Understanding and Manipulating Plant Attributes to Enhance Biological Control

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This paper demonstrates the necessity to consider plants as an essential and interactive component of biological control practices. Plants not only possess direct chemical and morphological defenses against herbivores but also benefit from indirect defenses provided by parasitoids and predators, which use herbivores as hosts or prey. Plants play an active role in the interplay between entomophagous arthropods and herbivores and actually mediate many of the interactions, thereby influencing the intensity of protection received. Herein, we review how plant attributes influence natural enemy efficiency by providing shelter, mediating host/prey accessibility, providing host/prey finding cues, influencing host/prey suitability, mediating host/prey availability, and providing supplemental food sources for natural enemies. In light of this crucial role, we suggest ways of manipulating morphological and chemical attributes of crop plants for a more sustainable and balanced control of insect pests in agro-ecosystems. © 2000 Academic Press

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INTRODUCTION

Plants and insect herbivores have long been competing in an evolutionary race in which plants evolve to reduce consumption, while herbivores evolve to increase it (Futuyma and Keese, 1992; Harborne, 1993; Mauricio and Rausher, 1997). As a consequence, plants have developed a number of direct chemical and morphological defenses that limit herbivore attack (Rosenthal and Berenbaum, 1991; Harborne, 1993). Direct chemical defenses include production of toxins, repellents, and digestibility reducers, while morphological defenses include trichomes, spines, waxes, and tough

foliage. The value of these defenses was realized early in agriculture, and production practices based on the selection and use of different herbivore-resistant crop varieties have frequently been implemented (see Smith, 1989, for a historical review). Furthermore, with the progress of genetic engineering it is now possible to directly manipulate these defenses by inserting new genes into crop plants (Gasser and Fraley, 1989; Meeusen and Warren, 1989).

In addition to these direct defenses against herbivores, plants also benefit from indirect defenses provided by parasitoids and predators that use herbivores as hosts or prey (i.e., extrinsic defenses in Price, 1986). Protection from herbivores by entomophagous arthropods can be so striking that they are sometimes referred to as "plant bodyguards" (Dicke and Sabelis, 1988; Whitman, 1994). Plant protection by means of natural body guards is well documented and has led to the development of biological control practices in many crops (see DeBach and Rosen, 1991, for a historical review). Plants are not passive in the interplay between entomophagous arthropods and herbivores. Rather, they actually mediate many of the interactions and thereby increase or decrease the intensity of protection received. Chemical and morphological plant attributes can directly influence survival, fecundity, and foraging success of natural enemies on hosts or prey. These traits can also have indirect effects by affecting qualities of an herbivore that in turn affect the physiology, behavior, or development of natural enemies.

Plant breeding and biological control have mostly been parallel but independent pest management practices in the past (Price, 1986; van Lenteren *et al.,* 1995; Thomas and Waage, 1996). While plant breeders have almost exclusively focused on selecting varieties with enhanced direct defenses against pests, biological control workers have mainly concentrated on improving natural enemy traits, such as reproduction and host-finding efficacy. We feel that there is an urgent need for bridging these two pest management practices (Fig. 1). Studies are revealing substantial interactions be-

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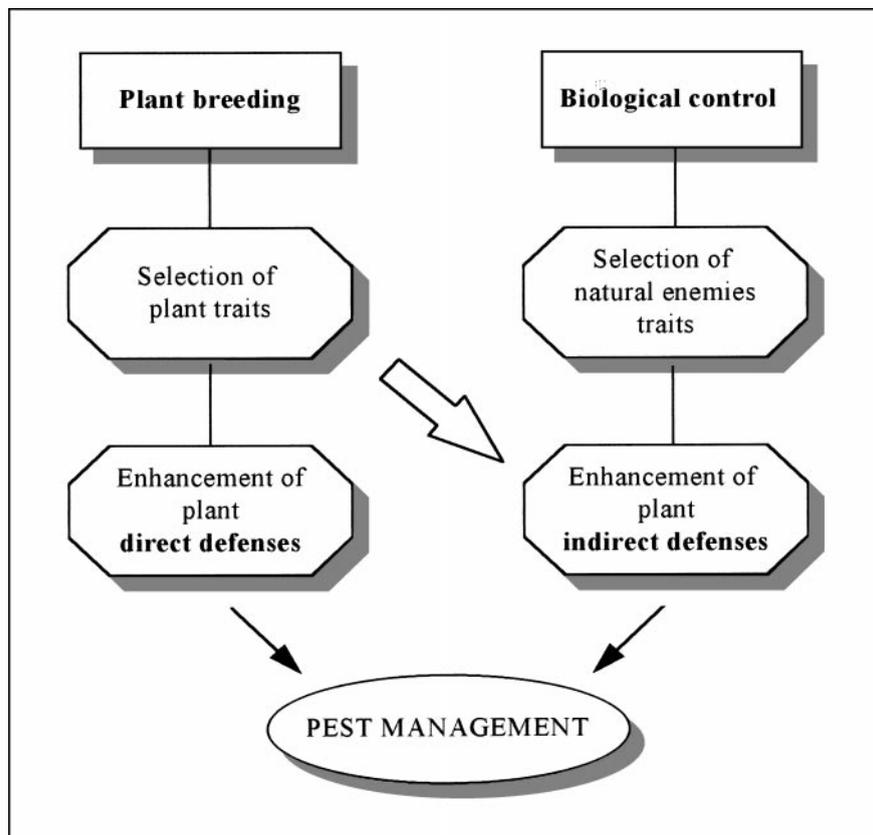
FIG. 1. The necessity of bridging plant breeding and biological control practices to improve crop protection. Crop plants should also be selected and bred for their capacity to enhance natural enemy efficacy (i.e., indirect defenses).

tween plant traits conferring herbivore resistance and biological control agents (see reviews in Bergman and Tingey, 1979; Boethel and Eikenbary, 1986; Shepard and Dahlman, 1988; Hare, 1992; Panda and Khush, 1995; Thomas and Waage, 1996; Gould, 1998), thereby emphasizing the importance of managing plant attributes from a tritrophic perspective. Yet, a key interaction is still often overlooked in current crop protection strategies: the possibility of manipulating the presence and expression of plant attributes to promote the third trophic level. Therefore, special emphasis should now be placed on breeding crop plants with natural enemy-enhancing traits.

In this paper, through key examples, we aim at demonstrating the essential role of plants in the interactions between natural enemies and herbivores. In light of this crucial role, we suggest ways of incorporating this important knowledge into future pest management strategies.

IMPORTANCE OF PLANT ATTRIBUTES TO NATURAL ENEMY EFFICIENCY

Several plant structures and products can supply parasitoids and predators with essential resources.

These plant attributes have the potential to affect abundance, survival, rate of herbivore attack, fecundity, and development of natural enemies and therefore are crucial in determining their efficacy as biological control agents.

Plants Provide Shelter

Many plants, including several cultivated species, have special structures that provide shelter for natural enemies (Fiala *et al.,* 1989, 1994; O'Dowd and Willson, 1989; Turner and Pemberton, 1989; O'Dowd, 1994; O'Dowd and Pemberton, 1994, 1998; Karban *et al.,* 1995; Rozario, 1995; Maschwitz *et al.,* 1996). Leaf domatia are examples of such structures. They are small pockets, cavities, pits, and/or tufts of trichomes located at the junction of primary and secondary veins on the leaf undersurface (Metcalfe and Chalk, 1979; Pemberton and Turner, 1989; Turner and Pemberton, 1989; Walter and O'Dowd, 1992; Whitman, 1994). Studies in which domatia were sampled for their occupants showed that many contained mites, predominantly predatory or fungivorous species (Pemberton and Turner, 1989; Walter and Denmark, 1991; Karban *et al.,* 1995; Rozario, 1995; Agrawal, 1997; Agrawal and

Karban, 1997; O'Dowd and Pemberton, 1998). Pemberton and Turner (1989), for example, sampled 32 plant species and found that the domatia of 31 of these species harbored mites. Beneficial mites were found in the domatia of 84% of the plants, while only 19% contained phytophagous mites. Leaf domatia not only shelter adult mites from adverse climatic conditions and other predators but they also serve as protected nurseries for mite eggs and larvae (Walter and O'Dowd, 1992; Whitman, 1994; Walter, 1996). Their presence has often been hypothesized to be correlated with plant protection and was even demonstrated in one study (Grostal and O'Dowd, 1994). When the domatia from leaves of *Viburnum tinus* L. were removed, the abundance, distribution, and reproduction of predatory mites were reduced as well as their prey consumption (Grostal and O'Dowd, 1994). More recently, Agrawal and Karban (1997) showed a positive correlation between presence of domatia on cotton plants (*Gossypium hirsutum* L.) and number of predatory arthropods, such as *Frankliniella occidentalis* (Pergande), *Geocoris* spp., and *Orius tristicolor* (White). In addition, they demonstrated that plants with domatia hosted smaller populations of herbivorous mites and had an overall yield improved by almost 30%.

Ant domatia are other plant structures that provide shelter to natural enemies. They usually are cavities or holes in a variety of plant parts, including stems, roots, leaves, and spines (see Whitman, 1994 for detailed descriptions), which are used as nesting sites by a variety of ant species (e.g., Fonseca, 1993; Fiala *et al.,* 1994; Maschwitz *et al.,* 1996). These ants are usually aggressive and protect plants against herbivore damage (Schupp, 1986; Fiala *et al.,* 1989, 1994). Mutual benefits to plants and ants can be so important that some species are unable to survive without each other (Janzen, 1966).

Other plant morphological traits, such as prominent leaf veins or moderate pubescence, can provide sheltered habitats for small natural enemies and promote their abundance (Drowning and Moillet, 1967; Walter and O'Dowd, 1992; Karban *et al.,* 1995; Walter, 1996). In temperate regions, such structures can supply shelter for overwintering predators and parasitoids and constitute a key factor in the maintenance of their populations (Hance and Boivin, 1993; Corbett and Rosenheim, 1996; Elkassabany *et al.,* 1996).

Plants Mediate Host/Prey Accessibility

Morphological plant traits can also affect the foraging success of natural enemies. Factors such as foliar pubescence, glandular trichomes, waxy leaf surface, leaf toughness, and plant architecture can either impede or facilitate predator and parasitoid movement and thus significantly influence encounter rate with hosts or prey (Obrycki *et al.,* 1983; Obrycki, 1986;

Schuster and Calderon, 1986; Kauffman and Kennedy, 1989; Kareiva and Sahakian, 1990; Grevstad and Klepetka, 1992; Farrar *et al.,* 1994; Weisser, 1995; Vohland, 1996; Sutterlin and van Lenteren, 1997).

A negative influence of plant pubescence on parasitism by insect parasitoids has been shown in a number of crop species (Elsey and Chaplin, 1978, in tobacco [*Nicotiana tabacum* L.]; Obrycki *et al.,* 1983, in potato [*Solanum tuberosum* L.]; Treacy *et al.,* 1986, in cotton [*G. hirsutum*]; McAuslane *et al.,* 1995, in peanut [*Arachis hypogaea* L.] and soybean [*Glycine max* L.]). van Lenteren *et al.,* (1995) provide examples of the different effects that leaf features, such as dense trichomes, can have on parasitoid behavior. The host-killing and parasitizing capacity of the whitefly parasitoid *Encarsia formosa* Gahan was lower on all evaluated cucumber varieties (*Cucumis sativus* L.) having high leaf hairiness. By comparing several cucumber varieties differing in their hair density, they found that the walking speed of this parasitoid was inversely proportional to the hairiness of the leaves. Moreover, the rate of turning of the parasitoid on hairy leaves was much higher, which decreased its searching efficiency. Also, hairy leaves retained whitefly honeydew, which increased parasitoid mortality, increased the time spent grooming, and decreased time available for searching for hosts.

Glandular trichomes can also have adverse effects on parasitoids and predators. These effects include toxicity (e.g., Kauffman and Kennedy, 1989) and reduced mobility (e.g., Obrycki and Tauber, 1984; van Haren *et al.,* 1987) and generally lead to reduced efficiency. However, this morphological trait can also favor natural enemies. For example, the development, reproduction, and prey consumption by the predatory mite *Phytoseius plumifer* (Canestrini and Fanzago) was enhanced on leaves with glandular trichomes (Rasmy and Elbanhawy, 1974).

A waxy surface and the shape of a leaf are other morphological traits that can affect prey- or host-finding rate by natural enemies. For example, slipperiness due to a waxy leaf surface caused ladybird beetles to frequently fall off crucifer plants and substantially decreased their consumption rate of aphid prey (Grevstad and Klepetka, 1992). However, leaf shape appeared to counter this effect. Predators did not fall as often from plants that had waxy leaves but also had more edges and fewer flat surfaces. In another study (Eigenbrode *et al.,* 1995), predators such as *Chrysoperla carnea* (Stephens), *Orius insidiosus* (Say), and *Hippodamia convergens* Guerin-Meneville were shown to be more effective in reducing populations of *Plutella xylostella* L. on a cabbage (*Brassica oleracea* var. *capitata* L.) variety with glossy surface waxes than on a normal-wax cabbage variety. Increased effectiveness was related to improved mobility of these predators on

glossy leaf surfaces. Wax debris that accumulated on tarsae impeded the mobility of predators walking on the normal-wax cabbage variety but not on glossy cabbage (Eigenbrode *et al.,* 1996).

Plants Provide Host/Prey Finding Cues

Plants play an important role in the ability of natural enemies to find hosts or prey. Not only are herbivores small components of a complex environment but in addition they have evolved to be inconspicuous in order to avoid predation and parasitization (Vet and Dicke, 1992). Therefore, parasitoids and predators often need to resort to plant information to locate their victims from a distance. Plants provide both olfactory and visual signals that are used as cues by foraging parasitic and predaceous arthropods (Nordlund *et al.,* 1988; Lewis and Martin, 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; Takabayashi and Dicke, 1996; Drukker *et al.,* 1995; Potting *et al.,* 1995; Geervliet *et al.,* 1996; Bertschy *et al.,* 1997; Sullivan *et al.,* 1997; Powell *et al.,* 1998).

Parasitoid foraging behavior offers striking evidence of the active involvement of plants in the recruitment of arthropods as body guards against herbivores. Most compounds emanating from herbivores (other than pheromones) are slightly volatile or nonvolatile and can only be detected at close range (Vet and Dicke, 1992). Therefore, to restrict prospected areas, parasitoids often first search for habitats where hosts are likely to be present (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 in this process (e.g., Elzen *et al.,* 1983, 1984; Vinson *et al.,* 1987; Navasero and Elzen, 1989; Martin *et al.,* 1990; Turlings *et al.,* 1991a,b, 1995; Udayagiri and Jones, 1992, 1993; McCall *et al.,* 1993; Agelopoulos and Keller, 1994a,b; Ngi-Song *et al.,* 1996). Some species use volatiles emitted by undamaged plants to locate the habitat of their host (e.g., Elzen *et al.,* 1983; Ma *et al.,* 1992; Cortesero *et al.,* 1993; Ngi-Song *et al.,* 1996; Benrey *et al.,* 1997; Takabayashi *et al.,* 1998). However, these volatiles are poor indicators of actual host presence and parasitoids must also resort to signals more directly correlated with host presence. Once again, such signals may originate from plants in many cases. Many volatiles released as a result of mechanical damage inflicted on plants by herbivores, such as green leafy 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; Steinberg *et al.,* 1993; Mattiacci *et al.,* 1994). These volatiles released concomitantly with herbivore feeding

damage are reliable indicators of herbivore presence and can potentially bring parasitoids into close proximity to their hosts. For example, wind tunnel experiments with *Cotesia glomerata* (L.), a parasitoid of larvae of several pierid species, showed that this parasitoid was attracted to artificially damaged Brussels sprouts (*Brassica oleracea* L. var. *gemmifera*) leaves (Steinberg *et al.,* 1993; Mattiacci *et al.,* 1994). *C. glomerata* females had a strong preference for artificially damaged leaves over undamaged leaves but host-damaged leaves, although free of hosts and host by-products, were far more attractive than artificially damaged leaves. Actually, studies with corn (*Zea mays* L.), lima bean (*Phaseolus lunatus* L.), and cotton (*G. hirsutum*) demonstrated that plants were actively involved in the production and release of chemical cues guiding host-foraging parasitoids (see reviews in Dicke, 1994; Stowe *et al.,* 1995; Turlings *et al.,* 1995). Indeed, when plants are attacked by insect herbivores, they may emit specific compounds that are not produced after artificial damage only (Dicke *et al.,* 1990a; Turlings *et al.,* 1990a; Paré and Tumlinson, 1997). These herbivory-induced compounds are emitted not only at the damaged site but also systemically by the entire plant (Dicke *et al.,* 1990a; Turlings and Tumlinson, 1992; Turlings *et al.,* 1995; Röse *et al.,* 1996; Cortesero *et al.,* 1997). The release of such induced compounds appears to be triggered by a factor present in the herbivore's saliva (Turlings *et al.,* 1993a; Mattiacci *et al.,* 1995; Potting *et al.,* 1995; Alborn *et al.,* 1997). In corn (*Z. mays*), for example, applying herbivore regurgitate onto artificially damaged sites or placing the cut stem of a plant in herbivore regurgitate solutions induced the release of volatiles highly attractive to the parasitoids *Microplitis croceipes* (Cresson) and *Cotesia marginiventris* (Cresson) (Turlings and Tumlinson, 1992; Turlings *et al.,* 1993a). The active compounds in the herbivore saliva have been identified in a few host plant complexes (*Pieris brassicae* L./*B. oleracea:* Mattiacci *et al.,* 1995; *Spodoptera exigua* [Hübner]/*Z. mays:* Alborn *et al.,* 1997). Different types of elicitors were involved in these two host plant complexes; cabbage responded to an enzyme, the β-glucosidase, while corn responded to *N*-(17-hydroxylinolenoyl)-L-glutamine, a compound named volicitin.

Furthermore, in some cases, plants not only signal general herbivore attack but also provide more specific information on the identity or the developmental stage of the herbivore causing the damage (Turlings *et al.,* 1990b, 1993b; Takabayashi *et al.,* 1995; Du *et al.,* 1996; DeMoraes *et al.,* 1998). In such cases, plant signals can facilitate the recruitment of specialized body guards.

Remarkable similarities exist between the involvement of plants in host finding by parasitoids and in prey finding by predatory mites (Dicke *et al.,* 1990a; Dicke, 1994; Takabayashi *et al.,* 1994). Plant-induced

volatiles allow predatory mites to discriminate between plants infested with spider mite prey and uninfested plants (Sabelis and van de Baan, 1983; Takabayashi *et al.,* 1994). Infested plants emit a number of volatiles that are not emitted by undamaged or by artificially damaged plants (Dicke and Sabelis, 1988; Dicke *et al.,* 1990b). Differences in volatiles released by plants that are attacked by different species of spider mites allow predatory mites to discriminate between these plants from a distance (Takabayashi *et al.,* 1991a). The release of volatiles induced by herbivore damage is systemic (Dicke *et al.,* 1990a; Takabayashi *et al.,* 1991b). Furthermore, uninfested plants exposed to volatiles emitted by spider mite-infested plants may also release volatiles that attract predatory mites (Bruin *et al.,* 1992, 1995) and attract even more natural enemies to a pest-infested area.

The role of plant chemical signals in the orientation of other predator species toward their prey is less well documented. However, evidence of use of plant-produced signals exists for predators such as lacewings (e.g., Flint *et al.,* 1979), predatory pentatomids (e.g., Greany and Hagen, 1981), predatory wasps (e.g., Spadbery, 1973), coccinellids (e.g., Ponsonby and Copland, 1995), and other predatory beetles (e.g., Wyatt *et al.,* 1993).

Finally, even though it is generally recognized that olfaction is not the only sensory modality involved in locating hosts or prey (Vinson, 1981; Wäckers, 1994), few studies are available on the influence of physical factors, such as color or shape of the plant, involved in this process. Studies on the foraging behavior of parasitoids illustrate the potential importance of vision for host- and prey-finding by natural enemies. Not only do parasitoids show innate preferences for specific visual cues but they are also able to learn cues that are consistently associated with the presence of their hosts (Arthur, 1966; Weseloh, 1972, 1986; Wardle, 1990; Wardle and Borden, 1990; 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 complex and dynamic. Numerous intrinsic as well as extrinsic factors can influence quantity and quality of plant signals (Nettles, 1979; Elzen *et al.,* 1985, 1986; van Emden, 1986; Dicke *et al.,* 1990a; Turlings *et al.,* 1993b; Takabayashi *et al.,* 1994, 1995; Loughrin *et al.,* 1995; Du *et al.,* 1996; Rapusas *et al.,* 1996). As we will discuss in the second part of this paper, manipulation of these factors could be used to enhance the abundance and host-finding efficiency of natural enemies in the field.

Plants Influence Host/Prey Suitability

Plant quality influences the suitability of herbivores as hosts or prey for natural enemies. Toxic allelochemicals occurring in plants are often sequestered in the herbivores' hemolymph and the presence of these chemicals can affect development and survival of parasitoid progeny (Barbosa *et al.,* 1982; Duffey and Bloem, 1986; Duffey *et al.,* 1986; Barbosa, 1988; van Emden, 1995; see Kester and Barbosa, 1991 for a review of the detrimental effects of nicotine absorbed in the hemolymph of *Manduca sexta* L. larvae on the parasitoid *Cotesia congregata* [Say]). Sequestered secondary plant compounds can also affect host or prey acceptance. For example, larvae of the sawfly *Rhadinoceraea nodicornis* Konow store in their hemolymph toxic alkaloids originating from their host plant (Schaffner *et al.,* 1994). These authors found that the hemolymph of sawfly larvae was highly deterrent and toxic to ants, spiders, and bushcrickets.

Also, the nutritious quality of plants for herbivores can be altered by environmental conditions, which in turn affect their usability for parasitoids and predators (Fox *et al.,* 1990; Fox and Eisenbach, 1992; Roth and Lindroth, 1995; Walde, 1995; Stadler and Mackauer, 1996). Plant nitrogen content, for example, appeared to influence parasitization of the diamondback moth by the parasitoid *Diadegma insulare* Cresson (Fox *et al.,* 1990). Fewer larvae were parasitized when they fed on unfertilized collard plants (*B. oleracea*) than on fertilized plants. Similar results were found with *E. formosa* (Bentz *et al.,* 1996). Parasitization of the whitefly *Bemisia argentifolii* Bellows and Perring and host feeding were higher on fertilized than on nonfertilized poinsettias (*Euphorbia pulcherrina* [Willd.]).

Furthermore, with the recent advent of genetically engineered crops that produce insecticidal or antifeedant proteins, the question of the influence of plant quality on natural enemies has reached a new dimension. While biopesticides (such as *Bacillus thuringiensis* Berliner (*Bt*) insecticides) used in foliar applications are generally considered highly selective with little or no detrimental effect on natural enemies (Croft, 1990), transgenic plants that produce toxic compounds could affect these beneficial organisms quite differently (Hilbeck *et al.,* 1998a,b). Indeed, with most transgenic plants, phytophagous insects are exposed to high levels of toxic compounds for extended periods of time (Koziel *et al.,* 1993). Therefore, most, if not all, available herbivores (whether sensitive to the toxic compounds or not) are likely to ingest large quantities of toxic plant tissues, making them less suitable as hosts or prey for natural enemies. Furthermore, even when based on the same microorganism, some toxic proteins expressed in transgenic plants are known to differ from proteins found in biopesticides (Perlak *et al.,* 1990; Fujimoto *et al.,* 1993; Koziel *et al.,* 1993), and these proteins may affect natural enemies differently.

Few studies have investigated the biology of natural enemies after feeding or parasitizing herbivores that were fed transgenic plants and those available studies

give variable results. Some studies (e.g., Dogan *et al.,* 1996) reported no adverse effects on a predator. When the convergent lady beetle (*Hippodamia convergens* [Guérin-Ménéville]) was exposed to aphids (*Mysus persicae* [Sulzer]) that were reared on transgenic *Bt* potato plants, no effect on survival, prey consumption, development, or reproduction was found. Other studies, however, (e.g., Hilbeck *et al.,* 1998a,b) reported important detrimental effects on predator survival and development. Increased mortality was observed in *C. carnea* larvae reared on transgenic *Bt* corn-fed prey. This increased mortality appeared to be directly associated with the presence of *Bt*-related factors in the prey (Hilbeck *et al.,* 1998a). Furthermore, in *C. carnea,* feeding on *Bt*-intoxicated prey not only affected longevity but also slowed development time (Hilbeck *et al.,* 1998a). Therefore, apart from lethal effects, insecticidal proteins in plant tissues can have indirect detrimental effects (i.e., sublethal effects) on natural enemies. These indirect effects should always be screened before transgenic plants become commercially available. Furthermore, for a realistic assessment of potential detrimental effects of transgenic plants on natural enemies, laboratory screening tests should be complemented with long-term field studies (see Gould, 1998, for a review of potential effects of transgenic plants on insect population dynamics and evolution).

Plants Mediate Host/Prey Availability

Plant quality also can have an indirect effect on the efficiency of natural enemies by delaying the development of the herbivores. Indeed, it has often been hypothesized that longer developmental time could make herbivores more vulnerable to natural enemies (see Benrey and Denno, 1997, for a review). Through prolonged feeding, traits such as tough leaves, digestibility reducers, allelochemicals, or poor nutritional quality could increase exposure time of vulnerable herbivore stages (Feeny, 1976; Moran and Hamilton, 1980; Price *et al.,* 1980; Price, 1986; Osier *et al.,* 1996). Although little empirical evidence exists of this indirect effect, it has been demonstrated in *Pieris rapae* (L.) larvae when feeding on plants with low nutrition (Loader and Damman, 1991). Also, Benrey and Denno (1997) found that a positive relationship existed between slow development in *P. rapae* larvae and high mortality inflicted by its parasitoid *C. glomerata.*

Indirect effects of plant quality are receiving renewed attention with the use of genetically engineered, herbivore-resistant crops (Daly, 1994; Gould, 1994). In tobacco plants (*N. tabacum*), a moderate level of *Bt* endotoxin-mediated resistance was shown to enhance parasitism of *Heliothis virescens* F. larvae by the parasitoid *Campoletis sonorensis* (Cameron) (Johnson and Gould, 1992). This increase in parasitization appeared to be related to a prolonged development time of vulnerable larval instars on resistant tobacco plants. Also, increased movements of larvae on toxic plants may augment their vulnerability to foraging parasitoids (Johnson and Gould, 1992). The importance of such sublethal effects on improving pest control deserves more attention. Not only is it advantageous for natural enemies to have suitable prey available for extended times but it is also crucial that prey populations are sufficient for natural enemy populations to be maintained. The benefits of keeping a weakened pest population available for natural enemies to feed or reproduce on (e.g., through low-dose expression of toxins) versus trying to eliminate pest populations (e.g., through high-dose expression of toxins) should be addressed and investigated whenever genetically engineered crops are to be implemented.

Plants Provide Supplemental Food Sources

Many members of the third trophic level are not exclusively carnivorous but also feed on various plant products, including pollen, food bodies, floral nectar, post floral nectar, and extrafloral nectar (Whitman, 1994; Jervis and Kidd, 1996). Adults of some parasitoid species are actually entirely dependent on plant-supplied food sources (Jervis and Kidd, 1996). Moreover, the availability of such food sources is important to supply not only energy for locomotion or flight but also to maintain high longevity and fecundity in many species of natural enemies (Leius, 1963; McMurtry and Scriven, 1965; Syme, 1975, 1977; DeLima and Leigh, 1984; Hagley and Barber, 1992; Idris and Grafius, 1995; Olson and Nechols, 1995; White *et al.,* 1995; Taylor and Foster, 1996; Baggen and Gurr, 1998). The squash bug egg parasitoid, *Gryon pennsylvanicum* Ashmead, for example, lived on average fewer than 3 days in the absence of food, whereas it lived more than 17 days when it was supplied with squash (*Cucurbita pepo* L.) extrafloral nectar (Olson and Nechols, 1995). In addition, *G. pennsylvanicum* fecundity was more than three-fold higher in the presence of this food source.

Other important effects of plant food sources include increased attraction, retention, and efficiency of natural enemies in targeted fields. Such is the case, for example, for *M. croceipes,* a parasitoid of *Helicoverpa zea* (Boddie) larvae. Detailed behavioral studies in patches of nectaried or nectariless cotton plants containing host larvae revealed that when nectar was present in the patch, *M. croceipes* females stayed longer and parasitized more hosts than when nectar was absent (Stapel *et al.,* 1997). Also, Pemberton and Lee (1996) showed that within the same forest, levels of parasitism of the gypsy moth (*Lymantria dispar* [L.]) were higher on trees with than on trees without extrafloral nectaries.

Many species of ants have been reported to feed on plant secretions and to protect the plants from herbi-

vore attacks (Bentley, 1977; Keeler, 1980, 1981; O'Dowd, 1982; Smiley, 1986; Rocha and Bergallo, 1992; Rico-Gray, 1993; Yano, 1994). The effect of food absence on the abundance and effectiveness of natural enemies has been addressed in cotton crops. Significant reductions in predator populations were found in fields planted with varieties lacking extrafloral nectaries (Schuster *et al.,* 1976; Adjei-Maafo and Wilson, 1983). An important decline in the parasitism of *H.* zea by the egg parasitoid *Trichogramma pretiosum* Riley was also found in the same crop (Treacy *et al.,* 1987).

Phytophagy is widespread among natural enemies and its effect on the effectiveness of biological control agents should always be considered. In addition to ants and parasitoids, many other predacious arthropods are known to use plant food sources: predatory wasps, predatory mites, lacewings, ladybeetles, syrphids, predatory hemipterans, carabids, mantispids, and even spiders (Rogers, 1985; Schuster and Calderon, 1986; Bugg *et al.,* 1989; Cowgill *et al.,* 1993; Pemberton, 1993; Pemberton and Vandenberg, 1993; White *et al.,* 1995; Taylor and Foster, 1996). However, many of these studies are essentially descriptive and record only which natural enemies were seen feeding on what food sources. The factors affecting food encounter, acceptance, usability, and profitability remain unknown for the majority of parasitoids and predators. Such knowledge is essential if crops that supply better quality food are to be developed.

ENHANCEMENT OF FAVORABLE ATTRIBUTES IN CROP PLANTS

The previous section documents the multiple roles of plants in the complex interplay between natural enemies and their herbivore prey and hosts (Table 1). Given these roles, knowledge of how plant attributes affect natural enemy efficiency must be actively integrated into pest management strategies. Despite the vast, although often disparate, information available on plant/herbivore/natural enemy interactions, much research is still needed. For example, little is known about the way environmental factors and/or physiological conditions modulate the expression of these vital indirect plant defenses. Such knowledge is crucial for understanding indirect effects of stress and agronomic practices on crop protection.

Furthermore, we must actively select and incorporate traits favorable to natural enemies into new crop varieties (see Thomas and Waage, 1996, and Bottrell *et al.,* 1998, for a discussion on the challenges of plant variety selection). Because of earlier neglect of indirect defenses, many such traits have most likely been "bred out" or weakened in current crop varieties (Brattsten, 1991; Loughrin *et al.,* 1995; Pickett *et al.,* 1997). Considering the multiplicity of existing indirect plant

TABLE 1

Literature Reporting the Influence of Plant Attributes on Natural Enemy Performance

Influence on natural enemies	Literature references
Plants provide shelter	
Leaf domatia	4, 5, 72, 85, 124, 132, 151, 206, 207, 208, 215.
Ant domatia	54, 55, 57, 81, 103, 155.
Other morphological traits	24, 39, 46, 75, 85, 206, 208.
Plants mediate host/prey accessibility	
Pubescence	47, 108, 120, 179, 196.
Glandular trichomes	87, 119, 144, 195.
Waxy surface	44, 45, 70.
Plants provide host/prey finding cues	
Volatiles from undamaged plants	12, 25, 48, 100, 116, 176.
Green leafy volatiles	91, 93, 104, 107, 165, 190, 216.
Herbivory-induced volatiles	6, 20, 21, 26, 32, 33, 34, 35, 36, 41, 56, 68, 105, 129, 136, 137, 148, 152, 162, 166, 172, 173, 174, 175, 181, 182, 183, 186, 187, 188, 218.
Visual cues	7, 100, 200, 203, 204, 209, 210, 212.
Plants influence host/prey suitability	
Toxic allelochemicals	9, 10, 41, 43, 91, 154, 194.
Nutritious quality of plants	14, 58, 59, 150, 163, 205.
Transgenic plants	28, 37, 78, 79, 83.
Plants mediate host/prey availability	
Low nutritious plants	11, 53, 98, 113, 127, 141, 142.
Transgenic plants	29, 65, 83.
Plants provide supplemental food sources	
Extrafloral nectar, floral nectar, post floral nectar, pollen, food bodies	1, 8, 13, 22, 27, 31, 74, 80, 82, 88, 89, 94, 110, 121, 126, 130, 131, 133, 145, 146, 147, 156, 157, 160, 164, 169, 170, 177, 180, 214, 215, 219.

defenses, much could be learned from traits present but overlooked in wild species. Although the debate on this subject is still active (Marquis and Whelan, 1996), in natural ecosystems, plant traits are likely to be under constant natural selection for increased protection by natural enemies. Therefore, attributes involved in indirect plant defenses should be looked for in wild species and selected varieties. Subsequently, their expression should be maximized by breeding and agronomic practices. Also, the selection of traits potentially detrimental to natural enemies should be avoided whenever possible. For a sustainable and balanced control of insect pests in agro-ecosystems, natural enemy populations have to be maintained. In addition to their obvious pest-regulating effect, natural enemies can be an important factor in the development of resistance to direct defense mechanisms in herbivores (Gould *et al.,*

1991; Johnson *et al.,* 1997). By maintaining multiple selection pressures on insect pests, natural enemies may delay the appearance of resistant strains.

Manipulating Morphological Traits in Crop Plants

Morphological traits constitute a typical example of defense attributes selected only in a bitrophic context in many crops. Many varieties have been bred for their capacity to directly resist herbivores through traits such as increased hairiness or tough foliage (see Panda and Khush, 1995, for a review) but information on interactions between these traits and natural enemies is often limited to description of their occurrence or investigations of their detrimental effects. However, as we described previously, morphological traits can enhance abundance, protection, and foraging efficiency of natural enemies. Traits providing shelter or facilitating host or prey discovery should receive more attention in future breeding programs. To demonstrate how morphological crop traits could be manipulated to enhance biological control, we will focus on two key plant attributes, leaf domatia and trichomes.

Leaf domatia. Leaf domatia are small morphological structures that provide shelter to predatory arthropods. Because they increase predator populations on plants, presence of these structures can indirectly result in enhanced plant protection. Removal of leaf domatia can severely reduce abundance, distribution, reproduction, and prey consumption of predators (Grostal and O'Dowd, 1994), while addition of leaf domatia can significantly increase populations of predatory arthropods and decrease populations of phytophagous arthropods (Agrawal and Karban, 1997). In cotton, addition of artificial domatia early in the season resulted in a fruit production increase of 30% and thereby substantially improved overall yield in this crop (Agrawal and Karban, 1997).

As leaf domatia are very common structures in angiosperms (Pemberton and Turner, 1989), many crop plants are likely to have close relatives which have naturally occurring leaf domatia. Therefore, breeding or genetically engineering crop plants that employ domatia to enhance predator activity should be feasible, provided enough attention is devoted to the development of such a crop protection strategy.

Trichomes. The importance of manipulating morphological traits in crop plants to promote biological control has been clearly demonstrated by van Lenteren *et al.* (1995). The control of whiteflies in cucumber (*C. sativus*) using the parasitoid *E. formosa* was successful only when varieties with a lower hair density than found in traditional commercial varieties were used. As we already mentioned, high leaf hairiness in cucumber interfered with movement, decreased host encounter rate, and increased mortality in this small parasitoid. Similar detrimental effects of plant hairiness on effi-

cacy have been found in many other crops for other parasitoids (Obrycki *et al.,* 1983; Schuster and Calderon, 1986; Keller, 1987; McAuslane *et al.,* 1995) and for some predators (Gurney and Hussey, 1970; Shah, 1982; Schuster and Calderon, 1986).

Because traits such as trichomes presumably incur little metabolic cost (Walter and O'Dowd, 1992; Whitman, 1994) and have already been manipulated for direct herbivore resistance purposes, their implementation as indirect defense mechanisms should be feasible in many crops. Breeding programs aimed at decreasing leaf hairiness to enhance efficiency of small predators and parasitoids appear to be a realistic option in many crop protection programs.

Manipulating Chemical Traits in Crop Plants

As we have seen, indirect plant chemical defenses are numerous. These defenses include provision of supplemental food, provision of cues for finding hosts or prey, and mediation of host or prey quality. Here, in order to illustrate how these traits can be manipulated, we will focus on two essential plant attributes: plant signaling and extrafloral nectaries.

Plant signaling. Manipulation of plant signals offers the most promising perspectives for enhancing the effectiveness of biological control agents in the field. Although signaling has never been part of plant breeding criteria, cultivars are known to differ in their production of natural enemy-attracting volatiles (e.g., Elzen *et al.,* 1985, 1986, in cotton [*G hirsutum*]; van Emden, 1986, in Brussels sprouts [*B. oleracea* var. *gemmifera*]; Dicke *et al.,* 1990a, in bean plants [*Phaseolus vulgaris* L.]; Rapusas *et al.,* 1996, in rice [*Oryza sativa* L.]). Therefore, instead of this selection being accidental, breeding varieties for their attractiveness to natural enemies should be pursued. Furthermore, it appears that bitrophic-oriented breeding programs may have deprived some crops of this indirect defense or at least may have weakened it. In cotton, for example, a recent comparison of the volatiles emitted by damaged leaves showed that commercial cultivars emitted almost a sevenfold lower quantity of volatiles than a naturalized cotton variety found in southern Florida (Loughrin *et al.,* 1995). As we described in the first part of this paper, plant volatiles that are emitted as a result of herbivore damage are an important component of parasitoids' ability to locate hosts. Therefore, maintaining and even enhancing the attractiveness of crop plants to natural enemies should be part of the list of selection criteria for breeding new crop varieties. However, these possibilities may sometimes be constrained by the effect of these changes on the attractiveness of the plant to herbivorous pests, as volatiles that attract more natural enemies could also attract more herbivores.

Since the role of volatiles (coming either from prey/

hosts or from plants) in host or prey finding was discovered, pest managers have been willing to artificially produce them and apply them in the field to attract and stimulate biological control agents. Unfortunately, as demonstrated in field studies (Chiri and Lagner, 1983; Gross, 1981) application of artificial attractants has shown little promise to successfully enhance biological control. As previously pointed out by Dicke *et al.* (1990a) and Vet and Dicke (1992), naturally produced attractants are far more desirable for biological control purposes. Indeed, to be effective, attractants must lead parasitoids and predators to real host or prey locations. A failure to do so results in time and energy losses as natural enemies forage in incorrect host or prey locations (Powell, 1986). Unless pinpointing of host-infested zones in the field is possible, artificial application of attractants will be unsuccessful. In contrast, volatiles released by plants as a result of herbivory are excellent candidates for the enhancement of natural enemy efficiency in the field: their presence is a reliable indicator of herbivore presence and in some cases they even can inform specialized entomophages on herbivore identity and developmental stage (Turlings *et al.,* 1993b; Takabayashi *et al.,* 1995; Du *et al.,* 1996; DeMoraes *et al.,* 1998). More research should be directed toward understanding the biochemical and physiological processes that are involved in the production of herbivore-induced plant volatiles. Such knowledge may allow us to genetically modify plants to produce herbivore-induced signals more quickly and at lower herbivore infestation levels.

Very little is known about the influence of environmental factors on the signaling ability of plants and on the quality of the signals. Recent studies with cotton show that water stress and soil nitrogen have a strong effect on the plant's ability to systemically release parasitoid-attracting volatiles (Cortesero, unpubl. data). The effect of abiotic factors on the attractiveness of plants was also investigated in a few other studies (Nettles, 1979; Takabayashi *et al.,* 1994). Factors such as water stress, season, and light were shown to affect the emission of volatiles in lima bean (*P. lunatus*) plants (Takabayashi *et al.,* 1994). Again, such knowledge is crucial for determining growing conditions that are likely to enhance plant signaling and thereby improve the ability of natural enemies to effectively find hosts or prey.

Finally, for an efficient and sustainable use of plant signaling in biological control, both large-scale and long-term field studies are necessary. Although laboratory studies are useful in understanding the role of synomones in interactions among plants, herbivores, and natural enemies, they may not always be reliable predictors of real natural enemy activity in the field. Furthermore, laboratory studies rarely consider interactions between different natural enemies, even though

biological control is a complex process often involving different species of predators and parasitoids with different ecological characteristics. Also, long-term field studies are necessary to better understand the influence of naturally produced plant attractants on pest and natural enemy population dynamics.

Extrafloral nectaries. Extrafloral nectaries in cotton offer a good example of the prevalence of reductionist, bitrophic logic in past pest management strategies. Because extrafloral nectar attracts many lepidopterous pests, resistant varieties lacking nectaries were developed. However, when these varieties were used in the field, the absence of nectaries not only reduced the number of pest insects, but also reduced populations of a wide range of entomophagous arthropods (Rogers, 1985; Schuster and Calderon, 1986). The benefits of breeding out extrafloral nectaries in cotton were so minimal that nectariless varieties are not even bred anymore.

Rather than eliminating nectaries, an alternative should be to try to limit their use by herbivore pests by developing varieties with nectar palatable only to beneficial species, as suggested by Rogers (1985). We believe that extrafloral nectaries should not only be maintained in crop plants but further improved. In cotton, for example, leaves usually bear only one nectary. However, as many as three nectaries per leaf occasionally can be observed. More emphasis should be directed toward breeding varieties with an increased number of nectaries and a higher and longer production of nectar. As for nectar composition, however, a less than optimal nutritional quality may be, to some extent, advantageous. For example, the lack of essential amino acids in nectar may force predators to complement their diet by feeding on nearby herbivores (Whitman, 1994).

Moreover, although conditions such as humidity, light intensity, and quantity of chlorophyll are known to influence nectar secretion in some plants (Gromer, 1937), very little is known about what causes quantity and quality variation in many crop plants. This knowledge is necessary to adopt agricultural practices that favor nectar production.

Evidence exists that plants advertise extrafloral nectar with olfactory signals that are used by natural enemies, such as parasitoids, to locate food (Lewis and Takasu, 1990; Stapel *et al.,* 1997). This characteristic of food sources may also be manipulated in crop plants to enhance natural enemy efficiency (Lewis *et al.,* 1998).

CONCLUSION

We hope this review has succeeded in demonstrating the need to consider plant attributes as an essential and interactive component of biological control practices. Because the role of crop plants in biological

control has been largely overlooked in the past, we concentrated on inherent crop attributes that could be improved to enhance natural enemy efficiency in the field. However, manipulating characteristics of the crop plant per se is not the only strategy available. Many of the key plant-related resources that we described can be supplied by managing other components of the agro-ecosystem (Powell, 1986; Verkerk *et al.,* 1998). Companion plants interplanted with crops can also provide shelter, supplemental food sources, alternate host or prey populations, and host- or prey-habitat finding cues for natural enemies.

When manipulating plant attributes, different effects can be expected depending on the species of natural enemies that are present. Pubescence for example, can be a favorable trait for predatory mites as a shelter but, conversely, the same trait can have negative effects on the searching efficiency of small parasitoids. Also, traits acting directly and indirectly on pest insects can have conflicting effects. For example, glandular trichomes, a herbivore-resistant trait in some tomato varieties, may negatively affect biological control because of their adverse effect on parasitoids (Farrar *et al.,* 1994). Clearly, there is no such thing as an ideal plant attribute. The relevance of each attribute for biological control depends not only on the nature of the plant, herbivores, and beneficial arthropods considered but also on the characteristics of the relationships among these trophic levels. It is, therefore, of utmost importance to identify the natural enemy species that play major roles in regulating pest populations and to understand their biology before plant attributes can be manipulated for a sustainable and balanced control of insect pests in agro-ecosystems.

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