

Review article

The impact of secondary pests on *Bacillus thuringiensis* (Bt) crops

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Summary

The intensification of agriculture and the development of synthetic insecticides enabled worldwide grain production to more than double in the last third of the 20th century. However, the heavy dependence and, in some cases, overuse of insecticides has been responsible for negative environmental and ecological impacts across the globe, such as a reduction in biodiversity, insect resistance to insecticides, negative effects on nontarget species (e.g. natural enemies) and the development of secondary pests. The use of recombinant DNA technology to develop genetically engineered insect-resistant crops could mitigate many of the negative side effects of insecticides. One such genetic alteration enables crops to express toxic crystalline (Cry) proteins from the soil bacteria *Bacillus thuringiensis* (Bt). Despite the widespread adoption of Bt crops, there are still a range of unanswered questions concerning longer term agro-ecosystem interactions. For instance, insect species that are not susceptible to the expressed toxin can develop into secondary pests and cause significant damage to the crop. Here, we review the main causes surrounding secondary pest dynamics in Bt crops and the impact of such outbreaks. Regardless of the causes, if nonsusceptible secondary pest populations exceed economic thresholds, insecticide spraying could become the immediate solution at farmers' disposal, and the sustainable use of this genetic modification technology may be in jeopardy. Based on the literature, recommendations for future research are outlined that will help to improve the knowledge of the possible long-term ecological trophic interactions of employing this technology.

Keywords: secondary pest, pest outbreak, ecological impact, genetically engineered insect resistance crops, *Bacillus thuringiensis*.

Introduction

With the intensification of agriculture and development of synthetic insecticides in the mid-20th century, scientists and farmers regarded technological development as the solution to reduce pest losses and enhance food production (Oerke, 2006). Insecticide use has enabled worldwide grain production to more than double in the last third of the 20th century (Krebs *et al.*, 1999). Conversely, the heavy dependence and overuse of insecticides has had many unintended consequences. Insecticides have been responsible for poisoning millions of people including numerous fatalities across the globe (Ecobichon, 2001; Jeyaratnam, 1990). Negative environmental impacts, such as a reduction in biodiversity, insect resistance to insecticides, negative effects on nontarget species (e.g. natural enemies) and the development of secondary pests, have also been attributed to the use of insecticides (Hardin *et al.*, 1995; Matson *et al.*, 1997; Vitousek *et al.*, 1997). Even so in 2011, about 1.3 thousand tons of insecticidal active ingredients were used in the world (FAOSTAT, data 2011). The use of recombinant DNA technology to develop genetically engineered (GE) insect-resistant crops could mitigate many of pesticide's negative side effects. The expression of toxic crystalline (Cry) proteins from the soil bacteria *Bacillus*

thuringiensis (Bt) by Bt crops is one such genetic alteration. This comes with the hope of supporting an agricultural revolution that is more productive (Conway and Toenniessen, 1999) while maintaining healthy and functional ecosystems for future generations (Poppy and Sutherland, 2004; Tilman *et al.*, 2001).

Overall, commercialized Bt crops have performed well against their target pests (Carrière *et al.*, 2010; Tabashnik *et al.*, 2008). Additionally, due to the high specificity and efficiency of Bt Cry toxins, it is generally accepted that any eventual detrimental impact on nontarget organisms (NTO) is lower than that caused by broad-spectrum insecticides (Areal and Riesgo, 2015; Cattaneo *et al.*, 2006; Marvier *et al.*, 2007). The reduced use of insecticides may then allow for a higher diversity and density of beneficial arthropods (Lu *et al.*, 2012; Naranjo, 2005). Also, in theory, the reduced reliance on insecticides enabled by Bt crops can lead to a reduction in farm operations with associated economic, environmental and social benefits (Areal *et al.*, 2013; Wolfenbarger and Phifer, 2000). Still, regardless of worldwide adoption of Bt crops, it remains a controversial technology which is surrounded by uncertainty, dividing the scientific community (e.g. the following debate: Andow *et al.*, 2009; Lövei *et al.*, 2009; Shelton *et al.*, 2009). These uncertainties are mainly based on alleged methodological research faults concerning the

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potential long-term impacts of *Bt* crops, such as the development of insect resistance and the impact on NTOs (Garcia and Altieri, 2005; Lövei *et al.*, 2009; Smale *et al.*, 2006). Two arguments are often mentioned in connection with possible long-term impacts: (i) ecological shifts can take several years to manifest (Ho *et al.*, 2009) and (ii) impacts of *Bt* crops vary temporally and spatially, which may not reflect the results obtained in laboratory studies (Andow *et al.*, 2006; Lövei *et al.*, 2009). A further concern is that other insect species that are not susceptible to the expressed toxin will develop into secondary pests and cause significant damage to the crop (Sharma and Ortiz, 2000; Wu and Guo, 2005). If these impacts materialize, they will certainly affect other trophic chains which, according to the magnitude of the impact, could become of high economic and ultimately of ecological relevance.

This study focuses on the development and effects of secondary pests on *Bt* crops. This issue, although of high importance, has to date received only limited attention in spite of Harper's warning (Harper, 1991, p. 22) that, 'ignoring secondary pests can lead to devastating crop damage that may continue over a considerable period of time'. By reviewing the relevant literature, this study has three main goals: (i) to assess the main causes of secondary pest outbreaks when arising in association with *Bt* crops; (ii) to review the impacts of these outbreaks, as currently understood; and (iii) to provide recommendations for future research.

Characterization of secondary pests in *Bt* crops

The concept of secondary pests is intrinsically linked with that of NTOs. NTOs in the broader context of GE crops include, 'all living organisms that are not meant to be affected by newly expressed compounds in GE crops, and that can be potentially exposed, directly or indirectly, to the GE crop and/or its products in the agro-ecosystem where GE crops will be released or in adjacent habitats' (Arpaia, 2010, p. 14). Although food webs in agro-ecosystems are typically simpler than those in natural habitats, they still include multitrophic relationships (Altieri, 1999; Arpaia, 2010). In any given cropping system, numerous species and scores of ecosystem functions can be found, although only a few can cause major losses in crop yield or quality (Hooper *et al.*, 2005; Matson *et al.*, 1997). A lethal or sublethal effect of a *Bt* crop upon one or a group of NTOs might occur through direct exposure to the *Bt* toxin or indirectly due to changes in the ecosystem on which that species depends (Snow *et al.*, 2005). To assess the impact of *Bt* crops on NTOs at different trophic levels, scientists would need to be acquainted with the majority of arthropod species prevalent in a given agro-ecosystem (Meissle *et al.*, 2010). Lövei *et al.* (2009), in summarizing published literature, concluded that stating that *Bt* crops will pose 'no harm' to NTOs is still a premature conclusion due to the limited number of nontarget species studied.

There are two relevant phenomena in agricultural systems that are considered as ecological backlash events: pest resurgence and outbreaks of secondary pests. The former refers to a situation in which a suppressed pest population unexpectedly rebounds following a pest control action, exceeding the economic injury level (Hardin *et al.*, 1995). The latter, and the focus of this study, refers to the emergence of a pest other than that originally targeted by an agricultural intervention (the 'targeted' or 'primary' pest), and can be seen as 'replacement' for the primary pest (Hardin *et al.*, 1995; Metcalf, 1980). According to the FIFRA Scientific Advisory Panel (1998), a secondary pest is a 'nontar-

geted' pest that has historically posed small or negligible economic threat, but which could be affected directly by a dose expressed in a *Bt* crop, or indirectly through changes in insecticide-use patterns. Berryman (1987, p. 3) defines outbreaks of secondary pests as 'an explosive increase in the abundance of a particular species that occurs over a relatively short period of time'. Termed a 'type II resurgence' by Metcalf (1986), this can arise when the primary pest is strongly affected by a pest management strategy, yet is replaced by another pest not affected by this strategy. The causes responsible for both pest resurgence and outbreaks of secondary pests are relatively similar which includes reduction in the number of natural enemies and removal of competitors (Hardin *et al.*, 1995; Ripper, 1956). In the event of a secondary pest outbreak, additional pest management interventions are required. In most cases, this results in crop spraying with a broad-spectrum insecticide (Gross and Rosenheim, 2011).

Causes for secondary outbreaks in *Bt* crops

The employment of *Bt* crops might have nonintuitive negative effects on agricultural ecosystem interactions and on farm profits (Sharma and Ortiz, 2000; Wolfenbarger and Phifer, 2000). Secondary pests, which before were of minor importance, might now find favourable conditions and themselves become major pests (Lu *et al.*, 2010). Three main drivers may trigger an outbreak of secondary pest species with the use of *Bt* crops: (i) a reduction in broad-spectrum insecticide applications; (ii) a reduction in natural enemy populations; or (iii) a decrease in interspecific competition with the target pest. Each of these is in turn explored below.

A reduction in broad-spectrum insecticide applications

The introduction of *Bt* technology, at least in the early years, brought significant decreases in insecticide application among adopters, considerably alleviating the negative impacts associated with such insecticides (Kouser and Qaim, 2011; Krishna and Qaim, 2012; Meissle *et al.*, 2010). Despite warnings from several authors (e.g. Sharma and Ortiz, 2000; Wu and Guo, 2005) that some NTOs could appear in such numbers that they become key insect pests in *Bt* crop fields, specific measures to combat their population increases were not taken. Consequently, there have been outbreaks of secondary pests which were previously controlled by the insecticide applications originally targeting the primary pest (Lu *et al.*, 2010; Pemsil *et al.*, 2011). This situation has been particularly evident in *Bt* cotton production in China. Less than 3 years after its introduction in 1998, several pest groups including whiteflies, plant hoppers, aphids, mirids and mealy bugs increased in number (Men *et al.*, 2004; Yang *et al.*, 2005a). Similarly in *Bt* maize, there is evidence that several secondary pests have acquired higher levels of agronomic importance (Eizaguirre *et al.*, 2010; Erasmus *et al.*, 2010; Gray *et al.*, 2009; Pérez-Hedo *et al.*, 2012) (see section Maize for further details). As a consequence, in some cases farmers have had to recommence the use of insecticide applications because *Bt* cropping systems have failed to control insect pest populations.

Reduction of natural enemies

Agro-ecosystem biodiversity is important not only because of its fundamental ecological, environmental and anthropocentric value but also because it is vital to a healthy and sustainable agriculture (Hooper *et al.*, 2005; Matson *et al.*, 1997). The

employment of *Bt* crops and the consequent reduction in insecticide usage increase the significance of the function of natural enemies to control secondary pests (Naranjo, 2005). Natural enemies include predators, parasitoids and pathogens. Natural enemies are critical to ecosystem functioning by inhibiting the excessive multiplication of potential pests in agricultural systems through 'biological control' (Bianchi *et al.*, 2006; Wilby and Thomas, 2002). Natural enemies alone may be sufficient in some cases to keep secondary pest populations under economic injury thresholds (Hardin *et al.*, 1995; Wolfenbarger *et al.*, 2008). Hence, a major concern related to the growing of *Bt* crops is their potential impact on the abundance of natural enemies (Marvier *et al.*, 2007; Poppy and Sutherland, 2004). The selectivity of Cry toxins is not entirely known, with the potential for unintended effects on beneficial species which may influence other non-susceptible pests (Lövei *et al.*, 2009). However, interactions between prey and natural enemies are extremely complex. Not all herbivores that feed on *Bt* plants take up the toxin, nor will all natural enemies be negatively affected by prey that have ingested the toxin (e.g. Dutton *et al.*, 2002).

Due to these complex uncertainties regarding ecological risks, many laboratory and field research studies have been conducted to evaluate the impact of *Bt* toxins on the natural enemies of potential secondary pests. While several laboratory studies reported no significant effects on natural enemies (e.g. Dutton *et al.*, 2002; Li and Romeis, 2010; Meissle and Romeis, 2009), several others have indicated negative effects (e.g. García *et al.*, 2012; González-Zamora *et al.*, 2007; Hilbeck *et al.*, 1998). Results from studies performed at a field level show similar variation; some found no significant impacts (e.g. Chen *et al.*, 2006; Eckert *et al.*, 2006; Pons *et al.*, 2005), while other studies reported negative effects (e.g. Meissle *et al.*, 2005; Obrist *et al.*, 2006; Stephens *et al.*, 2012). The overall dichotomy of results across the literature is striking (see Lang and Otto, 2010; Lövei and Arpaia, 2005; Lövei *et al.*, 2009; Marvier *et al.*, 2007; Wolfenbarger *et al.*, 2008 for detailed reviews). The main source of uncertainty relates to the degree to which laboratory studies are of relevance to the complexity of field-scale agro-ecosystems (Lövei and Arpaia, 2005; Lövei *et al.*, 2009; see also section 'Outstanding issues'). Natural enemies are often present in higher numbers in insecticide-free conventional fields than on *Bt* fields (Marvier *et al.*, 2007; Naranjo, 2009). It is also widely accepted that the use of insecticides has larger direct negative effects on natural enemies than does the use of *Bt* crops (Cattaneo *et al.*, 2006; Romeis *et al.*, 2009; Wolfenbarger *et al.*, 2008). Overall, this suggests that in field settings, while *Bt* crops do have an impact on natural enemies, this is not as strong as the direct effect of insecticide.

The impact of *Bt* toxins on natural enemies can occur through direct and/or indirect effects (Romeis *et al.*, 2006). Direct impacts might occur due to the ingestion of the insecticidal protein (Meissle *et al.*, 2005; Obrist *et al.*, 2006; Stephens *et al.*, 2012). The mechanism of action of several available *Bt* toxins is still unknown or inconclusive (Lövei and Arpaia, 2005; Lövei *et al.*, 2009). Thus, it is conceivable that *Bt* toxins may cause similar negative effects on predators as they do on the target herbivores (Andow *et al.*, 2006). In a recent study (Stephens *et al.*, 2012), *Bt* proteins were passed from the Cry3Bb *Bt* maize plant to the predator (*Harmonia axyridis*, a common coccinellid) via prey consumption (*Rhopalosiphum maidis*, the corn leaf aphid and *Rhopalosiphum padi*, the bird cherry-oat aphid), which significantly reduced their life span. Furthermore, although not yet

demonstrated in the context of *Bt* crops, there is also concern regarding toxin bioaccumulation through the food chain, possibly driving cascade effects within the ecosystem (Chen *et al.*, 2009). Indirect effects might manifest through reductions in prey/host populations or in the nutritional quality of the prey. Impacts of the toxin on herbivores may manifest at a sublethal level which can affect life parameters such as lifespan and fecundity (Meissle and Romeis, 2009; Romeis *et al.*, 2004). There is evidence that the low nutritional quality of prey items after they have ingested *Bt* proteins has a significant impact on the performance, development and even survival of natural enemies (Dutton *et al.*, 2002; Obrist *et al.*, 2006; Stephens *et al.*, 2012). Moreover, high mortality rates in the target species may cause a reduction in specialist natural enemies, which themselves can be important prey for generalist predators (Stephens *et al.*, 2012). Additionally, prey species in general might migrate to non-*Bt* fields in search of preferable food resources (Daly and Buntin, 2005; Naranjo, 2005). Thus, if prey availability for secondary pest predators in *Bt* fields is scarce, predators might be encouraged to 'migrate' to adjacent conventional crops, negatively affecting their abundance within *Bt* fields (Razze and Mason, 2012; Sisterson *et al.*, 2007). As a result, any lethal or sublethal impacts on pest predators will disproportionately affect insect population dynamics. Hence, it may be possible that these negative impacts will permit the development of secondary pests in the crop itself or even in neighbouring crops (Gross and Rosenheim, 2011; Gutierrez *et al.*, 2006). Understanding the direct and indirect effects of *Bt* cultivars on natural enemies is central for the management of insect pests as undoubtedly these insects play a major role in biological control of primary and secondary pests (Naranjo, 2009, 2011; Snyder *et al.*, 2006).

Species replacement

Competition may play an important role in the dynamics of herbivorous insects (Kaplan and Denno, 2007). However, the importance of replacement between primary and secondary pests has generally been ignored in conventional agriculture (Denno *et al.*, 1995; Hardin *et al.*, 1995), but especially in *Bt* cropping. *Bt* crops, as insecticides, are an artificially imposed disturbance on the ecosystem; hence, it is not surprising that niche rearrangement occurs (Catangui and Berg, 2006). It is possible that when a primary pest is successfully controlled by a *Bt* toxin, a non-susceptible species starts to utilize the newly available ecological resource (Gross and Rosenheim, 2011; Hardin *et al.*, 1995). This situation occurs in cases where, prior to the pest management treatment, the primary pest is a dominant competitor species and the secondary pest is a weak competitor (Shivankar *et al.*, 2007).

A notorious example of species replacement is the western bean cutworm (WBC) [*Striacosta albicosta* (Smith)] a noctuid moth native to West and Central America (Douglass *et al.*, 1957). In the mid-1990s, the WBC began an expansion of range size that correlated with the introduction of transgenic maize. It has now effectively established itself as a major Lepidopteran pest of maize crops in some areas of the Corn Belt in the US and Canada (Dorhout and Rice, 2010; Lindroth *et al.*, 2012; Michel *et al.*, 2010). This secondary pest shows low susceptibility to most transgenic maize currently commercialized (Eichenseer *et al.*, 2008). Transgenic crops expressing Cry1Ab and Cry9C toxins have larger populations of WBC compared to conventional maize (Catangui and Berg, 2006; Dorhout and Rice, 2010). It is possible that changes in cultural practices (e.g. conservation tillage and reduced insecticide use) due to the widespread adoption of *Bt*

maize across these areas might have contributed to the WBC's rapid expansion (Hutchison *et al.*, 2011). However, as the widespread planting of *Bt* maize hybrids has effectively eliminated intraguild competition with the European corn borer (ECB) (*Ostrinia nubilalis*) and the corn earworm (CEW) (*Helicoverpa zea*), it is possible that an ecological opportunity opened for WBC (Catangui and Berg, 2006; Dorhout and Rice, 2010).

To date, only one study appears to have been specifically conducted to assess the interaction between WBC and other species (Dorhout and Rice, 2010). CEW had a significant negative impact on WBC survival when both were fed on a meridic or isoline maize silk diet. CEWs are extremely aggressive by nature compared to the WBC (Douglass *et al.*, 1957), and CEW larvae often kill WBC larvae even when the latter are present in larger numbers (Dorhout and Rice, 2010). However, when both pests were fed with a transgenic silk diet, WBC presented high survival rates (Dorhout and Rice, 2010). Competition with the ECB exists because of their similar feeding behaviour on the kernels in corn ears (Catangui and Berg, 2006). Hence, along with the high flight capacity of WBC (Michel *et al.*, 2010), the reduction in direct competition very likely played a fundamental part in its territorial expansion.

Other examples of species replacement include the corn leafhopper (*Dalbulus maidis*) in maize in the absence of the target pest *Spodoptera frugiperda* in Argentina (Virla *et al.*, 2010). In Spain, the true armyworm *Mythimna unipuncta* could have competitive advantage in the absence of both the Mediterranean and ECB (Eizaguirre *et al.*, 2010; Malvar *et al.*, 2004). In *Bt* cotton in the USA, stink bug pests, specifically *Nezara viridula* L. and *Euschistus servus* S., have recently become a severe problem in the absence of the target pests *H. zea* and *Heliothis virescens* (Zeilinger *et al.*, 2011). *Helicoverpa armigera*, *Acantholeucania loreyi* and *Eublemma gayneri* could also gain competitive advantage following the displacement of *Busseola fusca* from *Bt* maize in South Africa (Van Wyk *et al.*, 2007). As *Bt* cropping expands worldwide, it is of critical importance to determine the key species–susceptible and nonsusceptible pests—which might compete for resources within the same transgenic crop.

Impact of secondary pests on *Bt* crops

In the early years of *Bt* cropping, there were reports of increased profitability in overall production due to 40%–60% reductions in insecticide applications alongside increased crop yields, as compared to nonadopters (e.g. Bennett *et al.*, 2004; Fitt, 2000; Huang *et al.*, 2002; Pray *et al.*, 2002; Qaim and Zilberman, 2003; Thirtle *et al.*, 2003). There was also a reduction in human insecticide poisonings (Huang *et al.*, 2002; Pray *et al.*, 2002). Nonetheless, there were early concerns about the potential for secondary pest outbreaks due to the decrease in insecticide applications (Morse *et al.*, 2005; Qaim, 2003; Wu *et al.*, 2002). Here, we focus on the development of secondary pests in two of the most important GE insect-resistant crops, *Bt* maize and *Bt* cotton.

Cotton

From the worldwide 24.3 million hectares cropped with *Bt* cotton, India, China and USA account for 11.0, 4.2 and 4.1 million hectares, respectively (James, 2013), with the adoption rate varying between 90% and 95% (James, 2013). The *Bt* cotton hectareage in Africa is increasing, for instance Burkina Faso

and Sudan cropped 50% and 300% more *Bt* cotton, respectively, compared with 2012 (James, 2013).

In China, in some areas where the bollworm incidence is higher, the adoption is close to 100% (Xu *et al.*, 2008) and undoubtedly, *Bt* cotton has reinvigorated Chinese cotton production. Historically, cotton and rice have required the largest number of insecticide applications in the world (Deguine *et al.*, 2008). Until the end of the 20th century, insecticides were intensively applied to control the cotton bollworm (Wu and Guo, 2005). However, in the early 1990s, the effective control of this pest became problematic, and the cotton bollworm became resistant to most insecticides due to their overuse (Deguine *et al.*, 2008; Wu and Guo, 2005). Following the introduction of *Bt* technology in 1999, insecticide applications in *Bt* cotton fields dropped from about 61 kg/ha (20 applications) per year, to approximately 12 kg/ha (6.6 applications) per year (Huang *et al.*, 2002). By 2002, this figure started to increase, reaching on average 15.6 kg/ha (10.7 applications) per year of insecticides, of which 4.7 kg were used against cotton bollworm, and the remaining against *lygus* bug and other pests (Pemsl *et al.*, 2011). By 2005, farmers applied roughly the same amount against the cotton bollworm, but the amount sprayed against secondary pests had increased by 20%, to a total of 18.6 kg/ha (14.2 applications) per year (Pemsl *et al.*, 2011). Within the space of approximately 10 years, the initial advantage of *Bt* crops had gone; Zhao *et al.* (2011) reported that *Bt* adopters were using on average between 16 and 22 insecticide applications, while conventional cottons farmer were using only 11–17 applications per year. Nowadays those insects once considered of minor relevance are actually the main concern of farmers' (Pemsl and Waibel, 2007). The drop in insecticide use and the ineffectiveness of *Bt* cotton against these secondary pests has led to a reversal of the ecological role of cotton (Li *et al.*, 2011; Lu *et al.*, 2010). Conventional cotton had been a population sink for the mirid bug secondary pest, while nowadays *Bt* cotton fields are a source of these pests (Lu *et al.*, 2010). This has led to a situation where there are no major differences in the total quantity and expenditure in insecticide application between *Bt* and conventional cotton farmers (Yang *et al.*, 2005b; Zhao *et al.*, 2011). When comparing with the period prior to *Bt* adoption, farmers are generally not worse off. Cotton production is still effective and farmers are applying fewer sprayings in early season, with fewer cases of human poisoning (Huang *et al.*, 2014). Moreover, a higher survival of generalist arthropod predators has been recorded (ladybirds, lacewings and spiders), providing additional biocontrol to neighbouring crops, such as maize and soybean (Huang *et al.*, 2014; Lu *et al.*, 2012).

Indian cotton farming is comparable with China, with numerous small-scale farmers (Huang *et al.*, 2002; Qaim *et al.*, 2009). Recent evidence shows that secondary pests are now posing a major problem (Nagrare *et al.*, 2009), with farmers battling against nontarget insects (Stone, 2011). Ramaswami *et al.* (2012) found no significant difference between adopters and nonadopters in terms of insecticide use. This is consistent with Indian *Bt* farmers' perceptions, who attributed a total of 77% of cotton damage to aphids and other sucking pests and only 23% to the primary Lepidopteran pests, leading to 99% of the farmers spraying against secondary pests (Stone, 2011). Elsewhere in the world, similar issues to the Chinese and Indian cases have been reported in cotton. Adopting farmers are either still using significant numbers of insecticide applications to control secondary pests, or the damage caused by these pests has increased.

Some examples include South Africa (Hofs *et al.*, 2006; Schnurr, 2012), Burkina Faso (Dowd-Urbe, 2014), Pakistan (Jaleel *et al.*, 2014), Australia (Wilson *et al.*, 2013), Brazil (Sujii *et al.*, 2013) and Mexico (Traxler and Godoy-Avila, 2004).

In the USA, for example, in the mid-southern and south-eastern cotton-producing regions, there has been a significant increase in the number of insects considered as secondary cotton pests, such as aphids, leafhoppers, mirid plant bugs and stinkbugs (Naranjo, 2011). The same author analysed National Cotton Council data, reporting that before *Bt* cotton adoption, farmers were applying an average of 17 applications per hectare, and this figure dropped postadoption to five applications (a 71% reduction). Additionally, *Bt* cotton losses due to pest damage are around 5.4%, a decrease of 27% when compared to pre-1996 levels. Nonetheless, while insecticide use to control primary pests has decreased, insecticide applications used to control secondary pests such as plant bugs have nearly doubled to approximately four applications per hectare to achieve adequate control (Naranjo, 2011). In contrast to the other cases around the world, most of the secondary pests in the US are being effectively managed with sensible use of insecticides and other integrated pest management (IPM) tactics (Naranjo and Ellsworth, 2009).

Maize

The economic benefit of *Bt* maize associated with the regional suppression of specific pest populations is significant (Areal *et al.*, 2013; Carpenter, 2010; Riesgo *et al.*, 2012). Hutchison *et al.* (2010) estimated the cumulative benefits of controlling ECB with *Bt* maize over the last 14 years at \$6.8 billion for maize growers in the US Midwest, with an estimated 60% of this accruing to non-*Bt* maize growers. This is due to savings in insecticide applications because of the regionwide suppression of ECB populations. Presently, in the USA the most problematic secondary pest in *Bt* maize is the WBC (see section Species replacement), causing up to 70% yield losses (Catangui and Berg, 2006). This value is not surprising, as only one WBC larvae per maize plant at dent stage can reduce yields by 232 kg/ha (Appel *et al.*, 1993). Both the CEW and the fall armyworm are considered important secondary pests too. Their moderate survival rates in *Bt* maize expressing Cry1Ab and Cry1F make them economically important (Archer *et al.*, 2001; Hardke *et al.*, 2011; Storer *et al.*, 2001).

Currently, the only *Bt* maize allowed for cultivation in Europe contains the transformation event MON810 (Monsanto Company) expressing Cry1Ab *Bt* toxin (EFSA, 2010), although several other events are under evaluation by the European Food Safety Authority (EFSA). This transgenic maize presents a highly efficient level of resistance to the two primary maize lepidopteran borers present in the EU, the Mediterranean “corn borer” and the ECB (Eizaguirre *et al.*, 2010; González-Núñez *et al.*, 2000). In European conditions, *Bt* Cry1Ab is not efficient against several secondary pests, such as the western corn rootworm and the true armyworm (Gray *et al.*, 2009; Pérez-Hedo *et al.*, 2012). The western corn rootworm was first noticed in Europe in the mid-1980s (Bača, 1994; Miller *et al.*, 2005), and it has been spreading across the continent at an average rate of 33–40 km/year (Gray *et al.*, 2009; Meinke *et al.*, 2009). Its presence is more common in central and eastern European countries and in the Po Valley in Italy where attributable yield losses of about 2%–3% have been reported (Meissle *et al.*, 2010).

Field research concerning secondary pests in Europe has mainly been conducted in Spain. Recent studies have revealed that the true armyworm is only mildly susceptible to *Bt* maize expressing

the Cry1Ab toxin (González-Cabrera *et al.*, 2013; Pilcher *et al.*, 1997). Furthermore, field trials found no substantial differences in the number of true armyworm larvae per plant nor in their larval development between *Bt* and its isogenic variety (Eizaguirre *et al.*, 2010; Pérez-Hedo *et al.*, 2012). Hence, it is possible that the increasing use of transgenic maize expressing Cry1Ab toxin will further amplify the true armyworm’s importance due to decreasing conventional insecticide applications. In time, this could lead to it becoming a major pest (González-Cabrera *et al.*, 2013; Pérez-Hedo *et al.*, 2012).

In South Africa, *Bt* maize has the potential, when well managed, to effectively control primary lepidopteran pests, such as *B. fusca*, *Sesamia calamistis* and *Chilo. partellus* (Kruger *et al.*, 2012; Van den Berg and Van Wyk, 2007; Van Wyk *et al.*, 2009). However, several important secondary pests are also present, including *Agrotis segetum*, *H. armigera* and *A. loreyi* (Erasmus *et al.*, 2010; Van Wyk *et al.*, 2008, 2009). Although these secondary pests may show some degree of susceptibility to Cry proteins (their densities are usually lower in *Bt* maize fields compared to non-*Bt* fields), they are able to seriously damage the crop under field conditions (Van Wyk *et al.*, 2007, 2008). Similar importance is now given to *H. armigera* in China, Australia and South Africa (Tabashnik *et al.*, 2003; Van Wyk *et al.*, 2008) and to the corn leafhopper, an efficient vector of several plant pathogens, in Argentina (Bastos *et al.*, 2007). Ecological explanations for higher attraction to *Bt* maize in some pest species have been found; for example, chemical and/or morphological characteristics expressed by the *Bt* maize make it especially attractive to the corn leafhopper secondary pest (Bastos *et al.*, 2007).

This review suggests that in both *Bt* maize and *Bt* cotton, the increased significance of secondary pests is intrinsically linked with insecticide use. On the one hand, as previously shown, decreases in insecticide applications can allow non-*Bt* susceptible insects to increase in numbers within the *Bt* crop. On the other hand, broad-spectrum insecticide spraying is the cheapest and most efficient solution for farmers avoiding severe crop damage due to a sudden pest outbreak of a nontarget pest species. Several other issues are also linked with insecticide use in *Bt* crops, including pest resistance caused mainly by the lack of refuge strategies, weak institutional structures, poor education and a lack of understanding concerning the technology (Dowd-Urbe, 2014; Morse *et al.*, 2007; Yang *et al.*, 2005a).

Outstanding issues

Regardless of the cause, if non-susceptible secondary pest populations exceed economic thresholds, the sustainability of the technology may be in jeopardy. If natural enemies are negatively affected by *Bt* maize, directly or indirectly, an ecological opportunity may appear for the emergence of a new pest which had previously been controlled through predation or parasitism. Consequently, insecticide spraying is the only immediate solution at farmers’ disposal, which will disrupt the natural enemies’ complex. If a secondary pest outbreak occurs due to an ecological opportunity arising from a drop in the density of a former major herbivore, the same immediate solution could be used with equivalent impacts. Hence, farmers growing *Bt* crops will potentially recommence running on the insecticide treadmill observed in the 20th century (van den Bosch, 1978), leading once again to the negative impacts of insecticides on the environment that it was hoped *Bt* crops would reduce (Krebs *et al.*, 1999;

Pemsl *et al.*, 2011). There are serious disadvantages associated with overuse of pesticides, including human poisonings (Ecobichon, 2001; Jeyaratnam, 1990), the emergence of pest resistance (Metcalf, 1987) and natural enemy mortality (Hardin *et al.*, 1995; Metcalf, 1987). Additionally, pests tend to increase their reproductive rate when stressed by sublethal quantities of a control agent; a phenomenon known as 'hormoligosis' (Luckey, 1968; Morse, 1998). It appears that to date, a potential 'hormoligosis' effect of *Bt* crops has not been studied, even though this may be partly responsible for past outbreaks of secondary pests related to the misuse of insecticides (Cordeiro *et al.*, 2013; Gross and Rosenheim, 2011; Guedes and Cutler, 2014). Research presented in this review suggests that secondary pests are eroding some of the economic and ecological benefits of *Bt* crops. Chinese cotton production is a clear example. In fact, we have shown that, even in successful *Bt* cropping systems (such as *Bt* cotton in the USA), insecticide applications remain a strategically important method of controlling secondary pest outbreaks.

New stacked events expressing several *Bt* toxins may temporarily overcome some of the drawbacks associated with secondary pests. Scientists are hopeful that these stacked crops will mitigate some of the concerns raised so far for single traits and still increase yields even further (e.g. Shi *et al.*, 2013). From an ecological perspective, such expectations have yet to be proven as stacked events may equally cause faster changes in ecosystem processes, affecting the resilience of the system as a whole to adapt efficiently. Furthermore, some agro-ecosystem responses occur over a long time frame, so only long-term studies could effectively detect any effects (see Symstad *et al.*, 2003 for a detailed discussion). For example, continuous exposure to a range of *Bt* toxins throughout the full season may affect prey species and food chains (Groot and Dicke, 2002), and the occurrence of resistance may be increased in pests with low susceptibility to *Bt* toxins over time (Brévault *et al.*, 2013). This lack of certainty regarding ecological impacts and the complexity of agro-ecosystems have led to questions about the conclusions of several studies assessing the impacts of transgenic crops due to their simplistic methodological approaches (e.g. Andow *et al.*, 2006; Dowd-Urbe, 2014; Glover, 2010a,b; Kruger *et al.*, 2012; Lövei *et al.*, 2009; Smale *et al.*, 2006; Stone, 2011). There is a risk that interactions evaluated over a short period fail to detect potential longer term impacts (Kouser and Qaim, 2011; Pemsl *et al.*, 2011). The occurrence of secondary pests is clearly linked with profitability, which in turn is affected by other important factors: quality of seeds (Xu *et al.*, 2008); development of resistance (Kruger *et al.*, 2012); farm size (Stone, 2011); regional, social and institutional variability (Dowd-Urbe, 2014; Smale *et al.*, 2006); and farmers' knowledge/education, skills and wealth (Mancini *et al.*, 2008; Yang *et al.*, 2005a). For example, making an assumption that early adopters are similar in terms of managerial performance to late adopters or small-scale farmers may introduce a bias to the results (Croft *et al.*, 2007; Morse *et al.*, 2007; Stone, 2011). Similarly, differences in agricultural systems—such as irrigated versus nonirrigated fields in India (Qaim and Zilberman, 2003)—are important factors that are often omitted from research (Stone, 2011). It is likely that such systems have differences in pest abundance and insecticide use (Stone, 2011).

Studies assessing the impact of *Bt* crops on NTOs remain controversial. Ecological criticisms are mainly based on the reliability of data, poor replicability, low numbers of possible response variables and short temporal frames, and the studies often do not take into consideration environmental variability

across regions (Andow *et al.*, 2006; Lövei and Arpaia, 2005; Marvier, 2002; Shantharam *et al.*, 2008). Laboratory studies are essential to assess the effects of *Bt* crops on NTOs, provided they are assessed across the full variety of relevant ecological contexts (Lövei and Arpaia, 2005). In the laboratory or in controlled field cages, most nonfield-scale studies have assessed the direct impact that the toxin has on the predator, on the prey or on the impact of a predator through prey consumption (see for example Lang and Otto, 2010; Lövei *et al.*, 2009; Marvier *et al.*, 2007; Wolfenbarger *et al.*, 2008). However, the relevance of these findings within the field agro-ecosystem is uncertain (Andow and Hilbeck, 2004; Lövei and Arpaia, 2005) and such studies often fail to account for indirect spatial and temporal effects on tritrophic population dynamics (Andow *et al.*, 2006). Further, the occurrence and distribution of insect pests in crops are nonuniform, depending instead on factors such as the agro-climatic conditions, agro-ecology, anthropogenic interventions, introduction of new crops, pest control management techniques and other hard-to-define random factors (Baker *et al.*, 2000; Sisterson *et al.*, 2005; Velasco *et al.*, 2007).

Conclusions

Like insecticides, *Bt* crops alter agro-ecosystem processes and functioning. In some cases, this may lead to large and complex landscape-level effects on pest dynamics, a rearrangement of niches and thus a possible outbreak of secondary pests. This review has explored the reasons for, and the results of, secondary pest outbreaks in *GE insect-resistant* crops, with a focus on *Bt* maize and *Bt* cotton. Undoubtedly, *Bt* crops have led to several economic and environmental advantages, but many claim that those gains, although real, have been overemphasized (Smale *et al.*, 2006; Stone, 2011). Although secondary pest outbreaks are a well-known phenomenon, they have generally been overlooked in transgenic cropping research. While *Bt* crops are highly efficient at controlling target pest levels, they may not be as effective at controlling other pests that have historically posed less or even no threat (Sharma and Ortiz, 2000). The three potential mechanisms related to secondary pest emergence: (i) a reduction in broad-spectrum insecticide applications; (ii) a reduction in control by natural enemies; and (iii) a decrease in interspecific competition with the target pest, have relevance for better *Bt* crop management.

It is evident from the literature that, due to lower insecticide applications, secondary pests that are not susceptible to the expressed toxin are becoming an increasing concern in some agro-ecosystems where *Bt* crops are grown. The potentially negative influence of *Bt* crops on natural enemies has generated considerable debate among scientists, although there appears to be agreement that a negative impact is conceivable (e.g. Andow *et al.*, 2009; Lövei *et al.*, 2009; Shelton *et al.*, 2009). This impact can be direct through the ingestion of the toxin or indirect due to changes in the agro-ecosystem on which that species depends, such as reduced prey density (Andow *et al.*, 2006; Snow *et al.*, 2005). Less attention has been given to ecological opportunism by competitive species (but see Dorhout and Rice, 2010; Virla *et al.*, 2010). Secondary pests may take several years to develop to a point where they actually become a major concern (Ho *et al.*, 2009). Hence, it has been suggested that additional research is needed to evaluate the potential long-term effects of the wide-scale adoption of new *Bt* events and their impacts on ecosystems (Krishna and Qaim, 2012). It is important that the ecological

relevance of such studies is properly acknowledged (Gatehouse *et al.*, 2011), especially with regard to the impact on ecological services across the agricultural landscape and on the resilience of regional agro-ecosystems (Tschamtko *et al.*, 2005). Based on this review of the literature, we conclude with five major issues that require further exploration:

1. Large-scale, multitrophic and multispecies field studies to reveal the extent and potential of impacts on ecosystems (Lang and Otto, 2010) as (i) *Bt* toxins concentrations vary throughout the season depending on expressed toxins and the cultivar (Nguyen and Jehle, 2009; Showalter *et al.*, 2009); (ii) interactions between *Bt* fields and adjacent ecosystems will surely occur (e.g. natural enemy migration or niche replacement) (Dorhout and Rice, 2010; Razzi and Mason, 2012), which might carry direct and/or indirect biotic impacts across the landscape (Lundgren *et al.*, 2009); and (iii) in the case of stacked *Bt* crops, potential interactions between the expressed events may occur (Zhao *et al.*, 2005) and resistance may be increased in pests with low susceptibility to *Bt* toxins (Brévault *et al.*, 2013). Hence, laboratory and/or single species studies may fail to capture the wider trophic impacts that occurs in field environment (Lövei *et al.*, 2009). Only a holistic knowledge of pests and the behaviour of natural enemies will enable the formulation of a sustainable IPM framework capable of effectively suppressing secondary pest outbreaks (Lundgren *et al.*, 2009; Sisterson *et al.*, 2007).

2. The baseline for risk analysis studies should be adjusted. Until now, studies have used conventional cropping with insecticide treatments as the main basis for comparison of risk of *Bt* crops (Meissle *et al.*, 2011; Sisterson *et al.*, 2007). However, this comparison should be broadened to include other scenarios, such as organic or untreated cropping systems (Andow *et al.*, 2006). The assessment of *Bt* cropping with other IPM strategies, such as crop rotation, tillage, selective insecticides and biological control (Deguine *et al.*, 2008; Musser and Shelton, 2003; Vasileiadis *et al.*, 2011), would be useful, especially taking into consideration the forecasted increase in global food demand (Park *et al.*, 2011). Failing to take this into account might lead farmers to neglect other good farming practices (Bergé and Riccio, 2010).

3. Economic studies should move towards a wider approach, taking into consideration farmers' heterogeneity (Glover, 2010a, b). Assessing the mean yielding/profits of a crop within an entire country/region will likely be biased towards wealthier and better informed/educated farmers (Sanglestawai *et al.*, 2014). This is especially relevant in developing countries, where institutional networks are weak, making the enforcement of laws, policies and agricultural recommendations less effective (Dowd-Urbe, 2014; Kruger *et al.*, 2011, 2012; Shantharam *et al.*, 2008; Stone, 2011; Xu *et al.*, 2008). As Stone (2011, p. 395) states, 'longitudinal, multi-village, multi-ethnic, probabilistically selected, ethnographically grounded studies that avoid bias are helpful'.

4. To identify possible secondary pests and other nontarget effects of *Bt* crops with insecticidal properties, data are needed on which arthropod species occur in a given agro-ecosystem (Truter *et al.*, 2014). Presently, several million hectares of crops with *Bt* traits are being grown, and we should take advantage of such 'large-scale field research' opportunities. Hence, continuous, post-market and spatiotemporal monitoring is critical for rapid identification of the development of ecological problems. This could lead to timely regulatory decisions and the efficient deployment of mitigation measures (Sanvido *et al.*, 2009; Smale, 2012; Waage and Mumford, 2008). Furthermore, we suggest

that postmarket monitoring could help build a robust spatiotemporal database of insect species according to their ecological functions and occurrence in the specific receiving environments. Such a methodical process would also help to select a number of relevant and practical surrogate species for detailed laboratory or field tests (Hilbeck *et al.*, 2014).

5. The importance of spatially dynamic, bio-mathematical and bio-economic multispecies models in pre- and post-GE crop risk-assessment research has been recognized for sometime (e.g. Bohanec *et al.*, 2008; Harper and Zilberman, 1989; Marino and Landis, 1996; Yang *et al.*, 2009). Rigorous assessments of the present and future economic impacts, based on ecological constraints, are required to provide sound information to policymakers (Ascough *et al.*, 2008; Holmes *et al.*, 2010; Keller *et al.*, 2007; McDermott *et al.*, 2013). By allowing the manipulation of key biological parameters with economic production and damage functions, it will be possible to analyse potential solutions under different IPM scenarios, real or hypothesized (Carrasco *et al.*, 2010; DeJonge *et al.*, 2012; Liang *et al.*, 2012). A robust assessment of the effects of agro-ecosystem heterogeneity on pest population dynamics might be obtained when a geographic information system approach is added to the model (Carrière *et al.*, 2006). From these models, it would be possible to assess which species are most likely to be susceptible to landscape or environmental changes (Maiorano *et al.*, 2014; Petrovskii *et al.*, 2014). It is therefore important to foster research collaborations between the fields of ecology, mathematics and economics (Codling, 2014; Crowder and Jabbour, 2014).

In summary, despite the widespread adoption of *Bt* crops and a continued increase in the area on which they are grown, there are still a number of unanswered questions associated with longer term agro-ecosystem interactions, for instance the impact of secondary pests. These may not be serious enough to undermine the use of the technology, but do require further exploration so that practical and economically viable advice can be given to farmers and so that regulators are aware of potential issues and risks during a crop's approval phase.

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