Interactions in Entomology: Plant-Parasitoid Interaction in Tritrophic Systems[1]

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J. Entomol. Sci. 34(1): 31-39 (January 1999)

Abstract Tritrophic plant-herbivore-parasitoid interactions are highly complex and often tightly interwoven. Plant-parasitoid interactions are a fundamental component of such systems with profound implications both for parasitoid foraging efficiency and plant defense. Chemical, plant-based cues are the dominant cues used by parasitoids in long-range foraging to locate cryptic, highly-dispersed hosts within a complex physical and chemical environment. It is well documented that volatile chemical signals produced and released by plants specifically in response to herbivore feeding play an important role in parasitoid foraging. 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.

Keywords Tritrophic interactions, parasitoids, plant chemicals, host location.

The diverse interactions between plants, insect herbivores and parasitoids are of considerable interest to researchers in evolutionary biology, behavioral and community ecology and the applied science of biological control. These complex tritrophic interactions occur in a dynamic physical and chemical environment and comprise all the aggressive and defensive interactions among trophic levels (including morphological, behavioral and physiological relationships) as well as the inter- and intra-specific interactions within each trophic level. Such interactions are often tightly interwoven with one another and highly interdependent. For example, the foraging efficiency of parasitoids may be mediated by chemical cues produced by plants in response to herbivory. 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. A similarly complex example is provided by herbivores that defend themselves from parasitoid attack by sequestering toxic defense compounds produced by plants.

Despite their tritrophic complexities, such systems provide 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). The consequences of failing to find a host or of ovipositing on an unsuitable or unfavorable host are obvious and relatively easy to measure. In this review we describe some of the recent work on one important aspect of plant-herbivore-parasitoid systems, that being plant-

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[1] Received 13 August 1998; accepted for publication 18 September 1998.

parasitoid interactions and the importance of plant-produced cues for parasitoid foraging and host location.

In addition to being of critical importance for understanding the community dynamics of tritrophic systems, plant-parasitoid interactions are of significant interest to the applied science of biological control. 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 and Huffaker 1983, DeBach and Rosen 1991, Knipling 1995). In order to expand and optimize these approaches it is necessary to understand the mechanics of parasitoid foraging and host location. The ability to manipulate plant cues and parasitoids responses may facilitate the development of more efficient and effective biological control techniques. Such strategies could be particularly important when parasitoids are imported to new plant species or strains, when host densities are low, or when parasitoids are reared in the laboratory (in the absence of natural environmental cues) for subsequent release.

Parasitoids and plant defense. The strategies that plants employ to counter herbivores may be classified as direct and indirect defenses. Direct defenses against herbivory include chemical defenses such as toxins, repellents and digestibility reducers and morphological defenses such as trichomes, surface waxes and tough foliage (see Smith 1989, for a historical review). In addition, plants rely on indirect defenses provided by parasitoids and predators that use herbivores as hosts or prey [called extrinsic defenses by 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 and Sabelis 1988, Whitman 1994, see DeBach and Rosen 1991, for a historical review).

Numerous interactions between entomophagous arthropods and herbivores are mediated by plants, which are well placed to influence the efficiency of parasitism and predation. Plant structures and products can supply essential resources for parasitoids and predators. Chemical and morphological plant attributes affect the efficacy of biological control agents by influencing their abundance, survival, rate of herbivore attack, fecundity and development. Moreover, such traits can affect qualities of a herbivore that, in turn, affect the physiology, behavior or development of natural enemies.

Parasitoid foraging behavior. Parasitoids face many challenges in completing their reproductive cycles. Successful reproduction depends on appropriate habitat identification, host location, host acceptance, host suitability and frequently host regulation (Laing 1937, Flanders 1953, Doutt 1964, Vinson 1975, Vinson et al. 1998). Ongoing natural selection (involving key factors such as host ecology, the presence of competing species of parasitoids, natural enemies, plant demographic and genetics) in combination with phylogenetic constraints determines the life history of parasitoids (Godfray 1994, De Moraes et al. 1998a); to be successful a parasitoid must develop an efficient strategy for locating hosts in a complicated heterogeneous environment and for overcoming host defenses and the obstacles presented by competitors and natural enemies. Such a strategy will likely involve multiple cues and foraging tactics employed at multiple spatial scales as well as the development of behavioral and physiological adaptations to the host's internal 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 very important. Thus, it is not surprising that parasitoid behavioral phenotypes are often plastic and that learning plays an important role in shaping the foraging strategy of an individual parasitoid (Lewis and Tumlinson 1988, Turlings and 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 and Lewis 1990), (2) phenotypic plasticity of individuals allowing behavioral adaptation to different hosts or habitats (Lewis and Tumlinson 1988, Wardle and 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 and Lewis 1993, Jervis and Kidd 1996, Sirot and 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 remain inconspicuous to parasitoids, a factor that 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 and 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. 1998b). These cue characteristics presumably enhance searching efficiency and hence fitness (Vet et al. 1991, Wäckers and Lewis 1994, De Moraes et al. 1998b). Environmental cues arising directly from the herbivore (Turlings et al. 1990a; Turlings and 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. 1993a) provide 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 be ideal cues for foraging parasitoids and predators, especially host-specific species. Moreover, these compounds often exhibit high information content as specific cues and may be released in response to individual herbivore species (De Moraes 1998b). 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 1990, Wardle and Borden 1989, Ma et al. 1992, Wäckers 1994; Wäckers and 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.

Plant signaling. Plants play an important role in determining the ability of natural enemies to find herbivorous hosts or prey. Arthropod herbivores are small, highly dispersed components of a complex environment and have evolved adaptations to avoid predation and parasitization (Vet and Dicke 1992). Thus, members of the third trophic level often rely on information originating from plants to locate hosts at long range. Plants provide both olfactory and visual signals which are used as foraging cues by many parasitic and predaceous arthropods (Nordlund et al. 1988, Martin et al. 1990, Lewis et al. 1990, Ma et al. 1992, Powell and Wright 1992, Wäckers and Lewis 1994, Dicke 1994, Godfray 1994, Whitman and Nordlund 1994, Turlings et al. 1995).

Most chemical compounds originating from herbivores (other than pheromones) are slightly volatile or non-volatile and can only be detected at close range (Vet and Dicke 1992). Thus, parasitoids rely on habitat cues for long-range searching (Salt 1935, Doutt 1964, Vinson 1975, 1981, van Alphen and Vet 1986). For parasitoids of herbivorous insects, many studies document the key role of volatile allelochemicals emitted by plants (e.g., Elzen et al. 1983, 1984, Vinson et al. 1987, Navasero and Elzen 1989, Martin et al. 1990, Turlings et al. 1991a, 1991b, 1995, Udayagiri and Jones 1992, 1993, McCall et al. 1993, Ngi-Song et al. 1996). Some parasitoids use volatiles emitted by undamaged plants to locate the habitat of their host (e.g., Elzen et al. 1983, Ma et al. 1992, Ngi-Song et al. 1996). Although parasitoids can detect semiochemicals from undamaged plants and can use these cues to locate the habitat or possibly even the micro habitat of their hosts, there are distinct advantages to parasitoids deriving from the ability to detect, differentiate, and respond to semiochemicals that distinguish plants damaged by their host from the surrounding chemical environment.

Plant volatiles released in response to mechanical damage inflicted by herbivores, such as green-leaf volatiles or constitutive secondary compounds, are known to be attractive to parasitoids (Lecomte and Thibout 1984, Whitman and Eller 1990, Kester and Barbosa 1991, McAuslane et al 1991, Udayagiri and 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 Pieridae caterpillars, demonstrated that this parasitoid is attracted to artificially-damaged cabbage leaves (Steinberg et al. 1993, Mattiaci et al. 1994). *Cotesia glomerata* females showed a strong preference for artificially-damaged leaves over undamaged leaves, but host-damaged leaves, even in the absence of hosts and host by-products, were far more attractive than artificially-damaged leaves (Steinberg et al. 1993, Mattiaci et al. 1994). 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. 1998b). Turlings et al. (1991a, 1993b) showed that some plants, when damaged, actively produce volatile chemicals in response to a substance produced by the 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 *C. marginiventris* (Cresson) learn to take advantage of the plant-produced volatiles to locate hosts after experiencing these volatiles in association with host or host by-products.

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

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

Herbivore-specific signals. De Moraes et al. (1998b) recently 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* (F.) and *Helicoverpa zea* (Boddie). By exploiting herbivore-specific volatile emissions, the specialist parasitic wasp *Cardiochiles nigriceps* (Vier.) is able to distinguish between host and non-host infestations on phylogenetically distant plant species that produce varying chemical blends (volatile signals vary across plant species for each herbivore). The ability to exploit these differences to distinguish host from non-host infestations implies a level of behavioral plasticity on the part of these parasitoids that is in keeping with demonstrations that behavioral repertoires are flexible, involving learning and context-dependent analysis of chemical cues (Lewis and Tumlinson 1998). As indicated by herbivore-specific plant signaling parasitoids can exploit diverse chemical cues in a context-dependent manner on the basis of information content. Such a keen yet flexible detection system allows parasitoids to locate polyphagous host over a range of potential habitats.

By providing specific and reliable signals, plants may obtain a competitive advantage in the attraction of natural enemies, parasitoids on the other hand can concurrently improve their foraging efficiency by using these signals to distinguish host from non-host. The production by these phylogenetically diverse plant species and exploitation by parasitoids of highly specific, information-rich chemical signals, keyed to individual herbivore species, demonstrated the high degree of sophistication that exists in plant-parasitoid chemical interactions.

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