

# Plant-Mediated Interactions Between Whiteflies, Herbivores, and Natural Enemies

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## Key Words

competition, induced response, indirect effects, insect-plant relationships, tritrophic relationships

## Abstract

Whiteflies (Homoptera: Aleyrodidae) comprise tiny phloem-sucking insects. The sessile development of their immatures and their phloem-feeding habits (with minimal physical plant damage) often lead to plant-mediated interactions with other organisms. The main data come from the polyphagous pest species *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood), which are intricately associated with their host plants. Although these associations might not represent aleyrodids in general, we rely on them to highlight the fundamental role of host plants in numerous ecological interactions between whiteflies, other herbivores, and their natural enemies. Plant traits often affect the activity, preference, and performance of the whiteflies, as well as their entomopathogens, predators, and parasitoids. Leaf structure (primarily pubescence) and constitutive and induced chemical profiles (defensive and nutritional elements) are critically important determinants of whitefly fitness. Pest management-related and evolutionary biology studies could benefit from future research that will consider whiteflies in a multitrophic-level framework.

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**Polyphagous:**  
feeding on a variety  
of plants belonging  
to several families

**Biotype:**  
intraspecific  
taxonomic category  
of a group of  
individuals with a  
similar genotype  
(may resemble race)

**Constitutive:**  
present regardless of  
attack

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## INTRODUCTION

There are approximately 1500 described species of whiteflies (Homoptera: Aleyrodidae), which are divided into two subfamilies: Aleyrodinae (of world-wide origin) and Aleyrodicinae (originating mostly in Central and South America), with most species occurring in the warmer, tropical, and subtropical regions (18, 42, 81). Whiteflies are phloem-feeders (131), excreting excess sugars as honeydew. The whitefly life cycle comprises an egg, four nymphal instars, and winged adults. The eggs hatch into crawlers, the only mobile immature stage. Once settled, crawlers molt to sessile second instars with dysfunctional legs. Following two additional molts, the pharate adults develop within the cuticle of the fourth instar, emerging as winged adults (~1–2 mm) that live up to several weeks (18). The life cycle is mainly temperature regulated (taking 2–3 weeks to several months to complete) but may include a long diapause (42).

Whiteflies have received much attention because of several polyphagous pest species, such as the spiraling whitefly (*Aleurodicus dispersus* Russell), the greenhouse whitefly [*Trialeurodes vaporariorum* (Westwood)] and the sweetpotato whitefly [*Bemisia tabaci* (Gennadius)] (42, 100). [The taxonomic status of *B. tabaci* (including *B. argentifolii*) and its biotype complex (5, 14) are beyond the scope of this review. Here we follow De Barro et al. (33) using the name *B. tabaci* throughout.] Overall information on whitefly biology was last published about 15 years ago (18, 42). Other recent whitefly-related reviews have addressed taxonomy, economic importance, pest management, parasitoids, and virus transmission (13, 14, 22, 63, 81).

The interactions between herbivores and the biotic environment rely largely on plant-mediated mechanisms (38, 98, 99, 108). Such indirect mechanisms are associated with constitutive plant traits or with herbivore-induced modifications in the plant's anatomy, physiology, and chemistry. Therefore, plant-mediated interactions can operate among spa-

tially and temporally separated organisms on a given shared plant, even at low herbivory levels (99). This review is devoted to plant-mediated interactions between whiteflies (primarily *B. tabaci* and *T. vaporariorum*), other herbivores, and natural enemies. Although some host plant-associated relationships exhibited by these extremely polyphagous species differ from those of other more host-specific (oligophagous) whitefly species (18), we consider them indicative of the family's potential in plant-mediated interactions.

The wide whitefly-plant associations resulting from their extensive geographical and host plant ranges provide ample opportunities for complex interactions with organisms at all trophic levels. Moreover, the economic damage caused by *B. tabaci* and *T. vaporariorum* have elicited numerous studies that, with the advent of new molecular and analytical tools, have contributed greatly to our knowledge base of these relationships. The new available data support the hypothesis that complex plant-mediated interactions may play a key role in both ecological and practical (management-related) whitefly arenas.

The importance of plant-mediated interactions in whitefly biology arises from several major life-history traits: (a) the polyphagy of some species that creates the opportunity to form complex interactions with numerous herbivores and natural enemies on a variety of plant species in different habitats; (b) the capacity of whiteflies to induce significant responses and manipulate host plant physiology; and (c) the mostly sessile nature of the immatures.

Because whitefly research has focused primarily on pest management, most information on plant-mediated interactions originates in studies on natural enemies, and many ecological interactions with other (non-whitefly) herbivores have been relatively overlooked. We first outline briefly the effects of whiteflies on their host plants and then discuss plant-mediated interactions among whiteflies and between them, other herbivores, and natural enemies.

## EFFECTS OF WHITEFLIES ON THE HOST PLANT

Whiteflies may affect the biochemistry, physiology, anatomy, and development of infested plants. They may deplete plant reserves, reduce primary production, and cause direct phytotoxic effects. They also cause secondary damage through honeydew excretion that enables sooty mold development, blocks sunlight, and reduces photosynthesis (19, 42, 62, 133). A few species, most notably *B. tabaci*, transmit plant-damaging viral diseases (13, 22). The basic physiological process in the plant may be modified by whiteflies. For example, *B. tabaci* causes increased stomatal resistance (impaired gas exchange), reduced transpiration and photosynthesis rates, and reduced chlorophyll content in tomato leaves (15). In cotton, the net photosynthesis rates are reduced and whitefly feeding causes the accumulation of soluble sugars in the infested leaves, suggesting interference with the export of fixed carbon (78, 79).

### Induced Plant Responses to Whiteflies

Plant physical, and more often chemical, defenses may be induced in response to herbivore attack (73). Induced plant responses may potentially operate in several capacities: accumulation of defensive compounds; influencing the behavior, feeding efficiency, reproductive success, and host plant selection by the herbivores; and/or volatile emission that recruits natural enemies. Compared with other feeding guilds, phloem-feeders cause minimal mechanical damage to plants. Thus, induced response to whiteflies partly resembles plant responses to pathogens via the salicylic acid (SA) and jasmonic acid (JA)/ethylene-dependent pathways (72, 132). Such pathways may potentially crosstalk, promoting or inhibiting plant resistance to various challenges (11, 122, 132).

As with pathogen attack, plants accumulate pathogenesis-related (PR) proteins in re-

sponse to *B. tabaci* feeding (70, 82). Infested tomato leaves produced higher levels of the PR proteins  $\beta$ -1,3-glucanase, chitinase, peroxidase, PR2, and PR4 both locally and systemically (66, 83). The induction is more pronounced in response to viruliferous whiteflies (89). In squash, two genes (*SLW1* and *SLW3*) are induced locally and systemically by *B. tabaci* (126). This study (and see the *Wf1* gene in tomato; 132) demonstrated the specificity of plant response to whiteflies: First, *SLW1* and *SLW3* transcripts increased only in response to feeding by nymphs but not adults; second, the level of systemic induction differed in *B. tabaci* biotypes (*B. argentifolii*). Moreover, induction of *SLW3* expression probably represents a specific, novel signaling pathway that is not primarily regulated by JA or SA (72, 126, 132). It is unclear how whiteflies elicit plant response; potential elicitors are saliva components, mechanical damage, and endosymbiotic-borne cues. However, the efficiency of plant defense systems in pest management still requires intensive research. Most research efforts have been focused on the mechanism involved (see above) and the application of exogenous elicitors (23, 65, 69, 94) and nonpathogenic rhizobacteria (74, 91) (see sidebar, Induced Responses in the Plant: Potential Role in Pest Management).

### Feeding Disorders

Gall formation, common among some hemipterans, is rare among whiteflies (17). However, feeding by *B. tabaci* may cause physiological and anatomical changes in the plants (27, 107, 126), but the mechanisms controlling these phenomena are not thoroughly understood. In tomato, the symptoms of irregular ripening, correlating with density of *B. tabaci* biotype 'B' (117), are restricted to the fruit, in which the synthesis, function, and balance of phytohormones are modified (55, 86, 107). Feeding by *B. tabaci* biotypes 'B' and 'Ms' on leaves of cucurbits may induce leaf silvering (27, 34, 70, 116). Actual whitefly

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**PR proteins:**  
pathogenesis-related  
proteins

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## INDUCED RESPONSES IN THE PLANT: POTENTIAL ROLE IN PEST MANAGEMENT

Induced resistance to whiteflies might be obtained through the use of microorganisms and/or elicitors of plant defense systems. Immunization of the plant to whitefly-transmitted viral diseases may be achieved through earlier elicitation of plant defenses by nonpathogenic microorganisms that rely on nonspecific resistance mechanisms. The nonpathogenic plant growth-promoting rhizobacteria (PGPR) can elicit defense against viral, bacterial, and fungal diseases. Tomatoes treated with formulations based on *Bacillus* spp. (PGPR) displayed a reduction in *Tomato mottle virus* infection severity. Moreover, in some trials the PGPR also reduced the density of *B. tabaci*, the virus vector. It is unclear whether the induced systemic resistance affected the virus, its transmission, the whitefly, or a combination thereof. Practically, induced resistance may also be achieved by the application of exogenous elicitors. Foliar application to tomato and cotton of benzo (1,2,3) thiazole-7-carbothioic acid (S) methyl ester (BTH), an elicitor of the SA-dependent pathway, was useful against *B. tabaci* at least in some experimental set ups.

feeding, however, might be more damaging to the plant than silvering (19).

### INTRASPECIFIC AND INTERSPECIFIC PLANT-MEDIATED INTERACTIONS BETWEEN WHITEFLIES AND OTHER HERBIVORES

One would expect that the pronounced effects of whiteflies on the plant, together with their polyphagy and the wide distribution of some species, would promote numerous interactions with conspecifics, other herbivores, or both. Yet the data on such interactions are scanty.

#### **Facilitation of Whitefly Feeding: Positive Intraspecific and Interspecific Interactions**

Phloem-feeders act as sinks for assimilates, potentially competing with plant sinks such

as fruits and young leaves. Drawing assimilates to the feeding sites can be enhanced by mutual sinks created by feeding aggregations, which may also alter the nutritional value of the sap. Such facilitation might benefit whiteflies when density does not promote competition.

Sink manipulations were demonstrated on cantaloupe (9), where, during the plant's vegetative growth phase, *B. tabaci* aggregations altered free amino acid composition and elevated their total concentrations in the phloem sap. The ability of *B. tabaci* to manipulate the sink-source flow (i.e., successfully compete with natural sinks) ended once the plants reached their reproductive phase (9). Recently, De Barro et al. (31) described cross-biotype facilitation; *B. tabaci* biotypes 'B' and 'AN' benefited from increased fecundity when occupying the same plant. However, we have no evidence indicating that adult females actually prefer or are attracted to leaves already infested with whiteflies (44). A different facilitation mechanism was demonstrated in the Sudan Gezira, where fruit damage by *Heliothis* larvae enhanced cotton vegetative growth and altered leaf age composition that benefited *B. tabaci* development and density (4).

### **Microorganisms Inducing Plant Susceptibility (Facilitation) to Whiteflies**

Fungi and especially viruses may alter the attractiveness and suitability of plants for whiteflies (22, 26, 71, 82, 89, 129). Plant viruses transmitted by whiteflies may also act as insect pathogens (113). Nevertheless, examination of facilitation in respect to virus transmission produced conflicting results, depending on specific (virus-plant) complexes. A few studies failed to detect any effects of plant viruses on the fitness of whiteflies (3, 124). A lack of unified effects was reported following analyses of *B. tabaci*: host plant selection and nymph performance conducted on six healthy and six begomovirus-infected commercially important plant species. Although the leaves of

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#### **Facilitation:**

enhancement of one population by another

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all virus-infected plants had higher amino acid levels than the leaves of healthy plants, these differences were not significantly correlated with *B. tabaci* fitness (26).

Much clearer, positive (perhaps mutual) virus-whitefly relationships have been reported in other studies. Viruliferous *B. tabaci* growing on tomato plants infected with *Tomato mottle virus* had higher fecundity and larger population increases than did whiteflies growing on healthy controls. Whether this difference was due to the direct effect of the virus or indirectly mediated by the quality of the tomato remains unclear (88, 89). The populations of *B. tabaci* on several plant species infected with *Tomato leaf curl virus* increased significantly (22). Similarly, cassava inoculated with the *East African cassava mosaic virus*-Uganda served as better hosts for *B. tabaci* than did healthy plants. The whiteflies probably benefited from a higher concentration of free amino acids detected in the phloem sap of the infected cassava plants (22). The mutualism between viruses and (specifically) the *B. tabaci* 'B' biotype may have resulted in plant-mediated facilitation, ameliorating its rapid spread to new habitats (71).

### Plant-Mediated Intraspecific and Interspecific Competition Among Whiteflies

Intraspecific competition may be an important driving force in *B. tabaci* dynamics, especially once plant quality drops because of heavy infestation. Special attention has been paid to competition among the *B. tabaci* biotypes that may lead to displacement and speciation (14, 30, 71, 102) and influence viral transmission and pest control (64, 115). Dominance of *B. tabaci* 'B' biotype on a particular plant species and its mutual association with viruses may promote its wide geographic spread (31). Interspecific competition between whiteflies is also influenced by the plant. In greenhouses *B. tabaci* shared the same plant with *T. vaporariorum* (80, 125) but did not coexist on the same leaf for more than

two generations (80). Species dominance was plant dependent, with *B. tabaci* dominant on poinsettia and *T. vaporariorum* on green bean. The high adult densities on the more suitable plant apparently reduced the settling of the competing species (80).

### Interactions Between Whiteflies and Other Herbivores

Interspecific interactions between whiteflies and other herbivores should be common (1, 36, 103, 110). In Latin America, the cassava mealybug may share the same plant with the whitefly *Aleurotrachelus socialis* Bondar. When coexistence was experimentally tested, the duration of larval development of the mealybug was significantly prolonged; reciprocal effects were not tested (36). When whiteflies interact with mobile herbivores, it is harder to discriminate between direct and plant-mediated mechanisms. For example, first-instar larvae of the cabbage looper, *Trichoplusia ni* (Hübner), placed on *B. tabaci*-infested collards appeared more frequently on the adaxial, whitefly-free side of the leaf; their developmental duration was prolonged; and their growth rate and survival were reduced (67). Early-instar caterpillars are severely affected, probably because the whitefly may prevent access to leaf tissue and induce resistance of the plant (67). The presence of *B. tabaci* negatively affected the preference and performance of leafminers (Diptera: Agromyzidae) on various crops (66, 135). These interactions were asymmetric, as leafminers show no notable effect on *B. tabaci* (66). The effects are obvious when both insects share a leaf, but they are also systemic (i.e., when whiteflies and leafminers are spatially separated), indicating that the mechanism is indirect and plant mediated.

The case of whitefly-mite interactions deserves special attention. In a factorial field experiment, cotton seedlings were initially infested with the strawberry spider mite, *Tetranychus turkestanii* Ugarov & Nikolski. Later, the induced plant responses to spider mites negatively affected *B. tabaci* densities

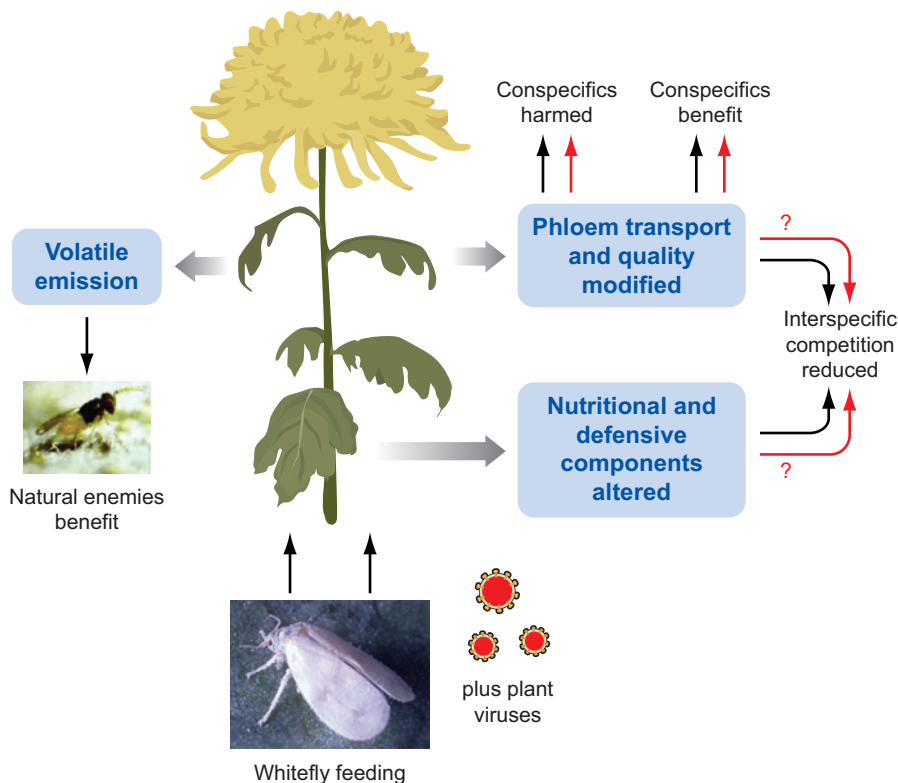
(1). The reciprocal effects of whiteflies on mites were not tested. Some mites established a unique phoretic relationship with whiteflies. The broad mite, *Polyphagotarsonemus latus* (Banks), is a widely distributed polyphagous pest of vegetables frequently shared with whiteflies (39). Although the mites may attach themselves to several phytophagous insects, they are attracted to Aleyrodidae (39, 101), reacting to whitefly wax particles as major olfactory attractants (119). Mites benefit via passive dispersal among hosts and sites, whereas the whiteflies may face direct competition with mites via their influence on the shared plants (1). The role of the host plant in such complex interactions awaits further research.

In conclusion, the outcomes of the interspecific interactions between whiteflies and other herbivores depend on several factors including the sequence of colonization, plant suitability and characteristics (constitutive

and induced), and the density and feeding mode of the other herbivores. Whiteflies may also benefit from conspecific feeding aggregation (facilitation) via sink modification, which may reduce the nutritional quality of the plants to other, especially non-sap-feeding, herbivores (Figure 1). It appears that *B. tabaci* is less sensitive to induced plant responses than other herbivores (66, 68, 82, but see 1).

## PLANT-MEDIATED INTERACTIONS WITH NATURAL ENEMIES

A thorough understanding of the role of natural enemies within the tritrophic pyramid is needed before we can comprehend the evolutionary processes and forces that shape trophic relationships (108). Multiple complex interactions and reciprocal selective pressures across all trophic levels have been widely demonstrated (35, 98). For example,



**Figure 1**

The effects of plant-induced responses to whitefly feeding on herbivores (whiteflies and non-whiteflies) and natural enemies. Red lines represent scenarios in which plant viruses are transmitted by the feeding whiteflies.

plant traits may protect herbivores (enemy-free space) or recruit, accommodate, and support natural enemies (plant guards). This concept has been extended to entomopathogens (25, 38) and has a significant role in agroecosystems (24).

Plant constitutive (chemical and morphological) and induced traits may affect natural enemies directly or indirectly (via their influence on the whiteflies) at all stages of attack, including plant and host location, handling, and feeding, as well as their persistence and survival. In their detailed review, van Lenteren & Noldus (128) concluded that the complex whitefly-plant interactions should be considered in the tritrophic context rather than as plain bilateral relationships. We agree with their view in the following discussion, which is taxonomically (rather than functionally) divided into arthropods (predators and parasitoids) and entomopathogens.

### Predators and Parasitoids

The direct and indirect effects of plants upon natural enemies have long been recognized as important factors in the tritrophic interaction and therefore have been the subject of numerous studies (35, 37, 54, 98). In the case of whiteflies, whose immatures are small sessile organisms that live closely within the sphere of the leaf's microatmosphere, the importance of plant features is compounded.

**Host plant location and selection.** Plant location precedes host location for both predators and parasitoids. For that purpose they may use visual and/or chemical plant traits that appear to be plant species related (51, 60, 63, 84, 127). For example, the parasitoids *Encarsia formosa* Gahan (112) and *Eretmocerus eremicus* Rose & Zolnerowich (10) were attracted from a distance to plant cues (leaf coloration). Sharon et al. (118) showed that *Eretmocerus mundus* Mercet used plant volatiles to differentiate between two cassava varieties, and that it frequented the variety that was also attractive to *B. tabaci*.

Induced volatile emission by plant-fed whiteflies may also attract natural enemies. Exposure of bean leaves to adult *B. tabaci* induced the emission of a blend of volatile compounds that differed from those emitted from uninfested bean plants. Females of *E. formosa* were attracted to synthetic samples of these compounds; the most effective was a mixture of (*Z*)-3-hexen-1-ol and 3-octanone (8). In contrast, *B. tabaci* did not induce volatile emission from cotton leaves but did suppress the volatile emission induced by simultaneously feeding caterpillars (111). Predators too are attracted to volatiles emitted from whitefly-infested plants (87, 97), although the specific cues have not been identified. The technological and conceptual progress in this field during the past decade should be more intensively used in whitefly research.

This review does not explore host plant selection by whiteflies (7, 68, 128). However, it is noteworthy that the presence of natural enemies (especially predators) may also affect plant selection by whiteflies. The oviposition rate of *B. tabaci* was reduced on leaves exposed to lacewing larvae (77), and adult whiteflies avoided cucumber plants with predatory phytoseiid mites (95). In both cases, the cues involved (direct or plant mediated) are unknown.

### The Effects of Leaf Surface Features on Predators and Parasitoids

Leaf surface features that affect the whiteflies may also critically affect the natural enemies (20, 21, 32, 56, 84, 120). Leaf tomentosity has enjoyed most research efforts (92; see below), although additional leaf surface features such as waxes are also important. For example, collard varieties with reduced leaf wax (glossy) are resistant to *B. tabaci* but exert mixed effects on the parasitoid community (85).

**Leaf pubescence and whitefly predators.** Varying degrees of leaf pubescence affect both prey and predators. Experiments on the detailed effects of tomentosity yielded

contradictory outcomes, which might stem from the predator species, differential influences of the plant, and specific environmental conditions. Some coccinellids such as *Serangium parcesetosum* Sicard and *Coleomegilla maculata* (DeGeer) appeared to prefer hairy plant species (2, 47), on which their larvae may escape predation (primarily cannibalism). The behavior (and fitness) of other species was negatively affected by leaf hairiness. Cotton leaf hairs prevented *Delphastus catalinae* (Horn) [as *D. pusillus* (LeConte)] from switching between intensive and extensive search patterns, blocking its innate searching activity (52). Searching for nymphs, the beetles adopted a unique foraging pattern: As they walked on top of the trichomes they dove onto the leaf surface instead of walking on it. On poinsettia, a 15% reduction in trichome density increased both oviposition and consumption rates of *B. tabaci* (59), whereas on hairy cotton leaves, *D. catalinae* collected trapped honeydew but would not consume adult whiteflies (52). Finally, leaf pubescence does not necessarily hamper the overall predation rates of the beetles. On tomatoes, longer residence time on the hairy leaves compensated for the relatively lower fecundity and reduced mobility of the lady beetles (61).

#### Leaf pubescence and whitefly parasitoids.

The affects of leaf pubescence on the level of parasitism is species (parasitoid) dependent (84). Although on completely smooth leaves parasitoids may walk too fast, failing to locate whitefly nymphs (127), in general, leaf pubescence influences parasitoid searching motivation, residence time, walking speed, ability to antennate, host probing, and oviposition, and may thus reduce parasitism rates (32, 49, 58, 127, but see 123). Leaf pubescence usually deters parasitoids, although several reports suggest that some performance parameters may actually increase on such leaves. For example, although finding, feeding, and parasitism of *B. tabaci* by *Encarsia* spp. increased on poinsettia cultivars with 15% less trichomes, adult wasp emergence rates were higher on

hairier plants (59). Female *Eretmocerus eremicus* (as sp. nr. *californicus*) seldom remained on hairy melon (versus smooth cotton), where their locomotion and host-finding abilities were reduced. However, those remaining on the melons had higher parasitism rates of *B. tabaci* (58). On hairy leaves the whitefly nymph margins often curl asymmetrically around leaf hairs, creating a gap over the leaf surface, making them more accessible to *E. eremicus*, which oviposits between the whitefly and the leaf (58, see also 32).

#### Leaf pubescence and whitefly morphology.

In the tritrophic context, leaf pubescence may induce morphological variations based on phenotypic plasticity in whitefly nymphs. Whiteflies reared on trichome-covered leaves often develop setose nymphs, in contrast to relatively asetose conspecifics on glabrous leaves (53, 54, 93). These features affect prey selection by predatory beetles in favor of asetose whitefly nymphs. However, the overall consumption rates of setose or smooth *B. tabaci* phenotypes were not affected (52).

#### The Influence of Leaf Chemistry (Nutrients and Defensive Compounds) on Natural Enemies

Plant chemical components can affect natural enemies both directly and through the quality of the whiteflies and their acquired secondary metabolites. Plant defense may be directly detrimental to natural enemies. For example, sticky latex exudates in lettuce inflorescence (*Lactuca sativa* L.) trap or deter lacewings and lady beetles (37, see also 48). Additional, direct (positive and negative) chemically based plant effects can operate on omnivorous enemies (especially predators) that also feed on plant material such as floral and extrafloral nectaries, pollen, and sap (43). Oviposition preference of the omnivorous mirid *Dicyphus hesperus* Knight is probably based on the plant's defensive traits and on its nutritional suitability for their progeny (114). Phytoseiid mites

used for whitefly control feed, survive, and reproduce on pollen, leaves, and *B. tabaci* honeydew (96). Omnivorous predators are also affected by induced plant responses. The only study examining this pathway found that resistance triggered by spider mites in cotton resulted in fewer minute pirate bugs, *Orius tristicolor* (White), whereas populations of bigeyed bugs (*Geocoris* spp.) remained intact. Both predators also feed on plant sap, but the eggs of the former only develop within the plant tissue, making them more vulnerable to defensive plant traits (1).

Indirect (via the whiteflies) plant-mediated effects on natural enemies are common, although the exact mechanism(s) is usually not known. Predatory lacewings failed to reach pupation when feeding on *B. tabaci* on lima beans and poinsettia, probably because of their poor nutritional value (77). Similarly, *S. parcesetosum* has probably become adapted to the natal host plant on which it had been maintained (76) and indeed, its fitness is highly affected by the host plant (2).

The nutritional quality of whiteflies and their honeydew to natural enemies depends largely on the plant species and its physiological status (9, 28). This in turn is expected to affect whitefly parasitoid species that feed on host body fluids and honeydew (16, 121). Significantly smaller and less fecund *Eretmocerus mundus* adults were produced on *B. tabaci* nymphs that developed on sunflowers than on nymphs that developed on cabbage, although the size of the whitefly was similar (46). *Encarsia formosa* preferred *B. tabaci* developing on fertilized plants than on unfertilized ones. Host feeding by the wasps was more frequent on the fertilized plants and parasitism rates rose only on plants treated with calcium nitrate (6), indicating that the resources available to the plants can influence the ratio between parasitism and host-feeding rates. Whitefly control could be enhanced by a better understanding of the mechanisms involved in the indirect effects by which the plant's physiological status affects the activity and efficiency of their natural enemies.

## Entomopathogens

Fungi can actively penetrate the insect cuticle, an essential factor with respect to sap-feeders. Indeed, several mycoinsecticide products are used commercially for biological control (41).

Entomopathogenic nematodes that penetrate the nymphs through the vasiform orifice may also be used in whitefly control (29). The chemical composition and the physical structure (in particular leaf surface components) of the plant may fundamentally affect pathogenesis of these natural enemies.

**The effects of plant chemistry on entomopathogens.** Plant secondary metabolites can affect the viability and germination of conidia, the development of mycelia of entomopathogenic fungi, and the susceptibility of whiteflies to infection (75, 90, 105, but see 130). Nymphs of *T. vaporariorum* reared on cucumbers were more susceptible to infection by the mitosporic fungi than were nymphs reared on tomato. In vitro experiments revealed that the increased susceptibility might be due to the tomatine and other secondary metabolites sequestered by the whiteflies (75, 104). Nymphs of *B. tabaci* reared on cotton were less susceptible to fungi than were nymphs reared on melon, although gossypol (a dominant terpenoid in cotton) did not inhibit conidial germination (105).

**The effects of leaf and canopy traits on entomopathogens.** Phyllospheric microbiota, including fungal pathogens and entomopathogenic nematodes, are sensitive to temperature, insolation, UV radiation, and humidity. Plant traits may fundamentally affect these conditions. For example, humidity is maintained by the transpiration rate and thickness of the leaf boundary layer, with broad and hairy leaves tending to create thicker layers (12, 40, 90). Likewise, the lowest rate of *Steinernema feltiae* Filipjev (entomopathogenic nematode) infection of poinsettia-attacking *B. tabaci* was associated

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**PGPR:**

nonpathogenic plant  
growth-promoting  
rhizobacteria

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with its smooth and waxy leaf surface, which reduces the thickness of the leaf boundary layer (57).

Interactions between natural enemies may disrupt whitefly control (92). Control efforts can suffer from the direct effect of entomopathogens on whitefly predators (106). Thus, leaf pubescence that promotes fungal infection may provide the whiteflies with an enemy-free space (49, 50, 127). Finally, ants attending whitefly honeydew or extrafloral nectaries could interfere with the activity and efficiency of various natural enemies, including pathogens (109, 121).

### CONCLUDING REMARKS AND FUTURE RESEARCH

Whiteflies continue to attract great ecological, physiological, and agro-economic interest, primarily because of a few highly polyphagous pest species. In contrast to most oligophagous or monophagous (rarely studied) species, the polyphagous species' diversity and adaptability have facilitated worldwide spread, reaching high densities (14, 42, 45, 100). We have listed various (and complex) plant-mediated interactions between whiteflies, other herbivores, and natural enemies (**Figure 1**). Such interactions with natural enemies are better documented owing to their practical (pest management related) implications. However, taking into account the polyphagy, high densities, and wide distribution of some whitefly species, it is reasonable to assume that nontrophic (intraspecific and interspecific) interactions, including competition and facilitation, with other herbivores should be common. Understanding the role of the host plant in such interactions will improve our understanding of the mechanisms contributing to the whiteflies' (*B. tabaci* and *T. vaporariorum*) ecological success.

As van Lenteren & Noldus (128) predicted, tritrophic interactions (plant-whiteflies-natural enemies) appear to be

important driving mechanisms in the field. The knowledge and tools available today suggest that whitefly-plant interactions should in fact be viewed and studied from a multitrophic perspective (82). Promising directions could include topics such as understanding the effects of plant resources (e.g., the availability of water and nutrients) on the outcome of whitefly competition with herbivores and their natural enemies (6). The role of viruses, endosymbionts, and other microorganisms (e.g., PGPR) in enabling whiteflies to exploit host resources and interact with other organisms (71, 91, 134) also seems highly interesting. The fact that whiteflies might be recognized by the plant as pathogens (72) opens a fascinating opportunity to look at the complex plant-mediated interactions between kingdoms and to explore the crosstalk between various induced defense mechanisms employed by the multichallenged plants. What are the differences between induced plant responses to whiteflies versus other sap-feeders such as aphids? Finally, the capacity of whiteflies to induce biochemical changes in plants and their response to exogenous application of elicitors of plant defense mechanisms (BTH) provide opportunities for new pest control approaches (8, 11, 69, 91, 94, 122, 132).

*B. tabaci* and *T. vaporariorum* are widely distributed and can be easily cultured and maintained. These are well-studied species, and considering the complex interactions in which they are involved, they could serve as convenient models for testing key hypotheses in insect ecology and evolutionary biology. Studying these models may contribute to our understanding of the enemy-free space concept (50), the evolution of polyphagy (7), the plant vigor and stress hypotheses (68), the relative importance of bottom-up versus top-down effects on herbivores, and the evolution of plant-induced defenses against phloem-feeders (132). Such ecological principles, however, need to underpin applied pest management strategies.

## SUMMARY POINTS

1. The wide distribution, polyphagy, and the profound effect of some whitefly species on plants promote extensive and complex interactions with other organisms at all trophic levels.
2. The interactions between whiteflies and other organisms are often plant mediated. Apparently, the interactions with other herbivores are influenced primarily by induced plant responses.
3. Leaf traits, in particular pubescence, are the dominant plant-mediated factor affecting the natural enemies of whiteflies.
4. The effect of plant-induced responses on whiteflies and their natural enemies may have a potential use in pest management.
5. Future research that will address whiteflies in the context of multitrophic-level interactions is highly promising. Such interactions may include the plant (and its resources), other herbivores, natural enemies, and microorganisms.
6. The information gained following intense research of *B. tabaci* and *T. vaporariorum* could serve as a useful platform to test fundamental ecological and evolutionary hypotheses on insect-plant relationships. Ecological principles and hypotheses could promote successful and sustainable pest management.

## DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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