches the last larval stage, prolonged development of the parasitoid is thought to result from delayed development of

its host rather than from an effect of rutin on the parasitoid (1, 6). Presumably the effect of rutin on *C. congregata* is greater at cool than warm temperatures. When nymphs of the predatory stink bug *P. maculiventris* were fed *M. sexta* larvae whose diet contained rutin, they experienced a reduction in weight gain at warm but not cool temperatures, a temperature effect opposite that seen for *M. sexta* larvae. Effects of rutin were observed when prey was scarce but not when abundant. In addition, *P. maculiventris*, which had previously preyed upon chlorogenic acid–fed larvae, subsequently rejected chlorogenic acid–fed *M. sexta* larvae as prey but not *M. sexta* larvae that had fed on diet that contained no chlorogenic acid (120).

Induced Defenses

Even minor injury to *L. esculentum* leaves by insects, pathogens, or mechanical wounding can elicit a systemic response that results in synthesis of more than 20 defense-related proteins, including antinutritional proteins, signaling pathway compounds, and proteinases (101a). These responses alter the suitability of foliage for some insect species and plant pathogens. Thus, feeding by *H. zea* larvae on *L. esculentum* induces elevated resistance to *H. zea* and *S. exigua*, as well as *M. euphorbiae*, *T. urticae*, and the phytopathogen *Pseudomonas syringae* (114).

Stout et al. (113) suggest that inducible defenses of *L. esculentum* consist of an array of sets of defensive compounds, with different sets being differentially inducible by different insects or pathogens or combinations thereof. Because individual insect and pathogen species vary in their sensitivity to each set of defensive compounds, injury to the plant by different agents may result in different patterns of resistance to any given array of insects and pathogens. For example, feeding by *H. zea* induces a systemic resistance to *H. zea*, mediated primarily by the induction of proteinase inhibitors, and resistance to the phytopathogen *P. syringae*, mediated primarily by induction of pathogenesis-related protein P4. The induced resistance to *P. syringae* is less than that induced by a localized *P. syringae* infection, which elicits a production of higher levels of pathogenesis-related protein P4. Because local infections of *P. syringae* induce levels of proteinase inhibitors comparable to those induced by *H. zea* feeding, *P. syringae* infections and *H. zea* feeding induce comparable levels of resistance to *H. zea* (39, 55, 113). Detailed descriptions of these induced defenses can be found elsewhere (10, 11, 39, 55, 56, 111, 112, 114, 115, 117, 119).

Caterpillar feeding on *L. esculentum* induces proteinase inhibitors, peroxidase, polyphenol oxidase, and lipoxygenase. The production of elevated levels of proteinase inhibitors, and to a lesser extent polyphenol oxidase, appears to be the primary mechanism for induced resistance to caterpillars (11, 111, 115, 117). Feeding on foliage from induced plants causes reduced growth and delayed development in *H. zea*, *M. sexta*, and *S. exigua*, as well as elevated mortality in *S. exigua* (11, 111, 112). Growth of *M. sexta* larvae on transgenic tobacco plants expressing the tomato gene coding for proteinase inhibitor II, which inhibits both trypsin and chymotrypsin, was reduced from 50% to 67% relative to controls, depending on expression level in the plant. In contrast, larval growth was only slightly reduced

on transgenic tobacco plants expressing tomato proteinase inhibitor I, which is a strong inhibitor of chymotrypsin but only weakly inhibits trypsin (59a) The induction of proteinase inhibitors and polyphenol oxidase is systemic, occurs within hours, and is long lasting ($\geq$21 days) (111). The systemic induction of defensive compounds reduces the ability of phytophagous arthropods to avoid locally induced compounds by moving to uninjured leaves (17a). However, induction is not uniform throughout the plant (98, 111, 112), and therefore some portions of the plant are more defended than others. Consequently, the distribution of insect feeding or damage on the plant may change following induction (5). In addition, levels of induction of proteinase inhibitors and polyphenol oxidase in response to feeding decline with plant age (16, 111). On plants of a given age, younger leaves have higher constitutive levels of polyphenol oxidase than older leaves but inducible levels of polyphenol oxidase are higher in older leaves (111). They also vary among *L. esculentum* cultivars (11).

The production of jasmonic acid via the octadecanoid pathway serves as a signal for expression of proteinase inhibitors, polyphenol oxidase, and peroxidase in tomato foliage in response to caterpillar feeding (39, 83a, 101a, 119). Thaler (117, 118) used foliar applications of jasmonic acid to induce elevated levels of these compounds in field-grown *L. esculentum* plants. In her experiment, the number of leaves damaged by insect feeding was 38% lower on the induced plants than on control plants (117). In a separate experiment, twice as many *S. exigua* larvae were parasitized by *H. exiguae* on the jasmonic acid–treated tomato plants as on untreated control plants (118). This difference was not due to an attraction of the wasps to jasmonic acid, nor was it due to a greater period of susceptibility to attack by *H. exiguae* resulting from slower growth of *S. exigua* larvae on induced plants. Thaler hypothesized that higher parasitism resulted from the attraction of *H. exiguae* adults to the blend of volatiles produced by the induced plants. Parasitoid survival was comparable when host larvae fed on induced or noninduced foliage; however, *H. exiguae* developing in *S. exigua* fed induced foliage developed more slowly than those developing in hosts fed foliage from noninduced plants. It seems unlikely that this delayed development would reduce the impact of elevated levels of parasitism on induced plants.

Effects on Predators

Although most research on tritrophic effects involving *Lycopersicon* has focused on parasitoids, effects involving predaceous arthropods have been documented as well. The predatory mite *Phytoseiulus persimilis* is used in the biological control of the two-spotted spider mite, *T. urticae*. Feeding on *L. esculentum* foliage by *T. urticae* induces leaves to produce volatiles that are attractive to the *P. persimilis*. The response of *P. persimilis* to *T. urticae*-induced plant volatiles is affected by starvation, specific hunger, and experience of the predator, as well as the presence of competitors and pathogen infestations (18a, 116a).

Type VI trichomes on the foliage and stems of *L. esculentum* entrap *P. persimilis*. Entrapment rates range from 2.5 to 20% (91) but vary among cultivars,

with higher entrapment rates associated with high trichome densities (121). Rapid increases in temperature appear to temporarily increase entrapment rates by reducing the rupture threshold of the trichome tips and may contribute to variation in the effectiveness of mite control by *P. persimilis* (91–93).

Oviposition by the whitefly *B. argentifolii* on *L. esculentum* is positively correlated with trichome density (type not specified) (50). Although lifetime fecundity and walking speed of its coleopterous predator *Delphastus pusillus* are significantly reduced on cultivars with high trichome densities, the ability of the predator to suppress whitefly populations is not reduced in the presence of high trichome densities. It seems that in the presence of high trichome densities, significantly longer residence time by beetles compensates for their reduced fecundity and walking speed (51).

In a three-year field study, populations of predaceous arthropods (*Coleomegilla maculata*, *Geocoris punctipes*, *Jalysus wickhami*, and spiders) were similar on PI134417, *L. esculentum*, F_1, and backcross plantings (4). Laboratory results confirmed that survival of adult *C. maculata* and *G. punctipes* was similar on these plant lines but demonstrated that consumption of *H. zea* eggs by adults and immatures of these predators was lower on PI134417 and F_1 than on *L. esculentum* foliage. *H. zea* egg consumption by *C. maculata* and *G. punctipes* adults on *L. esculentum* foliage was about 13 and 10 times greater than on PI134417 and about 2 times greater (both species) than on F_1 foliage. Reduced egg consumption on F_1 foliage appears to be due to the direct physical effects of the glandular trichomes on the predators, whereas the even greater reduction on PI134417 foliage appears to be due to the combined effects of high trichome densities and 2-tridecanone (3). The effects of tomato trichomes on prey consumption are consistent with observations of reduced searching efficiency of *Orius insidiosus* on tomato relative to bean and maize (17).

GENERAL CONCLUSIONS

The most intensively studied *Lycopersicon* species, *L. esculentum*, *L. pennellii*, *L. hirsutum f. typicum*, and *L hirsutum f. glabratum*, express a diverse array of defense traits. These include glandular trichomes that physically impede, entrap, and in some cases intoxicate phytophagous arthropods. They also include constitutively expressed and induced defenses associated with the leaf lamellae that act as growth inhibitors or toxins. A number of these traits affect parasitoids and predators as well as phytophagous species. Trichome-mediated defenses are particularly significant in *L. pennellii*, *L. hirsutum f typicum*, and *L hirsutum f. glabratum* and have been most extensively implicated in negative tritrophic effects in both the field and laboratory. These effects range from reduced searching efficiency due to direct physical interference with movement to elevated mortality due to entrapment or lethal intoxication of parasitoids and predators that discharge and contact sticky or toxic contents of trichome tips. Effects also include those that are indirectly mediated through the host or prey, such as those of 2-undecanone on *Trichogramma*

or *A. marmoratus*. Even seemingly simple traits, such as high concentrations of 2-tridecanone or 2-undecanone, can have profound and complex effects on the second and third trophic levels. The effects of any particular plant defensive trait on parasitoids and predators depend on the specific attributes of the plant trait and the details of the interaction between the natural enemy, its host (prey), and the plant, as well as the physiological ability of the natural enemy to de-toxify or sequester plant toxins. The great diversity that exists in parasitoid and predator biology with respect to the details of these interactions suggests that predictions linking types of plant defenses to tritrophic effects that are likely to be important ecologically or of value in deploying host plant resistance for crop protection may be limited and general. Clearly, one such generalization that emerges from work on *Lycopersicon*, as well as other species, is that glandular trichome-mediated resistance traits are more likely to exert general adverse tritrophic effects than nontrichome-mediated traits.

One striking feature of defense traits discussed in this review is the extent to which their expression is strongly influenced by environmental conditions, as well as plant age, leaf age, and leaf position on the plant. The implications of this variation for herbivore/parasitoid/predator interactions and adaptation to resistance traits represent an inviting avenue for future research. Only a limited portion of the research on tritrophic interactions in *Lycopersicon* has involved field studies. Virtually all these have been conducted in areas far removed from the plants' native habitats and have focused on phytophagous species that are pests on *L. esculentum* cultivars. Additional field studies of arthropod population and community dynamics involving a greater spectrum of *Lycopersicon* species, resistance traits, and locations, including native habitats of the plants under study, have the potential to provide new insights and understanding of the ecological impacts of plant defense traits.

Lycopersicon provides an excellent model system for research on the mechanisms, ecology, and evolution of plant defenses, and on tritrophic interactions. Recent progress in understanding the biochemical basis and molecular genetics of induced defenses in tomato, combined with the discovery in tomato of a gene that blocks biosynthesis of jasmonic acid and a gene that blocks the ability of the plant to respond to jasmonic acid (52a), provide the tools necessary to greatly advance our understanding of the mechanistic basis for and ecological consequences of tritrophic effects of induced defenses. *Lycopesicon* is also a rich source of resistance traits of potential use in breeding pest-resistant tomato cultivars. From a crop protection perspective, it is the net effects of plant resistance on the targeted pest(s) and their natural enemies that determine the final level of crop damage and the potential utility of a particular resistance trait or set of traits for crop protection.

ACKNOWLEDGMENTS

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Volume 48, 2003

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