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Review

Ecological compatibility of GM crops and biological control

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ABSTRACT

Insect-resistant and herbicide-tolerant genetically modified (GM) crops pervade many modern cropping systems (especially field-cropping systems), and present challenges and opportunities for developing biologically based pest-management programs. Interactions between biological control agents (insect predators, parasitoids, and pathogens) and GM crops exceed simple toxicological relationships, a priority for assessing risk of GM crops to non-target species. To determine the compatibility of biological control and insect-resistant and herbicide-tolerant GM crop traits within integrated pest-management programs, this synthesis prioritizes understanding the bi-trophic and prey/host-mediated ecological pathways through which natural enemies interact within cropland communities, and how GM crops alter the agroecosystems in which natural enemies live. Insect-resistant crops can affect the quantity and quality of non-prey foods for natural enemies, as well as the availability and quality of both target and non-target pests that serve as prey/hosts. When they are used to locally eradicate weeds, herbicide-tolerant crops alter the agricultural landscape by reducing or changing the remaining vegetational diversity. This vegetational diversity is fundamental to biological control when it serves as a source of habitat and nutritional resources. Some inherent qualities of both biological control and GM crops provide opportunities to improve upon sustainable IPM systems. For example, biological control agents may delay the evolution of pest resistance to GM crops, and suppress outbreaks of secondary pests not targeted by GM plants, while herbicide-tolerant crops facilitate within-field management of vegetational diversity that can enhance the efficacy of biological control agents. By examining the ecological compatibility of biological control and GM crops, and employing them within an IPM framework, the sustainability and profitability of farming may be improved.

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1. Introduction

Herbicide-tolerant and insect-resistant genetically modified (GM) crops have become dominant fixtures in agroecosystems of many of the world's agricultural regions (James, 2007), increasingly modifying the composition and dynamics of regional landscapes. Effects of GM crops may extend beyond their target pests to include non-target species, which often provide ecological and pest-management services. Environmental changes imposed by GM crops upon agroecosystems and on services provided by non-target organisms need to be evaluated as stand-alone pest-management strategies (especially in cropping systems where GM technologies are used as a sole management strategy for a pest), as well as with respect to alternative pest-management strategies (e.g., those strategies that are used as alternatives to or those replaced by GM crops).

The foundation of IPM strategies is commonly tripartite, and includes close monitoring of pest populations, decision rules based on pest density estimates (i.e., economic or other action thresholds), and application of an integrated suite of appropriate management tactics, including biological control (Kogan, 1998; Bernal, 2008). Thus, IPM systems rely (either intentionally or inadvertently) on predators, parasitoids, and pathogens, as fundamental sources of mortality to insect pests and weeds. It is unfounded to presume that GM crops fit well within an integrated pest and weed management frameworks simply because they reduce the use of conventional pesticides compared to conventionally managed crops. The ecological interactions, including the toxicological relationships, among biological control agents and GM crops thus become central to discussions concerning the

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compatibility of GM crops with IPM strategies. While field- and regional-level impacts of GM crops on biological control are difficult to predict, they are a crucial consideration when incorporating GM crops into pest-management systems.

Current strategies for assessing the impact of GM crops on non-target species are primarily based on the toxicity of the herbicides (or the active ingredient therein) applied to herbicide-tolerant GM crops, or the insecticidal toxins produced by insect-resistant GM crops, to specific indicator species representing various taxonomic or functional guilds (this insecticidal toxicity is addressed by Andow and Hilbeck, 2004; Hilbeck et al., 2006; Hilbeck and Schmidt, 2006; Romeis et al., 2006, 2008a). Industry, government and academic researchers have evaluated the potential ecological risks of GM crops to non-target organisms including natural enemies of insect pests such as predators, pathogens, and parasitoids (Romeis et al., 2006, 2008a, 2008b). Four risk assessment approaches are recognizable from these studies: (a) toxicity-based, (b) tritrophic interaction-based, (c) community-based, and (d) metadata-based (Table 1). This type of tiered framework is valuable in assessing the toxicological effects of GM crops on biological control agents. But biological control agents functionally interact with GM crops in some ways that are not easily measured using the tiered toxicological approach, but are potentially important for the interactions of these technologies within IPM systems.

This review departs from much of the literature on non-target effects of GM crops by focusing on the functional implications of GM crops for biologically based pest management. Here, we discuss not only how biological control agents may be affected directly by toxicity associated with GM crop technology, but also how GM crop-induced changes in the agroecosystem affect biologically based IPM in the absence of toxicity. Specific sections of the synthesis (I) point out that the toxicity and availability of required nutritional resources and quality of habitat for natural enemies are sometimes altered in GM crops, (II) discuss evidence of how natural enemies are affected by the adoption of insect-resistant and herbicide-tolerant cropping systems, and (III) suggest ways in which GM crops and biological control may act synergistically to manage pests within IPM programs. The discussion includes both insecticidal and herbicide-tolerant crops, considers several classes of entomophagous natural enemies (predators, parasitoids and entomopathogens), and addresses non-Bt insecticidal GM crops to expand the relevancy of the review as novel modes of action are commercialized to confront new pests. The main conclusion is that compatibility of biological control and GM crops within successful IPM programs depends as much on ecological interactions of these strategies as on their toxicological relationships.

2. Part I. Pathways through which natural enemies may be affected by GM crops

Biological control agents can be affected by GM crops when the quantity or quality (either reduced nutritional suitability or increased toxicity) of their food is affected by the GM crop, or when the GM crop alters the environment in which biological control agents live. The toxicity to biological control agents of insecticidal proteins produced by insect-resistant GM crops and of herbicides associated with herbicide-tolerant crops is testable under laboratory conditions using straightforward procedures (Table 1). Prey and crop-associated non-prey foods may harbor the insecticidal products of GM crops, and thereby function as a pathway for exposure to higher trophic levels. If hazard from a transgenic toxin or herbicide to a natural enemy is detected, then knowledge of the various routes through which natural enemies are exposed to these toxins can inform a more comprehensive assessment of potential deleterious effects of GM crops (Hilbeck et al., 2006; Andow et al., 2008).

Insect-resistant and herbicide-tolerant crops also affect natural enemies when the availability or nutritional quality of prey and non-prey foods is reduced in GM cropping systems relative to other production systems. Moreover, GM crops (especially herbicide-tolerant crops) potentially change the quality of cropland as habitat for biological control agents in ways unrelated to nutrition. Thus, understanding the physiological needs (dietary and other) of natural enemies, and how GM crops influence the availability of key resources, is essential to assessing the compatibility of GM crops and biological control agents within IPM systems.

2.1. *Toxicity-based pathways*

2.1.1. *Toxicity of non-prey foods from GM crops*

Most natural enemies of insects rely on non-prey foods as part of their diet. These foods sustain biological control agents when high-quality prey are scarce, and support various life-history functions, such as reproduction, dispersal, diapause and other physiological and metabolic processes (Hagen, 1986; Coll and Guershon, 2002; Wäckers, 2005; Lundgren, 2009). An obvious direct hazard posed by GM crops to natural enemies occurs when plant-based foods contain an insecticidal toxin.

The final distribution of toxins within GM crop tissues and exudates depends on a number of factors. These include the crop genotype and phenology, the insecticidal molecule produced, the gene promoter used in the transformation event, where the transgene is inserted within the crop's genome, and extrinsic environmental and geographical factors (Fearing et al., 1997; Duan et al., 2002; Grossi-de-Sa et al., 2006; Obrist et al., 2006a). The gene promoter used to regulate toxin expression has great influence on which tissues express a transgene. For many commercial Bt events, a constitutive cauliflower mosaic virus (CaMV 35S) promoter partially regulates the expression of the Cry toxin. This promoter is most active in vegetative and below-ground plant tissues, and thus beneficial arthropods that feed on roots, stems, shoots, and leaves of Bt crops are exposed to the highest levels of Cry toxins. Other promoters used in GM crops may be pollen- or phloem-specific, and will affect non-prey foods to varying degrees. For instance, those GM crops targeting phloem-feeding pests frequently have insecticide in nectar and honeydew derived from vascular tissues (Shi et al., 1994; Hilder et al., 1995; Rao et al., 1998; Couty et al., 2001; Wang et al., 2005; Wu et al., 2006). Each crop genotype interacts differently with gene promoters and the products they regulate, making it difficult to generalize where the transgenic toxins will ultimately reside in the plant. For instance, Cry toxins are not found in the phloem tissues of some maize events (Head et al., 2001), but these toxins are detectable in the phloem of some rice, oilseed rape, and other maize events (Raps et al., 2001; Bernal et al., 2002a; Burgio et al., 2007). The end result is that numerous factors influence whether non-prey foods will be contaminated with insecticides from GM crops.

2.1.2. *Toxin-containing prey on GM crops*

Natural enemies may be exposed to GM crop derived toxins or their metabolites through intoxicated prey or hosts. These concerns are not unique to GM crops and are equally relevant to conventional (especially systemic and seed-applied) insecticides and antibiosis from host-plant resistance. However, unlike insecticides that wax and wane with applications, and antibiosis which is often sublethal and induced by herbivory, transgene expression levels are generally constant and high. But it should be noted that Bt crops may be more target specific than other plant-incorporated insect resistance mechanisms, and Cry expression within plants varies with the developmental stage of the plant (Bird and Akhurst, 2005; Dong and Li, 2007).