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Field-resistance of the African maize stem borer to Bt maize: what did we learn?

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Introduction

In 1997 South Africa became the first country in Africa to commercially produce genetically modified (GM) crops in. Farmers started adopting Bt yellow maize (mainly used as animal feed) during the 1998/99 season. Bt white maize (mainly used for human consumption) was introduced during the 2001/2 season and the 2002/3 season saw the first large-scale Bt white maize production. Up to 2006, when event Bt11 was commercially released in South Africa all Bt maize hybrids contained Event MON810. These hybrids therefore all have the same gene that encodes for the Cry1Ab protein that is selectively toxic to larvae of the Lepidoptera.

Bt maize, expressing *Cry1Ab* protein was initially developed for the control of two stem borer species in North America i.e., *Ostrinia nubilalis* (Lepidoptera: Crambidae) and *Diatraea grandiosella* (Lepidoptera: Crambidae). These products also effectively control moth larvae of other economically important pests in Africa, which include *Chilo partellus* and *Sesamia calamistis* (Van Rensburg, 1999; Van den Berg & Van Wyk, 2007). Until 2006, effective control of the main target pest of Bt maize, *Busseola fusca*, was also reported in South Africa.

Since the first deployment of GM crops with insecticidal properties, there has been concern with regard to resistance development of target pests and possible non-target effects (Tabashnik, 1994; Gould, 1998). Resistance development as well as ineffective management thereof once reported could have several significant adverse effects. Firstly, if continued product failures occur and resistance becomes an area-wide problem, farmers will be back to where they were with management strategies 15 years ago. This will imply repeated application of broad-spectrum insecticides. Secondly, continued cultivation of specific GM events (for example cry 1Ab-producing maize cultivars), may compromise the future use of cultivars with similar stacked events, when these are deployed to control resistant pest populations.

Farmers perceptions of Bt maize in South Africa

Surveys conducted by Kruger *et al.* (2009, 2012) showed that the greatest benefit associated with Bt maize was the convenience of target pest management. An important advantage in the cultivation of Bt maize is the reduction in number of insecticide applications. However, Bt maize is only an advantage when target pests are present and there is no advantage in areas where infestation pressure is generally low. Stem borer populations can vary in abundance from year to year and their pest status is not predictable. This is evident from research done by Van Rensburg *et al.* (1987) on *B. fusca*, which indicated large-scale variation in infestation levels over seasons. In South Africa farmers have benefited from the adoption of Bt maize since its deployment during 1998 (Gouse *et al.*, 2005). Despite paying more for seed, adopters enjoyed increased income over conventional maize varieties through savings on pesticides and increased yield due to better pest control. Farmers also indicated that they did not need to scout their fields for pests any more since they assumed the technology was effective.

Resistance development

Two years after that start of planting Bt maize in South Africa, at harvest of the 1999 growing season, crop damage to the lower stems caused by *B. fusca* was noticed on a considerable scale at a number of localities, involving various Bt maize hybrids (Van Rensburg, 2001). No yield losses could be attributed to these infestations, but the observation caused concern due to the possibility that similar infestations may in future result in significant damage to maize ears. This concern was therefore only of "importance" due to the fact that it may result in yield loss

and no alarm seemed to have been raised about resistance development at that time. These observations were the first that should have indicated the possibility of resistance development and should have stimulated actions to address the issue.

1st report of resistance

The 1st official report of resistance of a maize pest to Cry 1Ab maize was made in South Africa during 2007 (Van Rensburg, 2007). This report of field resistance of *B. fusca* to Bt maize showed that the larvae on Bt maize at certain locations where some larvae were able to survive in the presence of the Bt-toxin but not without some detrimental effect on larval growth rate.

Within one year of the first report of resistance of *B. fusca* another reportedly resistant population was observed by farmers at the Vaalharts irrigation scheme, approximately 50 km from the initial site. Results from studies on fitness of stem borer population collected at the latter site showed that larvae survived on Bt maize and field-collected larvae were reared without problems for four generations on Bt maize plants in the laboratory. This study also indicated that larvae collected from non-Bt maize refugia, adjacent to maize fields survived until the moth stage on Bt maize. This indicates that the high dose/refuge strategy (see below) may be compromised in effectiveness in this geographical area.

Follow-up surveys conducted between 2010 and 2011 showed that resistant pest populations occurred in many areas within the maize production region of the country (Kruger *et al.*, 2012). Based on the incidence of farmers that spray insecticides for borer control on Bt maize, it can be concluded that *B. fusca* resistance to Bt maize (MON810) is wide spread in the country. The study by Kruger *et al.* (2012) showed irresponsible management of GM crop technology by the maize industry.

Insect resistance management (IRM)

Analysis of more than a decade of resistance monitoring data up to 2008 for six Lepidoptera species targeted by Bt maize and cotton suggested that the principles of the refuge strategy may apply in the field to limit resistance development (Tabashnik *et al.*, 2008a). To date field evolution of resistance has been detected only in *B. fusca* in South Africa (Van Rensburg, 2007), *Helicoverpa zea* (Lepidoptera: Noctuidae) in the South-Eastern United States (Tabashnik, 2008; Tabashnik *et al.*, 2008b) and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Puerto Rico (Matten *et al.*, 2008). Pink bollworm *Pectinophora gossypiella* (Lepidoptera: Gelechiidae) resistance to Bt cotton has also recently been reported from India and *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) resistance to Bt maize in the USA (Gassmann *et al.*, 2011). Except for the case of MON810-resistance of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Puerto Rico, poor refuge compliance was put forward as the major reason for resistance development in two of the three lepidopteran and one coleopteran species that have developed resistance to Bt crops.

Refugia

The importance of refugia in the delay of resistance development has been pointed out by several studies. Refuges are defined as habitats in which the target pest is not under selection pressure due to the toxin and it therefore provides a sustainable habitat for pest development.

The high dose/refuge strategy, employed to limit resistance development, comprises a combination of Bt maize plants producing high doses of toxin and non-Bt plants in close proximity to one another. The principle underlying this strategy is that any resistant insects emerging from Bt crops are more likely to mate with the one of the much larger number of susceptible pest insects emerging from refuges than with each other, thereby decreasing the selection for Bt-resistant alleles.

How did resistance develop so quickly in South Africa?

An effective high dose/refuge strategy requires three main components. First, the increase in fitness conferred by resistance alleles must be recessive. Second, resistance alleles must be rare so that few homozygotes survive on the Bt crops. Thirdly, one of the assumptions of the strategy is that resistant insects selected on Bt crops mate randomly, or preferentially with susceptible insects preserved on non-Bt crops (Bourguet, 2004).

Although the planting of refugia is compulsory, the level of compliance between 1998 and 2006 was shown to be low in the region where resistance was reported in South Africa (Kruger *et al.*, 2009, 2012). Furthermore, Van Rensburg and Van Rensburg (1987) indicated that rainfall and humidity are important environmental factors affecting the abundance of *B. fusca* moths. Moths possibly give preference to irrigated maize, which could have contributed to increased selection pressure towards the evolution of resistance to the Bt toxin (Van Rensburg, 2007). Van Wyk *et al.* (2008) also indicated that the strong linkage of stem borers to the maize ecosystem in irrigation areas and especially the planting of Bt-maize in these systems result in strong selection pressure for evolution of resistance.

The increased levels of resistance recorded for *B. fusca* was at least in part due to non-compliance by producers with the refuge principle (Kruger *et al.*, 2009, 2012). However, in retrospect it appears that the Bt-events currently available for control of *B. fusca* do not meet the high dosage requirement (Tabashnik *et al.*, 2009). Pest resistance to Bt maize most likely resulted from a combination of late planting dates with consequent increased levels of infestation and variance in time of planting providing a continuous supply of moths. Increased pest pressure combined with non-compliance with refuge requirements probably contributed to selection pressure that resulted in increased levels of pest tolerance to the Cry 1Ab toxin.

Lessons learned

Poor monitoring (and reporting?) of compliance to refugia requirement was shown to have played an important role in resistance development. Rapid adoption of Bt-technology, up to a level of nearly 100 % over a short period of 9 years probably created an environment in which farmers and seed companies did not foresee or realize the absence of refugia and the problem this was creating. A lesson that could be learned from this is that in areas where Bt-technology adoption rate is very high, refuge compliance should be followed-up and enforced.

No information exists on the levels of protein expression in Bt maize hybrids in South Africa. Low-dose expression of cry1Ab protein can contribute significantly to resistance development and the role that it could have played in this case should not be underestimated.

Apart from increased refuge compliance monitoring, no other actions relating to insect resistance management were taken in South Africa. Continued selection pressure could therefore

have contributed to the evolution of a pest population that could also rapidly evolve resistance to new Bt maize events.

The stacked event, MON89034, which expresses two different cry proteins, Cry1A.105 and Cry2Ab, was commercially released in South Africa during 2011 and large scale planting is expected from the 2012/13 growing season onwards. Only time will tell whether the continued planting of cry 1Ab-expressing maize after the first reports of resistance 6 years ago, will have an effect on the sustainability of the newly released stacked event in the country.

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