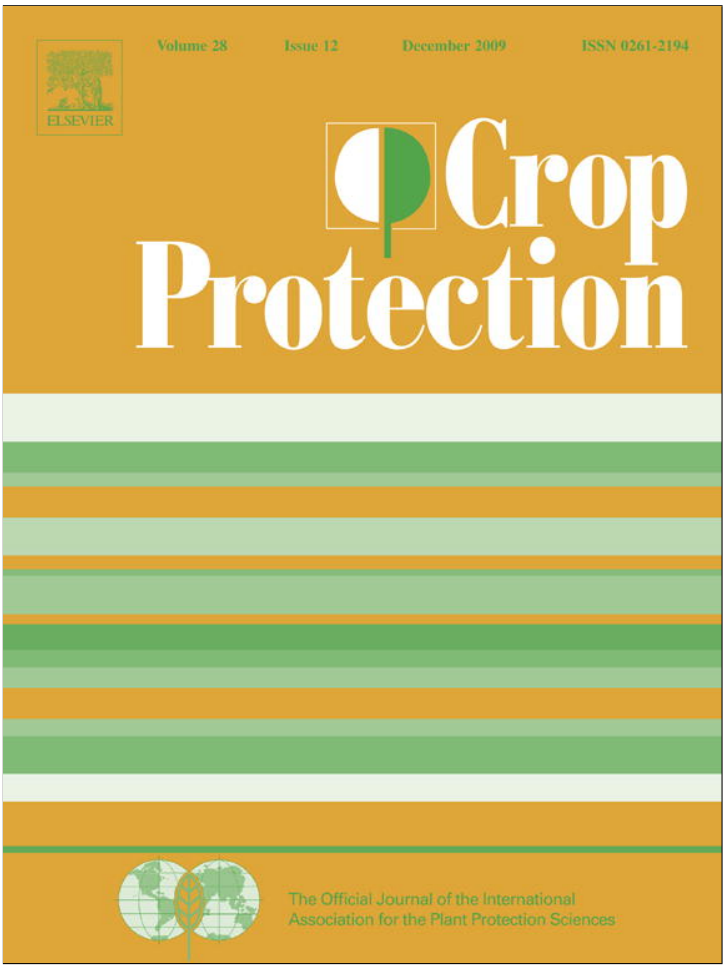

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Review

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).

Table 1
A summary of current approaches to assessing the compatibility of biological control agents and GM crops.

Assessment type	General approach	Experimental endpoint	Strengths	Weaknesses	Further reading
Toxicity-based	Evaluates direct toxicity of specific traits (e.g., Bt Cry proteins, protease inhibitors, herbicides used with herbicide-tolerant crops, etc.) to species indicative of certain functional or taxonomic arthropod guilds.	Measures mortality or sublethal effects, such as biomass of the test organism after a defined duration of exposure.	Lack of direct toxicity to arthropod natural enemies under worst-case conditions is considered first-tier evidence of compatibility between GM crops and particular biological control agents, and higher-tier studies (e.g., community-based assessment) may be unwarranted.	Toxicity-based assays are conducted under laboratory conditions in the absence of real ecological context. As a result, demonstrated direct toxicity to specific natural enemies may or may not equate to incompatibility of a GM trait and a natural enemy.	Hilbeck et al. (1998a, 1999), Zwahlen et al. (2000), Duan et al. (2006, 2007, 2008b), Torres and Ruberson (2007), Romeis et al. (2008a)
Tritrophic interaction-based	Detects prey- or host (hereafter referred to as prey)-mediated effects of GM crops on natural enemies, including both prey-based toxicity and prey quality. In these studies, prey are fed GM plant tissues or diets containing the transgene-derived products (e.g., insecticidal Bt Cry proteins).	Parameters measured are often the same as the toxicity-based assessments.	Measures the effects of GM-toxin induced changes to prey on natural enemies, the conclusions may provide a more realistic picture of the effects of GM crops on natural enemies than purely toxicological assessments.	Tritrophic studies cannot distinguish between prey-based toxicity and prey quality. Also, findings are limited to specific transformation events or cultivars of the tested GM plants rather than solely Cry toxins, and cannot be reliably extrapolated to other GM events or cultivars.	Hilbeck et al. (1998a, 1999), Zwahlen et al. (2000), Lundgren and Wiedenmann (2005), Torres and Ruberson (2007)
Community-based	Conducted under field conditions, where a natural enemy community and their prey directly and indirectly interact with GM crops.	Usually measure the relative abundance of natural enemies in GM, untreated, and/or conventionally managed cropping systems. Rarely measure diversity and ecological function.	Because they simultaneously measure responses of multiple species under realistic conditions, community-based assessments are often used as a higher-tier measure of the ecological impact of the GM crops. These are particularly important when lower tier assays indicate hazard to a non-target organism.	Logistically and economically difficult to conduct. For example, community-based assessments often require multiple field sites, or multiple years of study in order to have sufficient statistical power to detect reasonable effects of the GM crops.	Orr and Landis (1997), Pilcher et al. (1997), Reed et al. (2001), Al-Deeb and Wilde (2003), Hawes et al. (2003), Roy et al. (2003), Duan et al. (2004), Sisterton et al. (2004), Bhatti et al. (2005a, 2005b), de la Poza et al. (2005), Meissle and Lang (2005), Naranjo (2005a, 2005b), Ludy and Lang (2006a), Hoheisel and Fleischer (2007), Leslie et al. (2007)
Meta-data	A quantitative approach that simultaneously tests the effects of GM crops on specific taxonomic or functional groups across individual studies.	A unit-less effect size based on the treatment means, sample sizes, and standard deviations is generated for each study.	This evidence-based approach may provide the most convincing and statistically powerful conclusions concerning potential effects of GM crops on natural enemies. Studies based on this approach are prospective, and may generate testable hypotheses for subsequent experimental studies.	Causation for patterns are often difficult to tease out of the results, and the outcomes of specific studies that may have ecological relevance are overlooked in the identification of broader trends in the literature.	Marvier et al. (2007), Duan et al. (2008a), Wolfenbarger et al. (2008)

Exposure of natural enemies to toxins through their prey is contingent on the capability of the prey to acquire the toxin. Sensitive prey may be minimal conveyers of toxins to predators because of their rapid death following toxin ingestion. Less-susceptible prey species, on the other hand, may provide prolonged exposure to predators. Intake of transgene toxins by herbivores (targets and non-targets) has been well documented, with variations among taxa (Dutton et al., 2002; Meissle et al., 2005; Obrist et al., 2005, 2006b). In some cases, such as spider mites, herbivores concentrate the toxins at levels significantly exceeding the titers present in plants (Dutton et al., 2002; Obrist et al., 2006a). Numerous studies have documented the transfer of toxins from plants to various predatory taxa (Harwood et al., 2005; Meissle et al., 2005; Zwahlen and Andow, 2005; Obrist et al., 2006a). Retention of the toxin in the natural enemies appears to be relatively short-lived, but the relative abundance and season-long persistence of intoxicated prey make repeated exposure likely for many natural enemies in GM crops.

2.2. GM crop-induced changes to the crop environment

2.2.1. Unintended alterations to the crop plant

The quantity or nutritional quality of non-prey foods such as vegetative tissue, seeds, pollen, floral and extrafloral nectar, and honeydew may be influenced by transgenesis, and thus affect natural enemies that rely upon these foods. For instance, nectar production and sugar content is sometimes altered in GM crops from that observed in non-GM counterparts (Picard-Nizou et al., 1995). The quantity of honeydew produced by hemipterans may be

lowered (Rao et al., 1998; Kanrar et al., 2002), unaffected (Shieh et al., 1994), or increased (Bernal et al., 2002a; Faria et al., 2007) on GM plants compared with non-GM counterparts. In one case, planthoppers that consume Bt rice avoided the phloem sap and fed more heavily on the xylem, thereby changing the nutritional content of their honeydew (Bernal et al., 2002a). In other work, aphids were more abundant on Bt maize than on conventional hybrids, and the associated increase in honeydew production may provide an additional source of nutrition to natural enemies (Faria et al., 2007).

Natural enemies frequently rely on plant-based cues when searching for food or shelter (Vinson, 1977, 1981; Dicke et al., 1990; Verkerk et al., 1998; Cortesero et al., 2000), and it is unclear how or whether transgenesis will alter the chemical cues used by foraging biological control agents. Intraspecific variability is inherent in the nutritional quality of non-prey foods, including pollen (Karise et al., 2006; Lundgren and Wiedenmann, 2004; Lundgren, 2009) and nectar (Shuel, 1955; Cruden et al., 1983; Gottsberger et al., 1984). This variability highlights the importance of considering the relative quality or quantity of non-prey foods in GM versus non-GM crops when interpreting how these crops may affect natural enemies.

2.2.2. GM-induced reductions in prey quality and density

Impaired growth or development of prey resulting from their consumption of GM plant tissue may affect natural enemies (Bernal et al., 2004; Lövei and Arpaia, 2005; Hilbeck and Schmidt, 2006; Romeis et al., 2006). Developing on poor quality prey prolongs development and increases preimaginal mortality, which reduces population growth in natural enemies. As an example, parasitoids whose hosts suffer sublethal effects from feeding on GM crops (e.g., non-target pests of Bt crops) may themselves suffer sublethal reductions in fitness, such as lower fecundity (Baur and Boethel, 2003; Vojtech et al., 2005; Ramirez-Romero et al., 2007). Further, smaller adult predators and parasitoids may have impaired life-history traits, such as reduced fecundity and dispersal (Honěk, 1993; Kazmer and Luck, 1995), which may further delay population growth. Thus, prolonged consumption of low-quality prey could translate into smaller predator populations that grow at a slower rate in the field.

Populations of natural enemies are predicted to be less numerous as the strength of their reliance on herbivores susceptible to Bt crops increases. In an extensive set of simulation models, a theoretical pest was never eliminated from a 9000 ha landscape before its primary parasitoid (Sisterson and Tabashnik, 2005). A real life example of this scenario may occur in North American maize fields. Here, the widespread adoption of Bt maize has resulted in a geographically broad population decline of *Ostrinia nubilalis* (Hübner) (Abrahamson, 2007; Hutchison et al., 2007), whose primary parasitoid (*Macrocentrus grandii*) demonstrates density dependent foraging (White and Andow, 2005). An empirical study on the parasitoid–host interactions over broad geographic regions, and the potential implications of regional reductions in *M. grandii* to IPM of *O. nubilalis*, remain to be conducted.

2.2.3. Plant communities associated with herbicide-tolerant crops

Herbicide-tolerant crops are the most widely planted of GM crop technologies (James, 2007). This technology is primarily used in conjunction with glyphosate, with a smaller market share devoted to glufosinate-based crops, and most published research pertinent to the current discussion has focused on glyphosate. Glyphosate functions by disrupting the enzyme, 5-enolpyruvyl-shikimate-3-phosphate synthetase (EPSPS), that catalyzes the creation of aromatic amino acids (tyrosine, tryptophan, and phenylalanine) (Cerdeira and Duke, 2006). Glyphosate-tolerant crops overcome the enzyme inhibition caused by glyphosate by either producing a structurally altered EPSPS molecule for which glyphosate has a low affinity, or producing an enzyme that degrades the glyphosate molecule (Cerdeira and Duke, 2006). The commercialization of glyphosate-tolerant soybeans in 1996, followed by numerous other crop species (Cerdeira and Duke, 2006), has led to the rapid market domination of this product (Fig. 1) (Benbrook, 2004; Bonny, 2008). Also important is that the amount of glyphosate applied to soybeans on a per area basis continues to rise (Fig. 1). Thus, more glyphosate is being applied to manage the same area, and it is not clear when glyphosate application rates will reach an asymptote. But the degree to which herbicide usage is altered by the adoption of herbicide-tolerant varieties is largely dependent on crop-specific production practices. For example, overall herbicide use in canola is reduced in herbicide-tolerant fields versus conventional fields (Brimner et al., 2005).

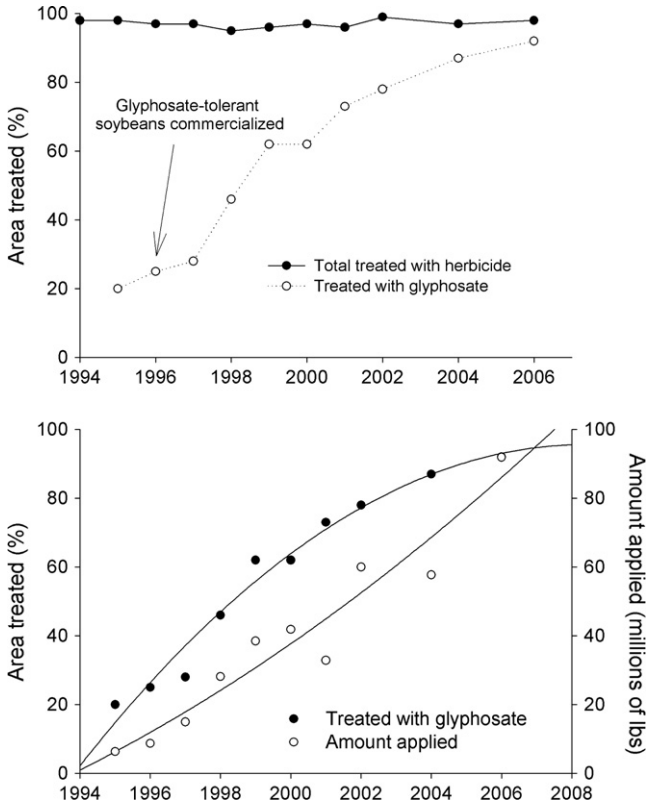

Fig. 1. Herbicide usage patterns in soybeans since the introduction of glyphosate-tolerant varieties. Data obtained from NASS 2008.

A major consequence of the rapid adoption of herbicide-tolerant crops is that the vegetational profile in agricultural lands has changed in response to the widespread application of glyphosate (Culpepper, 2006). The current approach to herbicide use in herbicide-tolerant crops reduces season-long vegetational diversity within farmland compared with conventionally managed crops, and this reduction in plant diversity is predicted to continue into the future (Heard et al., 2005). Non-crop plants vary in their innate tolerance to glyphosate, and excessive reliance on this chemical has led to resistance in several weed species. *Lolium* species, *Conyza canadensis* (L.) Cronquist, *Amaranthus tuberculatus* (Moq.) J.D. Sauer, and *Eleusine indica* (L.) Gaertn. are the best known examples of glyphosate resistance in weeds (Lutman and Berry, 2000; Owen and Zelaya, 2005; Cerdeira and Duke, 2006; Ott et al., 2007). Tolerance to glyphosate-intensive weed management systems are evident in at least *Ipomoea*, *Cyperus*, and *Commelina* (associated

with their natural tolerance of glyphosate), and *Chenopodium*, *Amaranthus* and annual grasses (because they germinate soon after glyphosate application) in portions of the USA (Culpepper, 2006). Thus, the non-crop vegetation community present in an herbicide-tolerant crop is either entirely removed, or shifted toward the dominance of these tolerant and resistant weed species. The abundance of higher trophic levels (predators and parasitoids) are closely tied to the local abundance of weeds (Hawes et al., 2003), and producing weed-free monocultures is often harmful to biological control (Lundgren, 2009). How shifts in the weed community resulting from the sowing of herbicide-tolerant crops affect biological control are often difficult to predict, but will likely depend on the crop, pest, and natural enemies under consideration (Heard et al., 2003a, 2003b; Hawes et al., 2009).

Within-field vegetational diversity usually increases natural enemy abundance and predation on insect pests in an array of agroecosystems (Russell, 1989; Andow, 1991; Coll, 1998b; Lundgren, 2009). Many natural enemies evolved in complex ecosystems with a diverse set of microhabitats and resources. Uniformity in habitat structure resulting from monoculture curtails resources available to natural enemies, even when prey are abundant. Increasing plant diversity may benefit natural enemies, and enable them to better respond to pest outbreaks (Speight and Lawton, 1976; Buckelew et al., 2000; Dewar et al., 2000; Haughton et al., 2001a; Bell et al., 2002; Dewar et al., 2003; Jackson and Pitre, 2004a, 2004b). But adding vegetational complexity to farmland does not always improve biological control (Bugg et al., 1987; Russell, 1989; Andow, 1991; Gurr et al., 1998). Sometimes diversifying a habitat can lead to unpredicted perturbations within complex food webs that ultimately disrupt biological control of a target pest. However, in the majority of research studies on this topic, increasing plant diversity in farmland improves natural enemy abundance and reduces pest pressure (Andow, 1991; Russell, 1989).

Application of herbicides disrupts entire communities of plants and the insects that live on them, and it takes a substantial amount of time for these communities to recover their normal compositions (Speight and Lawton, 1976; Prasse, 1985; Franz et al., 1997; Landis and Menalled, 1998; Kromp, 1999; Bianchi et al., 2006; Lundgren et al., 2009). In one study, carabid beetles avoided glyphosate-treated cropland for 28 days after the herbicide was applied, presumably because of the reduction of vegetational diversity in treated plots (Brust, 1990). The consequences of maintaining pure monocultures in farmland for biological control are not unique to herbicide-tolerant crops, but when herbicide-tolerant crops are marketed and employed with local eradication of weeds in mind, an important and unique opportunity to use herbicide-tolerant crops to promote IPM is missed (see Part III).

Another way that herbicide-tolerant crops can affect biological control agents is by shifting the weed community toward species that thrive under glyphosate-intensive production practices. As mentioned above, natural enemies are intimately coupled to the plants on which they reside, and show distinct preferences for those plants whose characteristics best provide them the nutritional resources and places to live. For example, *Orius insidiosus* chooses to lay eggs on non-crop plants whose characteristics facilitate the development of their progeny (Lundgren et al., 2008, 2009); the predatory heteropteran *Geocoris punctipes* also lays its eggs preferentially on specific cropland weeds (Naranjo and Stimac, 1987). Likewise *Coleomegilla maculata* lays its eggs on non-crop plants whose trichomes protect the progeny from intraguild predation (Griffen and Yeargan, 2002; Seagraves and Yeargan, 2006). In addition to removing susceptible members of a weed community, glyphosate application can sometimes affect the architecture of the remaining plants (Clements et al., 1990), which may also alter their suitability to natural enemies. Changing the relative abundance of certain non-crop plants within farmland could affect biological control by having indirect effects on natural enemies. Unfortunately, the relative quality of non-crop plants for specific natural enemies, as well as how changes in a vegetation profile affect higher trophic levels, remains to be explored for most systems.

2.3. Conservation tillage and biological control

In many parts of the world, weeds are controlled through tillage. In addition to being of questionable agronomic value (Triplett and Dick, 2008), tillage of farmland is extremely disruptive to soil-based food webs (Ammann, 2005), and to the communities and efficacy of biological control agent communities. Adoption of herbicide-tolerant crops (mainly cotton and soybean) has come hand-in-hand with a rapid expansion of no- or reduced-tillage production practices in North America (Triplett and Dick, 2008). This has led many to credit herbicide-tolerant crops as a cause of the adoption of conservation tillage practices, and some data support this notion (Fawcett and Towery, 2002; Ammann, 2005; Triplett and Dick, 2008). In one survey, 80% of US cotton producers have made fewer tillage passes after they adopted herbicide-tolerant cotton (Ammann, 2005). Likewise, most soybean producers associate the adoption of herbicide-tolerant varieties with their use of reduced-tillage practices (Fawcett and Towery, 2002).

Conservation tillage generally favors biological control. The communities of beneficial insects tend to be more diverse and abundant in cropping systems where conservation tillage practices are implemented (Stinner and House, 1990; Kromp, 1999). More importantly, insect pest and weed seed consumption is typically favored by reducing tillage and improving habitat stability (Stinner and House, 1990; Lundgren et al., 2006). It should also be noted that farmland under conservation tillage systems favors those pests who specialize on less disturbed habitats (Stinner and House, 1990). The result of these dynamics is that conservation tillage reduces pest performance in 43% of studies, and increases pest problems in 28% of studies (Stinner and House, 1990). Beneficial microorganisms are also more abundant in cropland under conservation tillage; these beneficial microbes antagonize plant pathogens within these systems and sometimes lead to lower crop disease incidence (Gil et al., 2008). For these reasons, the potentially deleterious effects of herbicide-tolerant crops on plant communities within cropland, and their associated effects on biological control agents, need to be weighed in concert with the potentially beneficial effects of reduced tillage on biological control.

3. Part II. Experimental assessments of the compatibility of GM crops on biological control agents

3.1. Effects of non-prey foods derived from insect-resistant crops

Laboratory feeding assays indicate that pollen, vegetative tissues, and seeds from commercialized Bt events do not affect natural enemies in the laboratory (Pilcher et al., 1997; Armer et al., 2000; Lundgren and Wiedenmann, 2002; Geng et al., 2006; Mullin et al., 2005; Ludy and Lang, 2006b; Obrist et al., 2006b; Torres et al., 2006; Li et al., 2008) and there have been no consistent direct deleterious effects of Bt crops on field populations of predators (see below for a discussion on primary parasitoids in Bt crops). Other insecticidal compounds expressed by not-yet-commercialized GM plants, such as those expressing snowdrop lectin (*Galanthus nivalis* L. agglutinin; GNA) appear to be more deleterious to natural enemies. For instance, offering sugar solutions containing GNA to

parasitoids significantly reduced their survival, longevity, and fitness (Romeis et al., 2003).

3.2. Prey-mediated effects of insect-resistant crops

3.2.1. Predators

Early studies on the effects of insect-resistant GM crops on predatory insects indicated adverse prey-mediated effects of these plant products on several predator species (Hilbeck et al., 1998a, 1998b; Ponsard et al., 2002). Immature predator development was delayed and survival reduced by the GM plants in these studies, or adult longevity was reduced (Ponsard et al., 2002). Subsequent detailed studies of several of these examples demonstrated that the observed effects were in most cases more appropriately ascribed to reduced quality of prey fed Bt plant tissues rather than the gene products themselves (Romeis et al., 2004; Torres and Ruberson, 2006a). Further, Rodrigo-Simón et al. (2006) found that Cry toxins did not bind to the gut of the predator *Chrysoperla carnea* (Stephens) and thus presented no serious direct risk to this predator. In several other studies indicating direct adverse effects, there were no isogenic control plants to allow differentiation of germplasm effects from effects of the Bt Cry toxin (Zhang et al., 2006a, 2006b). There is presently no clear evidence that Bt crops present a (direct) toxicological hazard to generalist predators through their prey.

Evidence to date suggests that commercialized Bt crops do not harm populations of most predators in the field (based on community-based and meta-analysis evaluations; Table 1). Meta-analyses of field studies that measured predator population dynamics failed to detect consistent effects attributable to the Bt crops (Marvier et al., 2007; Wolfenbarger et al., 2008). Overall abundance of predator populations was generally unaffected in GM crops relative to conventional crops in these studies, and a lack of impact on life histories is implied by the population data. The taxonomic resolution of these field-based studies is important to consider, since treating predators at feeding guild or familial levels may ignore species specific effects of GM crops on key natural enemies. Torres and Ruberson (2006a) used field cages to evaluate the life history of the big-eyed bug (*G. punctipes* Say) in Bt and conventional cotton with two prey types, one of which was an active herbivore that acquired toxin from the plant. Predators reared in field cages on low-quality prey (caterpillars adversely affected by the Bt toxin) were smaller than were those reared on high-quality prey. However, female feral predators (outside of cages) in the Bt and non-Bt cotton were the same size. Perhaps more importantly, feral predators were the same size as caged predators that received high-quality prey. Many generalist predators adjust their diets in the field to increase their fitness (Mayntz et al., 2005), and this appears to be the case for *G. punctipes* in Bt cotton. Ferry et al. (2006) observed that the carabid *Pterostichus madidus* (F.) preferentially fed on healthy prey, so that sickened prey in the field would have limited effect on the predator if other options are available. It is possible that generalist predators in GM crops may shift their prey base to less susceptible prey, or increase their consumption of low-quality, susceptible prey, in response to reductions in prey quality caused by the transgene products.

3.2.2. Parasitoids

Because they have particularly close relationships with their hosts and often possess a relatively narrow host range, parasitoids are more likely than predators (or certain pathogens) to suffer significant negative impacts from GM crops (Bernal et al., 2004; Bernal, 2008). Meta-analysis of the effects of Bt crops on parasitoids confirm that specialist parasitoids of the target pest are reduced consistently and substantially in Bt crops over conventional fields, a relationship best studied for *M. grandii* and *O. nubilalis* (Marvier et al., 2007; Wolfenbarger et al., 2008). The main mechanism behind this hypothesis is the substantial reduction in host populations.

A growing number of studies (conducted mostly in the laboratory) have sought to uncover how GM crops affect parasitoids. One vote-counting exercise showed negative impacts of Bt crops in ~40% of published laboratory studies (57% of these studies specifically involved Bt crops; 32% involved non-Bt crops) (Lövei and Arpaia, 2005). Specific studies reveal that the deleterious effects inflicted on parasitoids by GM crops occur as a result of reduced host quality (Bernal et al., 2002b; Setamou et al., 2002a, 2002b, 2002c; Baur and Boethel, 2003; Vojtech et al., 2005; Walker et al., 2007) rather than direct toxicity of contaminated hosts (Ramirez-Romero et al., 2007; Chen et al., 2008). Regardless of whether the population reductions incurred by some parasitoids stem from reduced host density or quality, the end result is that GM insect-resistant crops may pose certain hurdles to the adoption of parasitoid-based biological control of a susceptible host.

3.2.3. Entomopathogens

While data addressing effects of GM crops on specific entomopathogens (e.g., bacteria, fungi, nematodes, protozoa, and viruses; Lacey, 1997) are lacking, several studies measure the responses of soil-borne microbial communities to GM crops (Icoz and Stotzky, 2008). These data are relevant because many entomopathogens inhabit the soil. In two studies, the abundance of all nematodes (both entomopathogenic and non-entomopathogenic) did not differ among experimental soils from non-Bt maize fields, Bt maize fields, and soil amended with tissue of Bt maize (Saxena and Stotzky, 2001a; Al-Deeb et al., 2005). However, another comparison of samples from Bt and non-Bt maize fields revealed a lower abundance of nematodes in Bt fields (Griffiths et al., 2005). The compositions of bacterial communities (Devare et al., 2004; Baumgarte and Tebbe, 2005) and the relative abundances of bacterial classes (Brusetti et al., 2004) did not differ among Bt and non-Bt treatments. It should be noted that Brusetti et al. (2004) found no difference in the abundance of spore forming bacteria, which includes *Bacillus* entomopathogens. Protozoa and fungi are also unaffected by some commercialized Bt crops (Saxena and Stotzky, 2001a). Some entomopathogenic fungi, such as *Beauveria bassiana* (Bals.), form a symbiotic relationship with plants and can subsequently infect insects that feed on these plants; *B. bassiana* appears to establish equally well in maize producing or lacking Cry toxins (Lewis et al., 2001). Taken together, these studies suggest that direct effects of GM crops on entomopathogens are either subtle or absent. However, this hypothesis should be validated with experiments that measure the effects of GM crops on specific entomopathogens or that look specifically at the entomopathogen community.

There is evidence for both positive and negative indirect effects of Cry toxin on entomopathogens. Research in this area includes experiments in which Cry toxin or bacteria (e.g., *Bacillus thuringiensis kurstaki*) were added to the surface of plants or were media-incorporated. Sublethal exposure of the host to Bt chickpea enhanced pest susceptibility to the entomopathogenic fungus *Metarhizium anisopliae* (Lawo et al., 2008). Synergistic interactions also were found between Cry toxin and entomopathogenic fungi (Reardon et al., 2004; Wraight and Ramos, 2005). Additionally, Cry toxin and entomopathogenic fungi (Lewis and Bing, 1991; Pingel and Lewis, 1999; Costa et al., 2001) and nematodes (Baur et al., 1998) can function additively, although the nature of this interaction depends on the susceptibility of the host insect to Bt.

Unlike studies on entomopathogenic fungi and nematodes, antagonistic interactions often arise between Cry toxins and entomopathogenic viruses. Mortality of *Spodoptera frugiperda* from

entomopathogenic viruses was greater when insects consumed non-Bt maize compared with Bt maize (Farrar et al., 2004). Similarly, several studies report antagonistic interactions between Cry toxins, either alone or as part of a Bt strain (e.g., *B. t. kurstaki*), and entomopathogenic viruses (Bell and Romine, 1986; Pingel and Lewis, 1999; Farrar et al., 2004; Liu et al., 2006; Raymond et al., 2006). In these studies insects consumed plant material or diet treated with Bt (Cry toxin or bacteria), entomopathogenic viruses, or both in combination. The mortality from viruses in combination with Cry toxin was lower than expected from each agent individually. Because entomopathogenic viruses typically kill their host in order to reproduce, this antagonistic effect could also decrease virus reproduction.

The contrast in interactions of Bt with entomopathogenic viruses and entomopathogenic fungi with nematodes may result from differences in the manner in which these pathogens infect their host. Entomopathogenic viruses attack their host by infecting cells that line the midgut after ingestion (Moscardi, 1999). By contrast, entomopathogenic fungi and nematodes are not dependent on ingestion to initiate infection (Dowds and Peters, 2002; Roy et al., 2006). Antagonism between Bt and viruses could result from a reduction of leaf consumption by Bt-fed herbivores, which can in turn decrease exposure to entomopathogenic viruses (Farrar et al., 2004). Alternatively, Bt-imposed changes to cells that line the insect midgut may decrease the susceptibility of insects to subsequent infection with viruses (Raymond et al., 2006). These studies suggest that while control of pests in a Bt cropping system may be enhanced by entomopathogenic fungi and nematodes, control with entomopathogenic viruses may be less effective because Bt toxins may reduce the susceptibility of pests to viruses, but more data are needed before clear conclusions can be drawn.

3.3. Toxicology of herbicides associated with GM crops

3.3.1. Arthropod natural enemies

There are few reported cases of direct toxicity of glyphosate to arthropod natural enemies (Franz et al., 1997), largely because the amino acid synthesis pathway disrupted by glyphosate is not present in animals. Carabids (*Poecilus chalcites* [Say], *Agonom punctiforme* [Say], *Amara cupreolata* Putzeys, *Chlaenius laticollis* Say, and *Anisodactylus rusticus* [Say]) and a spider species (*Lepthyphantes tenuis* [Blackwall]) were unharmed by direct exposure to glyphosate (Brust, 1990; Haughton et al., 2001b), nor was there any apparent repellency of glyphosate to these carabid species in the greenhouse (Brust, 1990). Some evidence suggests that glyphosate may be directly toxic to at least one species of predatory mite, *Neoseiulus fallacis* (Garman) (Franz et al., 1997). By contrast, planting of glufosinate-tolerant crops may have more non-target effects because glufosinate-ammonium is directly toxic at label rates to at least two predatory mites, *Amblyseius womersleyi* Schicha and *Phytoseiulus persimilis* Athias-Henriot, and some immature stages of *Harmonia axyridis* (Pallas) and *Orius strigicollis* Poppius in the laboratory (Ahn et al., 2001).

3.3.2. Entomopathogens

Certain microorganisms that rely on EPSPS, including some entomopathogens, are deleteriously affected by direct exposure to glyphosate. *B. bassiana* (Balsamo) Vuillemin, *M. anisopliae* (Metchnikoff) Sorokin, *Nomuraea rileyi* (Farlow) Samson, and *Neozygites floridana* (Weiser and Muma) display reduced growth when exposed to a glyphosate formulation (i.e., Roundup) in the laboratory (Gardner and Storey, 1985; Morjan et al., 2002; Andalo et al., 2004). However, pure glyphosate had little effect on these entomopathogens, and it is possible that some of the inactive ingredients in commercial glyphosate formulations (i.e., Roundup) may contribute to the observed reduced fungal growth (Morjan et al., 2002). Glyphosate also had little effect on germination rates of *B. bassiana* (Gardner and Storey, 1985) and respiration rates of *M. anisopliae* (Mochi et al., 2005). Under field conditions, glyphosate does not reduce the infectivity of treated soils to insect hosts, and the number of colony-forming units of *B. bassiana* is similar in glyphosate-treated and untreated soils (Harrison and Gardner, 1992; Mietkiewski et al., 1997). All herbicides tested in one study (including glyphosate) decreased movement of the entomopathogenic nematode, *Steinernema feltiae* (Filipjev), but this pathogen remained highly infective after treatment (Forschler, 2003). Regardless of whether the direct effects of glyphosate formulations on natural enemies result from active or inactive ingredients, the potential direct influence of herbicide application on the outcome of biological control is worth additional research on a broader range of natural enemies, especially parasitoids which have escaped study in this regard. However, a more important consequence of herbicide applications is how these technologies shape the structures of agroecosystems in which natural enemies live.

4. Part III. Integrating GM crops with biological control

In addition to posing certain challenges, the evolution of GM crop technology also provides exciting opportunities for manipulating the cropland environment in ways that facilitate biological control and IPM. It falls upon the shoulders of scientists and stakeholders to meld these management tactics to promote sustainability and profitability for farmers. Three ways that biological control and GM crops can contribute to IPM are by (1) deferring pest resistance to insecticidal GM crops, (2) reducing abundance of non-target pest populations that attack insecticidal GM crops, and (3) promoting biological control agents as a source of insect pest mortality in herbicide-tolerant crops where herbicides are employed outside of an eradication mindset.

4.1. Biological control and resistance management in insect-resistant crops

Biological control has the potential to either enhance or diminish resistance management in GM crops. By magnifying fitness costs of Bt resistance, biological control agents may slow resistance evolution (Carrière and Tabashnik, 2001). However, natural enemies may also impose mortality that could intensify selection for resistance, and consequently, accelerate pest adaptation to Bt crops (Gould et al., 1991).

Biological control agents can slow resistance evolution if they increase fitness costs of Bt resistance. Fitness costs of Bt resistance occur in the absence of Bt toxin when resistant insects have lower fitness than susceptible insects. Fitness costs of Bt resistance may be especially effective for resistance management when Bt crops are grown in conjunction with a refuge of non-Bt host plants (Carrière and Tabashnik, 2001). Currently, refuges of non-Bt host plants are widely used for resistance management. The theory behind the refuge strategy is that any rare resistant individuals that develop in a Bt field will likely mate with susceptible individuals from non-Bt refuges (Gould, 1998). If Bt crops produce toxin at a sufficiently high concentration, only homozygous resistant individuals can survive (Tabashnik et al., 2004). The heterozygous progeny produced from the mating between resistant individuals from Bt fields and susceptible individuals from refuges will be unable to survive on the Bt crop. However, movement of resistance alleles into the refuge will break down this dynamic and lead to resistance in the population (Sisterson et al., 2005). If biological control agents magnify fitness costs, they will act to remove Bt

resistance alleles from refuges and thus delay pest resistance to GM crops.

Studies testing whether biological control agents alter the fitness costs of Bt resistance have thus far focused on entomopathogenic viruses and nematodes. Work by Raymond and colleagues (2006, 2007) tested how entomopathogenic viruses affect fitness costs of Bt resistance in the diamondback moth *Plutella xylostella* (L.). In cage studies, refuges treated with an entomopathogenic virus were more effective at slowing pest resistance to Bt than untreated refuges (Raymond et al., 2007). However, in an earlier study, there was no association between resistance to Bt and susceptibility to a virus across three insect strains (Raymond et al., 2006). In general, fitness costs of Bt resistance are greater when pests are more resistant to Bt (i.e., have a higher LC_{50}) (Gassmann et al., 2009). Entomopathogenic nematodes can also increase fitness costs of Bt resistance. Gassmann et al. (2006, 2008) found that fitness costs for Bt-resistant *Pectinophora gossypiella* (Saunders) were greater in the presence of some (but not all) entomopathogenic nematodes, a trend that was also present for diamondback moth (Baur et al., 1998). Because of variability in these interactions, specific host–pathogen interactions need to be considered when selecting entomopathogenic nematodes for resistance management strategies. Nonetheless, current evidence suggests that incorporating entomopathogenic viruses and nematodes into non-Bt refuges offers a promising avenue for integrating biological control with resistance management.

In addition to increasing the fitness costs of resistance, natural enemies can affect the evolution of pest resistance to GM crops by altering the strength of natural selection for resistance (Gould et al., 1991). These effects may arise though changes in pest density or pest distribution on Bt crops that in turn influence the foraging efficiency of natural enemies (Arpaia et al., 1997; White and Andow, 2005), or because Bt crops alter the development or behavior of herbivores in ways that affect susceptibility to natural enemies (Johnson et al., 1997a, 1997b). Such tritrophic effects on resistance evolution appear to be highly dependent on the specific set of interacting species, accelerating resistance evolution in some cases but slowing it in others.

Natural enemies may cause pest populations to evolve resistance faster if they intensify the selection of resistance. For example, if Bt crops have sublethal effects on herbivores, such as delaying development, natural enemies may more frequently prey on Bt-susceptible pests because of their longer development time on the Bt crop (Johnson and Gould, 1992). If evolution of Bt resistance results in faster development time on the Bt crop, the accompanying escape from predation will provide an additional advantage for Bt-resistant insects and will act to accelerate resistance evolution (Gould et al., 1991; Johnson and Gould, 1992). In contrast, if natural enemies preferentially remove resistant prey, then resistance development would be delayed.

Changes in pest density may affect how biological control agents influence evolution of resistance to insecticidal GM crops. If resistance alleles are rare within a population, pest density is expected to be higher on non-Bt crops than Bt crops, with the Bt-resistant genotypes occurring primarily at low density on Bt crops. Effects of lower pest density on the foraging behavior of natural enemies may in turn affect resistance evolution. For example, rates of parasitism of European corn borer, *O. nubilalis* (Hübner), by the specialist parasitoid *M. grandii* Goidanich are lower when this pest occurs at low versus high density. This suggests that Bt-resistant individuals can escape parasitism through a low initial density on Bt crops (White and Andow, 2005), and as a result this natural enemy may accelerate evolution of resistance. By contrast, the rate of egg predation for the Colorado potato beetle *Leptinotarsa decemlineata* Say by the generalist predator *C. maculata* is higher at low egg densities (Arpaia et al., 1997). Consequently, this natural enemy should delay resistance evolution in Colorado potato beetle populations.

Effects of Bt crops on herbivore behavior can alter some interactions between herbivores and natural enemies, which can affect how quickly pests adapt to Bt crops (Johnson et al., 1997a, 1997b). The interaction of *Heliothis virescens* (Fabricius) with the parasitoid *Campoletis sonorensis* (Cameron) and the entomopathogenic fungus *N. rileyi* (Farlow) illustrates two contrasting effects on resistance evolution. In the case of *C. sonorensis*, Bt-susceptible genotypes suffered lower rates of parasitism than Bt-resistant genotypes, which should slow the rate of resistance evolution (Johnson et al., 1997a). The authors hypothesized that this genotypic difference in parasitism arose because reduced feeding by the susceptible genotype on Bt plants decreased their attractiveness to parasitoids. By contrast, Bt-susceptible genotypes suffered greater mortality from *N. rileyi* than did Bt-resistant genotypes, which is expected to accelerate resistance evolution (Johnson et al., 1997b). Increased movement of Bt-susceptible larvae on Bt plants was hypothesized to have led to greater exposure to this entomopathogen.

4.2. Biological control of non-target pests

Reductions in insecticide use associated with some Bt crops create an environment conducive to conserving the function of resident and immigrant natural enemies. As noted above, numerous studies have failed to document consistent differences in enemy abundance between predator populations in Bt and non-Bt conventional crops. In this context, GM systems provide opportunities for integrating biological control with IPM. This is important because no insect-resistant GM crop produced to date is immune to all herbivores.

Current commercial GM varieties are effective against a subset of the herbivore community, and as the management system changes new pests can emerge. For example, widespread adoption of Bt cotton in the southeastern US has reduced insecticide use, which contributed to outbreaks of stink bugs that were not pestiferous in cotton since before the 1950s. Stink bugs are now one of the most important pests of cotton in this region (Williams, 2007). As a result, there is a continued need to have an effective complex of natural enemies in place to help manage pests that are not targeted by the transgene products.

There has been concern that the efficacy of natural enemies would be reduced in insecticidal GM crops due to reduction or elimination of the available prey base, and reduced prey quality. Although this is undoubtedly a reasonable concern for specialist enemies of pests targeted by the transgene products, it is less of an issue with generalist enemies and omnivores. In Bt cotton, the only prey removed from the system by transgene products are selected lepidopteran larvae beyond the first instar. But similar numbers of first-generation eggs of target species are present in Bt and non-Bt cotton fields (Torres and Ruberson, 2006b); thus, the GM system retains an abundant and heavily-used prey resource. In addition, the first instars of target pests are also equally abundant for a short period following hatch, although the quality of these prey will decline rapidly as they consume Bt foliage, sicken and die. Most mortality from natural enemies in lepidopteran populations in cotton in the southeastern US occurs during the egg and early larval stages (e.g., Ruberson et al., 1994). Thus, the overall prey base may be similar in Bt cotton and unsprayed cotton, and therefore generalist natural enemy populations would not be expected to suffer significantly.

As Romeis et al. (2006) noted, there are few studies of natural enemy efficacy in GM crops, but the few examples available indicate that biological control of non-target stages or species in insecticidal

GM crops is unaffected relative to that occurring in conventional varieties not treated with insecticides. Musser and Shelton (2003) observed that predation of sentinel *O. nubilalis* egg masses did not differ between untreated conventional maize and untreated Bt maize. Similarly, Sisterson et al. (2004) and Naranjo (2005b) noted that predation of several non-target prey species was comparable in Bt- and non-Bt cotton. Romeis et al. (2006) reviewed eight studies that assessed biological control in Bt cotton, maize, and tobacco, and none indicated any consistent effect of the GM crop on biological control function. The extent to which biological control would be affected in an insect-resistant GM crop will likely depend on (1) the relative contributions of generalist and specialist enemies to pest management in the system (if generalist enemies are important, then little or no change might be expected), (2) the degree to which pest stages targeted by the transgene products function as an important host/prey base for the enemy complex, (3) the relative abundance, acceptability and suitability of non-target hosts/prey for enemies in the system, and (4) the importance of the crop fields relative to extra-field habitats as food/host sources for enemies. In addition, genetic transformation of plants can have unintended effects on the plant's chemical attributes (Saxena and Stotzky, 2001b; Birch et al., 2002; Hjalten et al., 2007), some of which may elicit behavioral responses in natural enemies.

4.3. Biological Control and Habitat Management in Herbicide-tolerant Crops

Biodiversity is a valuable resource within and around cropland, and herbicide-tolerant crops provide a promising tool for managing non-crop vegetation as a basis for enhancing agricultural biodiversity. With respect to biological control, habitat complexity and diversity favors natural enemy communities by providing them with alternative foods, shelter, and favorable microclimates (Coll, 1998a; Landis et al., 2000). If used appropriately, GM herbicide-tolerant crops give farmers a flexible and powerful tool for managing non-crop vegetation in large acreages, and the biodiversity that accompanies it, in ways that improve biological control within farmland without reducing profitability.

Biodiversity and biological control within large farm fields can be encouraged using a variety of agronomically sound practices (Speight, 1983; Bugg and Pickett, 1998; Landis et al., 2000), which may be facilitated with the adoption of herbicide-tolerant crops. Vegetation management practices can be functionally categorized as strip management strategies and field-wide strategies (Lundgren, 2009). A related practice, and another source of within-field biodiversity, is intercropping, either in the form of relay intercropping (growing overlapping crops temporarily within a single field) or spatially integrated intercropping (growing two crops simultaneously in a single field). This section focuses on strip management and field-wide strategies as the most pertinent to large monocultures of herbicide-tolerant GM crops from a habitat-management perspective.

Strip management strategies often incorporate non-crop vegetation, or manage existing crop and non-crop vegetation in discrete patches or field-long strips. In the cases of cultivated weed strips (Zandstra and Motooka, 1978; Hausammann, 1996; Nentwig et al., 1998; Landis et al., 2000), beetle banks (Sotherton, 1995; Landis et al., 2000; MacLeod et al., 2004), and hedgerows (Wratten et al., 1998), perennial target areas are often entirely removed from crop production, and thus do not compete directly with the crop for resources. Herbicides can be used to maintain the distribution of these strips of biodiversity without harming the crop. Another approach to strip management involves spatiotemporally staggering the herbicide management of weeds (Barker, 1990; Bugg and Waddington, 1994; Dewar et al., 2003). Essentially, weedy strips are allowed to persist as temporary reservoirs of natural enemies within the field until non-crop vegetation can reestablish in treated areas. At that time, the untreated areas can be managed and the natural enemies immigrate to the initially treated regions of the field. Another tactic related to herbicide-tolerant GM crops that shows promise is removing non-crop vegetation at key times in the crop or pest phenology, in order to redistribute natural enemies to adjacent cropland when pest suppression is needed the most (Sluss, 1967; Perrin, 1975; Coll, 1998a). An important consideration when designing and implementing strip management systems is the dispersal capabilities of the natural enemies that the tactics are targeting. For species or life stages that disperse poorly, the benefits of non-crop vegetation and biodiversity need to be more finely integrated within large farm fields.

Field-wide management of non-crop vegetation can be easily and intricately managed within large-scale herbicide-tolerant GM cropping systems. In general, herbicide-tolerant GM crops provide farmers flexibility in the timing of weed management within their fields. Weeds can be allowed to establish and mature until they become competitive with the crop (Clay and Aguilar, 1998; Dewar et al., 2000), and these pre-economic populations provide a number of ecological services that include promoting natural enemies (Zandstra and Motooka, 1978; Altieri and Whitcomb, 1979; Norris and Kogan, 2005). Cover crops are another field-wide source of vegetation and biodiversity whose agronomic benefits are well documented (Clark, 1998), and whose management can be attuned in part to the dynamics of specific pests using herbicide-tolerant crops. Living mulches or ground covers are yet another form of field-wide management tactics that persist throughout a portion of the crop's life and can be subsequently removed or their competitive capabilities reduced using herbicides (Altieri and Letourneau, 1982; Bugg and Waddington, 1994; Landis et al., 2000; O'Neal et al., 2005; Prasifka et al., 2006).

When herbicide-tolerant crops are employed as an integrated component of weed management, the entire system benefits, including insect management. But when herbicide-tolerant GM crops are marketed and employed with a mentality toward complete weed eradication, then numerous opportunities for sustainable crop production and pest management are missed. Finally, while numerous instances indicate that biodiversity and biological control often accompany one another, this is far from universally the case (Russell, 1989; Bugg et al., 1987; Andow, 1991; Gurr et al., 2003), and each cropping system needs to be evaluated individually.

5. Conclusions

Herbicide-tolerant and insect-resistant GM cropping systems are primarily used in field-cropping situations, but are quickly becoming a cornerstone of modern IPM throughout agriculture. To date, integration of GM crops in pest-management strategies has benefitted pest-management efforts in many areas, and it is important to ensure that such benefits continue. However, it is also important to maintain the longstanding benefits of biological control to pest management. Key results of this synthesis are:

1) The interactions of insect natural enemies and GM crops transcend simple toxicological relationships, and the ways in which GM crops change the agricultural environment are also functionally important to the integration of biological control and GM crops. With insect-resistant crops, the agricultural environment is changed when prey populations are altered and if pleiotropic effects on the crop plant change the nutrition and abundance of non-prey foods (nectar, pollen, honeydew, etc.) or the structure of the vegetation on which

these insects live. From a natural enemy's perspective, the shifts in weed abundance and community structure brought about by herbicide-tolerant crops are likely more severe than deleterious effects caused by insect-resistant crops.

2) If employed as part of an IPM philosophy, then GM crops can be very compatible with biological control. Biological control agents may delay the onset of resistance to GM crop technologies in target insect pests, prolonging the life of an insect-resistant GM crop event. Natural enemies must be preserved within insect-resistant GM cropland, to cope with the dynamic changes to the populations of pests not targeted by the GM crop event. Finally, because of the profound effect of plant communities on natural enemy abundance and efficacy, the flexibility afforded by herbicide-tolerant crops in managing non-crop vegetation (and reducing soil disturbance) can be used to promote biological control within cropland. However, this is only possible if herbicide-tolerant crops are used in ways that preserve plant diversity over conventional herbicide treatment systems.

In conclusion, identifying and understanding the ecological pathways through which natural enemies interact with the crop environment, as well as how GM crops change agroecosystems relative to other pest-management tactics, is critical to evaluating the compatibility of biological control and GM crops. Moreover, recognizing the strengths and weaknesses of both GM crops and biological control provides opportunities for integrating these two strategies into effective and sustainable IPM frameworks. Many of the ecological challenges faced in the integration of GM crops and biological control are not unique to the former technology, but inevitably must be faced with this technology as it becomes more widespread.

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