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Examining Plant-Parasitoid Interactions in Tritrophic Systems

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Examinando Interações Plantas - Parasitóides em Sistemas Tritróficos

RESUMO - A demonstração de que os parasitóides são atraídos pelos compostos voláteis liberados pelas plantas, em resposta ao ataque dos insetos herbívoros, gerou considerável interesse nos últimos dez anos. A liberação dos compostos voláteis pelas plantas ocorre não somente em resposta aos danos causados aos seus tecidos, mas ela é também, especificamente, iniciada pela exposição às secreções salivares dos herbívoros. Alguns compostos voláteis são armazenados nos tecidos vegetais e liberados no momento em que o dano ocorre, outros são induzidos pelo dano causado pelo herbívoro e são, geralmente, liberados, não apenas pelo tecido lesado, mas também pelas folhas não atacadas. Desse modo o dano causado em somente algumas folhas, resulta numa resposta sistêmica e na liberação de compostos voláteis por toda a planta. Novas evidências sugerem que os compostos voláteis induzidos pelos insetos herbívoros, além de facilmente detectáveis e de serem indicadores seguros da presença de herbívoros, podem ainda, transmitir informação específica, que permite aos parasitóides discriminarem a longa distância, espécies de herbívoros muito próximas. Daremos aqui uma visão geral dos desenvolvimentos mais recentes na investigação das interações plantas-parasitóides.

PALAVRAS CHAVE: Insecta, interações tritróficas, parasitóides, compostos voláteis.

ABSTRACT - The demonstration that parasitoids are attracted to volatile compounds released by plants in response to herbivore feeding has generated a great deal of interest over the past ten years. The release of volatile signals by plants occurs not only in response to tissue damage but is also specifically initiated by exposure to herbivore salivary secretions. Although some volatile compounds are stored in plant tissues and immediately released when damage occurs, others are induced by herbivore feeding and released not only from damaged tissue but also from undamaged leaves. Thus, damage localized to only a few leaves results in a systemic response and the release of volatiles from the entire plant. New evidence suggests that, in addition to being highly detectable and reliable indicators of herbivore presence, herbivore-induced plant volatiles may convey herbivore-specific information that allows parasitoids to discriminate even closely-related herbivore species at long range. Here we give an overview of the recent developments in the investigation of plant-parasitoid interactions.

KEYWORDS: Insecta, tritrophic interactions, parasitoids, plant chemicals, host location.

In nature, trophic relationships among organisms within a community rarely, if ever, consist only of simple food chains. More commonly, they comprise an extensive web of interactions extending across several trophic levels. The trophic relationships between plants, insect herbivores, and their parasitoids provide a good example of these complexities. These tritrophic interactions occur within a spatially diverse and dynamic physical and chemical environment and include all the various aggressive and defensive interactions among trophic levels (including morphological, behavioral and physiological relationships) as well as the inter- and intraspecific interactions within each trophic level. Such interactions are often tightly interwoven and highly interdependent.

One well-documented component of this interdependence is the release of volatile compounds from plants attacked by insect herbivores (Fig.1). These volatiles are used as cues by natural enemies of the herbivores to locate their host or prey (Dicke *et al.* 1990, Takabayashi *et al.* 1994, Turlings *et al.* 1990a,b, 1991a,b, De Moraes *et al.*, 1998). Thus, potential competitive advantages exist for plants that produce more effective chemical signals, for parasitoids that employ such signals more efficiently, and for herbivores that minimize the plants' response. Herbivores that defend themselves from parasitoid attack by sequestering toxic defense compounds produced by plants provide a similarly complicated example of ecological interdependence (Barbosa and Saunders 1985, Malcolm and Zalucki 1996).

Despite, and often because of, their tritrophic complexities, plant-herbivore-parasitoid systems are of great interest to researchers in evolutionary biology, behavioral and community ecology and the applied science of biological control. Among other things these systems present an excellent opportunity to explore the role of alternative behavioral strategies in parasitoid reproductive success because there appears to be a very direct link between many aspects of parasitoid reproductive ecology and relative fitness (Godfray 1994). In this review I present an overview of the recent work on one important aspect of the plant-herbivore-parasitoid systems, the interactions between plants and parasitoids, and discuss the importance of plant-produced cues for parasitoid foraging and host location.

Plant-Insect Tritrophic Systems

Until recently most of the theory and research on plant-insect interactions was focused on plant-herbivore interactions or on the interactions between plants and pollinators. But, as Price *et al.* (1980) pointed out, any comprehensive discussion of plant-insect relationships must also address the third trophic level.

The response of plants to herbivory can be quite complex and may involve traits that allow plants to escape, defend or tolerate herbivore attack (Rausher 1992). Plants employ numerous morphological and physiological defenses against herbivory. The majority of attention has been given to direct chemical defenses including toxins, repellents, antifeedants and digestibility reducers and to morphological defenses such as trichomes, surface waxes, and tough foliage (see Smith 1989, for a historical review). In addition, plants rely on indirect defenses that facilitate 'top-down" control of herbivores mediated by parasitoids, predators, and pathogens that exploit the herbivores as hosts or prey (i.e., extrinsic defenses in Price 1986).

Plant protection by natural enemies is well documented and has been manipulated in the development of biological control strategies in many crops (Dicke & Sabelis 1988, Whitman 1994, see DeBach & Rosen 1991 for a historical review). Plants are well placed to influence the efficiency of parasitism and predation and they mediate numerous interactions between entomophagous arthropods and herbivores. Their structures and products often supply essential resources for parasitoids and predators. In addition chemical and morphological plant attributes can affect the efficacy of biological control agents

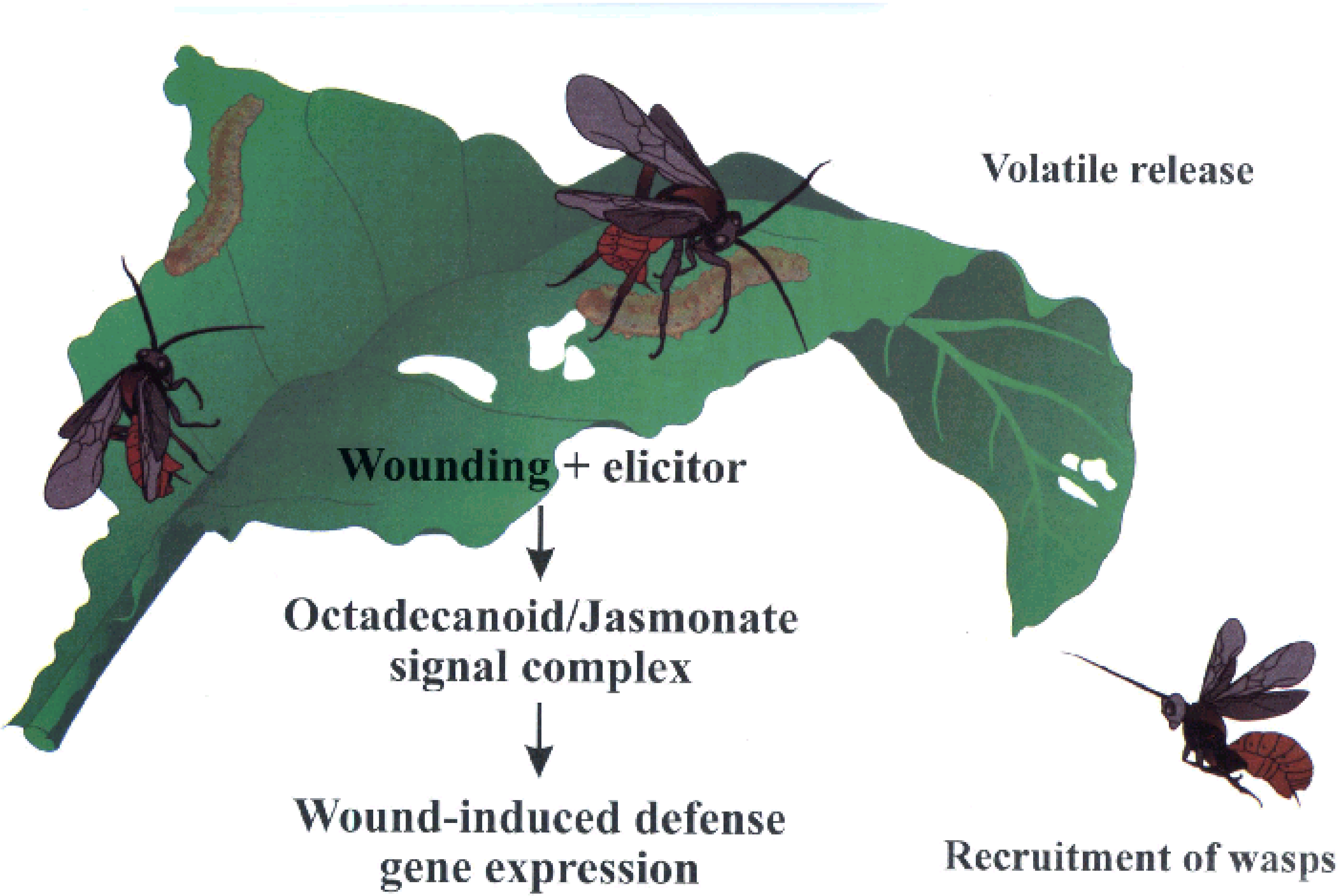

Figure 1. Volatile compounds are released by plants in response to insect feeding trigged by an interaction of elicitors from the oral secretions of insect herbivores with damaged plant tissue. These volatiles are used by some parasitoid wasps to locate their hosts.

by influencing their abundance, survival, development time, fecundity, and rate of attack.

Plants also influence the quality of parasitoids' herbivorous hosts by determining the quality of the host's nutrient intake (Vinson & Barbosa 1987). Several studies have shown that secondary compounds ingested by the host can negatively affect parasitoids (Vinson & Iwantsch 1980, Duffey *et al.* 1986, Rowell-Rahier & Pasteels 1990, Kester & Barbosa 1991). On the other hand secondary compounds can be positive to parasitoids. Toxins and low nutritional quality may weaken the herbivore's immune system, affecting its capacity to defend against parasitoid eggs (Salt 1964, van den Bosch 1964, Vinson & Barbosa 1987). For example, the ability of *Pieris rapae* (L.) to encapsulate the eggs of *Cotesia glomerate* (L.) depends on the species of plant which the host herbivore has fed upon (Benrey & Denno 1997).

Plant Signaling

In order to exploit arthropod herbivores, natural enemies must be able to locate small, highly dispersed targets within a complex spatial and chemical environment. Moreover, herbivores have evolved numerous adaptations to avoid being discovered and attacked (Vet & Dicke 1992). Members of the third trophic level often rely on information originating from plants to locate hosts. Plants provide both olfactory and visual signals used as foraging cues by parasitic and predaceous arthropods (Nordlund *et al.* 1988, Martin *et al.* 1990, Lewis *et al.* 1990, Ma.*et al.* 1992, Powell & Wright 1992, Wäckers & Lewis 1994, Dicke 1994, Godfray 1994, Whitman & Nordlund 1994, Turlings *et al.* 1995).

Apart from pheromones, the chemical compounds originating from herbivores are at most slightly volatile and can only be detected at close range (Vet & Dicke 1992). Thus parasitoids often rely on habitat cues for long range searching (Salt 1935, Doutt 1964, Vinson 1975, 1981, van Alphen & Vet 1986). Numerous studies document the key role of volatile allelochemicals emitted by plants as long range cues for parasitoids of insect herbivores (e.g., Elzen *et al.* 1983, 1984, Vinson *et al.* 1987, Navasero & Elzen 1989, Martin *et al.* 1990, Turlings *et al.* 1991a, 1991b, 1995, Udayagiri & Jones 1992, 1993, McCall *et al.* 1993, Ngi-Song *et al.* 1996). Some parasitoids use volatiles emitted by undamaged plants to locate the habitat and possibly the microhabitat of their host (e.g., Elzen *et al.* 1983, Ma *et al.* 1992, Ngi-Song *et al.* 1996). However, there are distinct advantages for parasitoids that can detect, differentiate, and respond to semiochemicals that distinguish plants damaged by their host from the surrounding environment.

Plant volatiles released in response to mechanical damage by herbivores, including green-leaf volatiles and constitutive secondary compounds, are known to be attractive to various parasitoids (Lecomte & Thibout 1984, Whitman & Eller 1990, Kester & Barbosa 1991, McAuslane *et al.* 1991, Udayagiri & Jones 1992, 1993, Steinberg *et al.* 1993, Mattiaci *et al.* 1994). Volatiles released in response to herbivore feeding are generally reliable indicators of herbivore presence and can potentially bring parasitoids in close proximity to their hosts.

Wind tunnel experiments with *Cotesia glomerata* (L.), a parasitoid of several pierid caterpillars, demonstrated that this parasitoid is attracted to artificially damaged cabbage leaves (Steinberg *et al.* 1993, Mattiaci *et al.* 1994). *C. glomerata* females prefer artificially damaged leaves over undamaged leaves, but host-damaged leaves, even in the absence of hosts and host by-products, are far more attractive than artificially damaged leaves (Steinberg *et al.* 1993, Mattiaci *et al.* 1994 De Moraes & Lewis, 1999). In a study with two parasitoids, *Cardiochiles nigriceps* (Vier.) and *Microplitis croceipes* (Cresson), De Moraes and Lewis (1999) demonstrated that these two species both depend primarily on herbivore-induced signals although these two species demonstrate a significant plant species preference: *C. nigriceps* for tobacco and *M. croceipes* for cotton. In choice experiments the odor of damaged plants of the less-preferred species was more attractive than that of undamaged plants of the preferred species. Additional studies with corn, lima bean, and cotton have demonstrated that plants are actively involved in the production and release of chemical cues that guide foraging parasitoids (see reviews in Dicke 1994, Stowe *et al.* 1995, Turlings *et al.* 1995, De Moraes *et al.* 1998). Turlings *et al.* (1991a, 1993a) showed that plants actively produce volatile chemicals in response to a substance associated with attacking herbivores. They demonstrated that plants produce chemicals in response to damage by larvae of several lepidopteran species and that the females of the generalist larval parasitoid *Cotesia marginiventris* (Cresson) learn to take advantage of the plant-produced volatiles to locate hosts after experiencing these volatiles in association with a host or host by-products.

When plants are attacked by insect herbivores (Fig.1), they emit compounds that are not produced in response to artificial damage (Dicke *et al.* 1990, Turlings *et al.* 1990a, De Moraes *et al.* 1998). These herbivore-induced compounds are emitted not only at the damaged site but also systemically from undamaged tissues (Dicke *et al.* 1990a, Turlings & Tumlinson 1992, Turlings *et al.* 1995, Röse *et al.* 1996, Cortesero *et al.* 1997, De Moraes *et al.* 1998). Production and release of volatiles is triggered at least in part by substance(s) in the oral secretion of herbivores (Turlings *et al.* 1993b, Mattiacci *et al.* 1995, Potting *et al.* 1995, Alborn *et al.* 1997). In the case of beet armyworm an elicitor has been identified and named as volicitin (Alborn *et al.* 1997). In cotton, the production of some volatiles is known to be an active process where several terpenoids are synthesized *de novo* in response to insect feeding (Paré & Tumlinson 1997).

In corn, application of herbivore regurgitate to artificially damaged sites induced the release of volatiles highly attractive to *M. croceipes* and *C. marginiventris* (Turlings & Tumlinson 1992, Turlings *et al.* 1993b). In some cases, plant volatiles provide specific information regarding the identity or developmental stage of the attacking herbivore (Turlings *et al.* 1990b, 1993a, Takabayashi *et al.* 1995, Du *et al.* 1996, De Moraes *et al.* 1998).

De Moraes *et al.* (1998) demonstrated that plant emissions can transmit herbivore species-specific information that is detectable by parasitoids. It was shown that tobacco and cotton each produce distinct volatile blends in response to damage by two closely related herbivore species, *Heliothis virescens* (Fab.) and *Helicoverpa zea* (Boddie). The specialist parasitic wasp *C. nigriceps* exploits these differences to distinguish infestations by its host, *H. virescens* from nonhosts. The production by these phylogenetically diverse plant species and exploitation by parasitoids of highly specific, information-rich chemical signals, keyed to individual herbivore species, demonstrates the high degree of sophistication that can exist in plant parasitoid chemical interactions.

Biosynthesis of Induced Plant Volatiles

As mentioned above the release of volatiles in response to herbivory is well documented. But little is yet known about how plants produce and regulate the blend of compounds released. So far four biosynthetic pathways (Fig. 2) have been identified which appear to be involved in the production of volatile signals (Paré & Tumlinson 1999). An outline of the metabolic pathways leading to plant volatile emissions is shown in Fig. 2. The isopropenoid precursor isopentenyl pyrophosphate serves as a substrate for monoterpenes and sesquiterpenes, the fatty acid/lipoxygenase pathway generates green leaf volatiles and jasmone, and the shikimic acid/tryptophan pathway results in the nitrogen containing product indole (Mann 1987). Green leaf volatiles are produced when leaves are damaged, independent of the agent causing the damage, and are primarily emitted from damaged leaf tissues. They are typically mixtures of C_6 alcohols, aldehydes, and esters produced by oxidation of membrane-de-

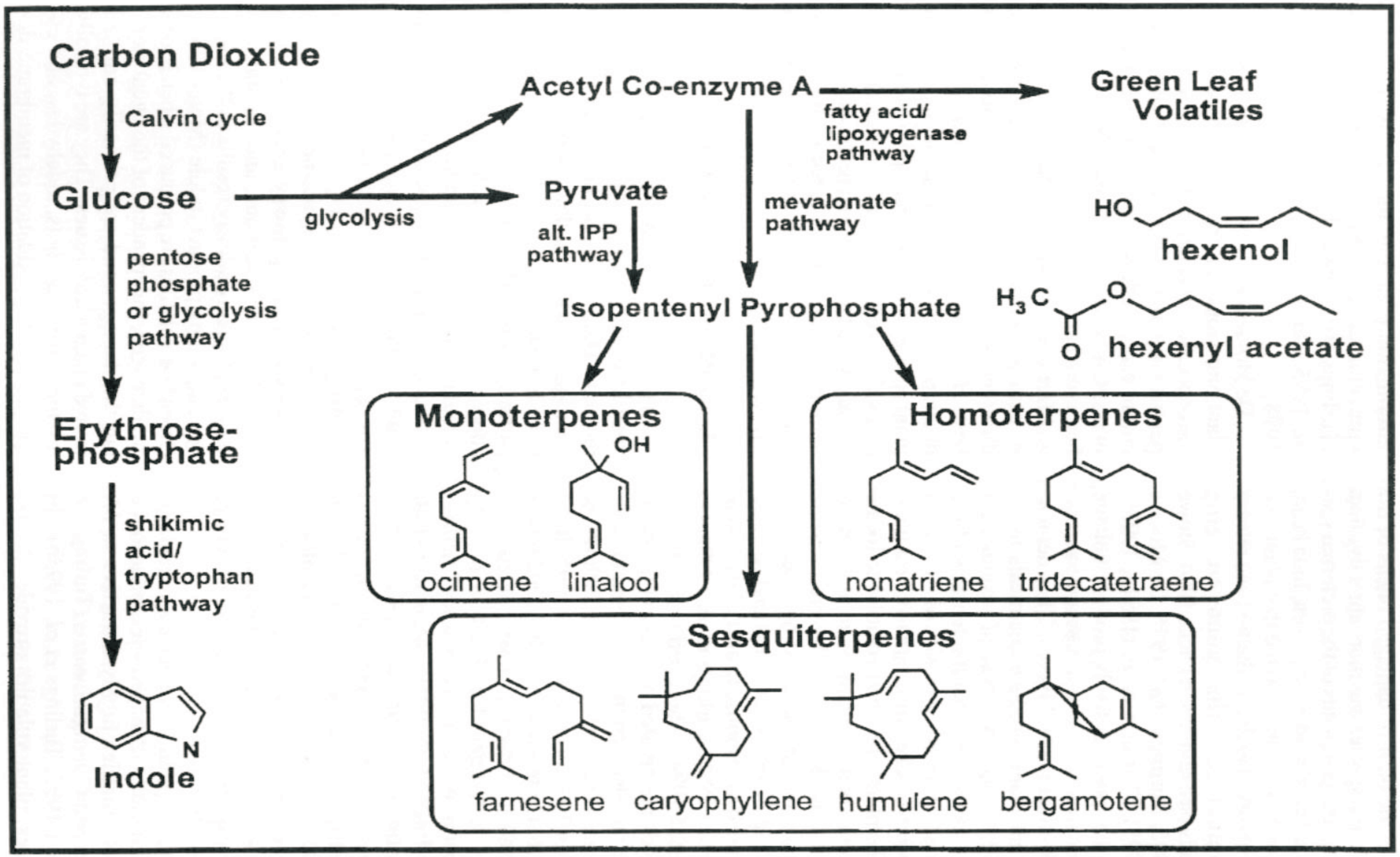

Figure 2. Metabolic pathways leading to volatile emissions from herbivore damaged plants and exemplary structure of volatile components (Paré & Tumlinson 1999).

rived fatty acids. In contrast, monoterpenes, homoterpenes, and sesquiterpenes are produced in response to herbivore damage and generally released not only from damaged tissue but also from undamaged leaves (Turlings *et al.* 1991a).

In the case of cotton, several monoterpenes and sesquiterpenes, along with the lypoxygenase products, are released immediately in response to damage. Another set of terpenoids and indole follow a diurnal pattern of release with a peak in the middle of the day (Loughrin *et al.* 1994). It is important to keep in mind that the release of compounds is highly variable across plant species and varieties and is also sensitive to the species of the herbivore (Dicke *et al.* 1990, Turlings *et al.* 1990b,1991a,b, Turlings & Benrey 1998, Takabayashi *et al.* 1991, Röse *et al.* 1996 & De Moraes *et al.* 1998).

Elicitors of Plant Volatiles

So far two elicitors of plant volatiles have been identified in the oral secretions of insect herbivores. Mattiaci *et al.* (1995) found that beta-glucosidase in *Pieris brassicae* (L.) caterpillars elicits the release of volatiles from cabbage leaves. The major active elicitor of the oral secretion of beet armyworm larvae was recently identified by Alborn *et al.* (1997) as (*N*-[17-hydroxylinolenoyl]-L-glutamine) and, as noted, was named volicitin. Volicitin, in both its natural and synthesized forms, induces corn seedlings to release the same blend of volatiles induced by herbivore feeding. This blend has been shown to be exploited as a host location cue by the parasitic wasps that attack this herbivore.

Despite the identification of these two elicitors, little is known about the pathway that leads to the synthesis and emission of these volatile compounds. It has been suggested that jasmonic acid, which is produced from linolenic acid by the octadecanoid signalling pathway, may be involved in the transduction sequence that triggers synthesis of volatile compounds by plants (Krumm *et al.* 1995). In the case of volicitin, which is an octadecatrienoate conjugated to an amino acid, this may suggest that the elicitor molecule interacts with the octadecanoid pathway in herbivore damaged plants (Alborn *et al.* 1997).

Parasitoid Foraging Behavior

For parasitoids, success in reproduction depends on overcoming the challenges of habitat identification, host location, host acceptance, host suitability and host regulation (Laing 1937, Flanders 1953, Doutt 1964, Vinson 1975, Vinson *et al.* 1998). As with all organisms, the life history characteristics of parasitoids are shaped by natural selection (involving key factors such as host ecology and the presence of competing species of parasitoids) acting within a framework of phylogenetic constraints (De Moraes *et al.* 1999). To succeed, parasitoids must develop efficient strategies for locating hosts in complicated heterogeneous environments and for overcoming host defenses and competitors. Such strategies will likely involve exploitation of numerous cues and foraging tactics at multiple spatial scales as well as the development of behavioral and physiological adaptations to the internal host environment. Given the complex and dynamic nature of the foraging environment, behavioral flexibility and the ability to interpret foraging cues in a context-dependent manner are at a premium. Thus it is not surprising that parasitoid behavioral phenotypes are often plastic and that learning based on prior experience plays an important role in shaping the foraging strategy of an individual parasitoid (Lewis & Tumlinson 1988, Turlings & Tumlinson 1992).

Parasitoid foraging efficiency is influenced by the interaction of many sources of variation including (1) genetic variation between individuals adapted to different foraging environments (Vet 1983, Drost *et al.* 1988, Hoy 1988, Prevost & Lewis 1990), (2) phenotypic plasticity of individuals allowing behavioral adaptation to different hosts or habitats (Lewis & Tumlinson 1988, Wardle & Borden 1989, Vet *et al.* 1990 Lewis *et al.*

1991), and (3) the parasitoids' physiological state with regard to non-host resources such as food, egg load, or mating opportunities (Takasu & Lewis 1993, Jervis & Kidd 1996, Sirot & Bernstein 1996). Numerous additional factors, such as climatic conditions, habitat type, and host density (Godfray 1994) also contribute to the foraging success of natural enemies.

Godfray (1994) recognized three broad categories of environmental cues used by parasitoids to locate hosts: (1) stimuli arising from the host itself, (2) stimuli indirectly associated with the presence of the host (e.g., odors released by the feeding activity of the herbivore such as plant allelochemicals and mandibular and labial gland secretions), and (3) stimuli arising from the host's microhabitat or food plant. Parasitoids' hosts presumably have faced continuous selection to avoid detection by remaining inconspicuous. This may be a major constraint on the evolution of long-range, host-searching strategies by parasitoids and may drive the evolution of indirect searching strategies, i.e., the exploitation of environmental information indirectly associated with the presence of the host (Vet & Dicke 1992).

The quality of an environmental host-location cue depends on its reliable association with the presence of a herbivore, the detectability of the stimulus (the ease of stimulus discovery) (Vet *et al.* 1995) and the information content of the signal (e.g., its taxonomic specificity) (De Moraes *et al.* 1998). All these characteristics presumably enhance searching efficiency and hence fitness (Vet *et al.* 1991, Wäckers & Lewis 1994, De Moraes *et al.* 1998). Environmental cues arising directly from the herbivore (Turlings *et al.* 1990a, Turlings & Tumlinson 1992) may be highly reliable and taxonomically specific indicators of host presence but are probably quite difficult to detect because herbivores are minor components of complex environments and because herbivores have evolved mechanisms to avoid detection by natural enemies (Vet *et al.* 1995). In contrast, constitutive plant cues are highly detectable but, in general, are not reliable indications of herbivore presence or identity.

The production and release by plants of specific volatile compounds in direct response to herbivore feeding (Turlings *et al.* 1993b) provides an additional set of cues that are reliably linked to the presence of the host and yet are produced in large quantities that increase their detectability. Indeed, such compounds seem to have been tailored by natural selection to serve as effective host-location cues for foraging parasitoids and predators. Moreover, these signals can have high information content. De Moraes *et al.* (1998) showed that highly specific signals are often released in response to individual herbivore species. Thus, plant-released compounds appear to represent the most effective cues for long-range host detection by parasitoids. Once an infested plant is located, cues directly or indirectly arising from the host itself become more important in short-range host location.

While it is generally recognized that olfaction is not the only sensory modality employed by natural enemies in locating hosts or prey (Vinson 1981, Wäckers 1994), few studies have examined the role of other factors in this process. Some investigators have stressed the importance of visual cues for host and prey finding by natural enemies. Not only do parasitoids show innate preferences for specific visual stimuli but they also are able to learn cues that are consistently associated with the presence of their hosts (Arthur 1966, Weseloh 1972, 1986, Wardle & Borden 1989, Wardle 1990, Ma *et al.* 1992, Wäckers 1994, Wäckers & Lewis 1994). Thus, the role of plant signals in the recruitment of natural enemies appears to be very complex. Numerous intrinsic and extrinsic factors can influence the quantity and quality of plant signals.

Conclusion

We are only beginning to appreciate the complexity of the physiological changes that occur within plants in response to herbivore attack and their effects on tritrophic interactions. It is clear that more detailed information will enhance our understanding of natural and agricultural ecosystems. Historically, the major approaches to biological control (i.e., importation, augmentation and conservation), have focused on identifying natural enemy species with desired characteristics and finding economical ways to generate large populations, either endemically or by release (Rosen & Huffaker 1983, DeBach & Rosen, 1991, Knipling 1995). Regardless of the approach used to employ parasitoids for biological control, knowledge of the mechanisms governing their host foraging behaviors will be important to the success of the program. Therefore, in order to extend and optimize biological control systems, it is important to gain insight into the mechanisms by which natural enemies locate and exploit their hosts, as well as the dynamics of competition between parasitoid species for host resources.

Our ability to achieve consistent and effective pest suppression through biological control depends on our ability to understand the complex interactions between natural enemies, herbivores and plants and to develop effective techniques for managing the genetic makeup and phenotypic expression of host plants and natural enemy populations as well as critical components of the target environment to optimize the performance of natural enemies. While a considerable amount of practical development remains to be done, it appears that parasitoids may be managed to enhance their effectiveness as biological control agents. Given the current decline in the effectiveness of available pesticides and the growing concern over their effects on ecological and human health, it is imperative that we develop the technology that is necessary to implement effective biological control methods as quickly as possible. Manipulating the behavior of parasitoids to improve their foraging effectiveness will clearly be an important component of any future integrated pest management program employing these agents.

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