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Chemical ecology and conservation biological control

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Abstract

Elucidating the chemical ecology of natural enemies, herbivores and host plants is important in the development of effective and successful integrated pest management (IPM) strategies where abundance and distribution of natural enemies could be manipulated by semiochemicals for improved conservation biological control (CBC). In response to attack by herbivores, plants produce semiochemicals called Herbivore-Induced Plant Volatiles (HIPVs) which act to repel pests and attract their natural enemies. Damaged, and in some cases, intact plants may also produce volatile signals that warn other plants of impending attack. Some of these intact plants are used as intercrops in 'push–pull' strategies; cropping systems based on stimulo-deterrent principle, where the target crop is intercropped with herbivore repellent plants (push) while attractant plants (pull) are planted around this intercrop. The intercrop, in addition to repelling the herbivores, attracts and conserves natural enemies thereby ensuring continued suppression of the pests. This natural delivery of semiochemicals for CBC is currently being exploited by smallholder farmers in eastern Africa in the management of cereal stemborers in maize and sorghum. Synthetic HIPVs also have the potential to effectively recruit natural enemies, thereby improving CBC as has been demonstrated in a series of field experiments in vineyards and hop yards in the Pacific Northwest of the United States. Potentially, plants could be 'turned on' by synthetic HIPV signals, and therefore become sources of natural enemy-recruiting volatiles. With the rapid development of plant molecular biology, modification of secondary plant metabolism is also possible which could allow appropriate semiochemicals to be generated by plants at certain growth stages. By identifying the promoter sequences associated with external plant signals that induce biochemical pathways, plant defense genes could be 'switched on' prior to insect attack. We review recent research on 'push–pull' strategies and synthetic HIPVs in recruitment of beneficial arthropods and warding off pest attack.

Keywords: Chemical ecology; Semiochemicals; Herbivore-Induced Plant Volatiles; 'Push–pull' strategy; Natural enemies; Conservation biological control

1. Introduction

Attraction of insects to plants and other host organisms involves detection of specific semiochemicals (natural signal chemicals mediating changes in behavior and development) or specific ratios of these semiochemicals (Pickett et al., 2006). Plants colonized and damaged by herbivorous insects produce a group of volatile organic compounds (VOCs) often referred to as Herbivore-Induced Plant Volatiles (HIPVs), which may include semiochemicals that act as repellents for herbivorous pests and as attractants for organisms antagonistic to these pests, such as predators and parasitoids. In the dual-purpose role, these signals indicate that the plant is already infested and, therefore, less suitable as a host but, on the other hand, they may increase foraging by predators and parasitoids (Pickett et al., 2006).

It is widely accepted that plants respond to attack by specific herbivore species through their induced direct and indirect defenses (Karban and Baldwin, 1997; Lou et al., 2006). In direct defenses, the chemicals target the herbivore resulting in its retarded development or death (Lou and Baldwin, 2003), whereas in indirect defenses, the chemicals (i.e., HIPVs) increase herbivore mortality through the recruitment of parasitoids and predators (Thaler, 1999;

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Kessler and Baldwin, 2001). Studies on the mechanisms leading to the production of HIPVs have revealed the role of herbivore-specific elicitors (Mattiacci et al., 1995; Alborn et al., 1997; Halitschke et al., 2001). These elicitors can activate various signaling pathways in the plant resulting in accumulation or release of defensive chemicals (Kessler and Baldwin, 2002). Additionally, we have observed that there are also intact plants that naturally produce similar VOCs without any herbivore damage (Khan et al., 1997a). Biological control agents (natural enemies) use a range of these VOCs to locate their prey.

Conservation biological control (CBC) is an approach that seeks to preserve the resident natural enemy populations in a cropping setting and enhance their abundance and activity, particularly through cultural techniques. Exploitation of chemical ecology in this approach involves incorporating practices that attract these natural enemies into the cropping system while providing suitable nutrient sources within the system. The latter involves provision of sources of nectar and other carbohydrates such as honeydew that enhance the longevity and fecundity of natural enemies thereby maximizing their impact on pest populations. Alternatively, refuges in the form of unsprayed plants or provision of alternative hosts that feed on deliberately sown and managed grasses, trap crops, windbreaks or hedgerows can significantly enhance and maintain natural enemies in and around crops.

CBC research in many cropping systems is frequently focused on improving the reliability of this strategy to suppress pests. Strengthening the natural enemy community both in terms of population density and species diversity is the aim of much of this research (Cardinale et al., 2003). Inevitably there are two aspects of this problem that need to be addressed: (1) attraction of beneficial arthropods to the crop during early cropping phases and (2) maintenance of these populations throughout the life of the crop. Manipulation of on-farm habitats to improve the attractiveness of crop ecosystems to beneficial arthropods is a major area of current research (Landis et al., 2000). This strategy is based on the idea that providing more and better resources (e.g., nectar, refugia) will allow larger populations of beneficial arthropods to reside in and near crops. Numerous examples of the potential and practicality of such approaches are available (Landis et al., 2000; Midega and Khan, 2003; Gurr et al., 2004; Midega et al., 2006; Koji et al., 2007). One of the most practical of these approaches is the 'push–pull' strategy (Cook et al., 2007). 'Push–pull' is a novel approach in integrated pest management (IPM) which uses a repellent intercrop and an attractive trap plant. Insect pests are repelled or deterred away (push) from the main crop and are simultaneously attracted to a trap crop (pull). The 'push–pull' strategy uses a combination of behavior-modifying stimuli to manipulate the distribution and abundance of insect pests and/or natural enemies (Khan et al., 1997a,b; Cook et al., 2007; Hassanali et al., 2008). Accordingly, we discuss how chemical ecology is exploited in conservation of natural enemies using Herbivore-Induced Plant Volatiles and 'push–pull' strategies.

2. Exploitation of chemical ecology in CBC: an overview

Predators and parasitoids, like their prey and hosts, often use sex or aggregation pheromones to bring the sexes together for mating. In this developing research area, the identification, synthesis and use of pheromones to manipulate populations of natural enemies in pest management are potentially important (Aldrich, 1999; Wermelinger, 2004). One of the few examples of commercialization of a predator pheromone to enhance biological control is the aggregation pheromone of the spined soldier bug, *Podisus maculiventris* (Say). Spined Soldier Bug Attractors ™ (Sterling International, Veradale, WA, USA) are mainly targeted at the home garden market, but this approach has also been used to suppress Colorado potato beetle, *Leptinotarsa decemlineata* Say, populations in potato fields (Aldrich, 1999). The use of semiochemical attractants (e.g., host/prey-derived chemicals) to increase recruitment and retention of beneficial arthropods in crop ecosystems is another area of opportunity for enhancement of CBC. Kean et al. (2003) identified 'spatial attraction' of natural enemies as the best way of enhancing CBC. Their results suggested an almost linear relationship between natural enemy attraction and prey equilibrium.

Although the exploitation of semiochemical attractants in pest management to date is limited, research on semiochemicals and the natural enemies of herbivores has expanded greatly in recent years (Pickett et al., 2006). Suggestions for possible utilization of these chemicals in pest management include (1) enhancing searching efficiency of natural enemies (Lewis and Martin, 1990), (2) bringing natural enemies into search mode (Gross, 1981), and (3) making novel or artificial host–prey species acceptable in a mass rearing program (Vinson, 1986). A good example of enhanced searching efficiency is manipulation of the green lacewing, *Chrysoperla carnea* (Stephens), through the use of tryptophan (Hagen et al., 1976). Tryptophan is present in honeydew (a sugary by-product of feeding by aphids, scale insects, etc.) and spraying honeydew in crops can attract chrysopid lacewings (McEwen et al., 1994). Planting molasses grass, *Melinis minutiflora* Beauv., between the rows of maize significantly increases the parasitism of maize stemborer larvae by *Cotesia sesamiae* (Cameron) (Khan et al., 1997a) and is being used as a strategy to control stemborers in eastern Africa (Khan et al., 2001 and this review). More recently, 2-phenylethanol, a volatile emitted from some plant species, was also found to be attractive to lacewings, particularly female *C. carnea,* indicating that this compound may be an ovipositional stimulant (Zhu et al., 1999). This volatile is also attractive to some lady beetle species and a predator lure based on this compound has recently been developed and marketed as Benallure® (MSTRS Technologies, Ames, IA, USA).