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Insect Resistance Management in Bt Maize: Wild Host Plants of Stem Borers Do Not Serve as Refuges in Africa

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Abstract

Resistance evolution by target pests threatens the sustainability of Bt maize in Africa where insect resistance management (IRM) strategies are faced by unique challenges. The assumptions, on which current IRM strategies for stem borers are based, are not all valid for African maize stem borer species. The high dose–refuge strategy which is used to delay resistance evolution relies heavily on the presence of appropriate refuges (non-Bt plants) where pests are not under selection pressure and where sufficient numbers of Bt-susceptible individuals are produced to mate with possible survivors on the Bt maize crop. Misidentification of stem borer species and inaccurate reporting on wild host plant diversity over the past six decades created the perception that grasses will contribute to IRM strategies for these pests in Africa. Desired characteristics of refuge plants are that they should be good pest hosts, implying that larval survival is high and that it produces sufficient numbers of high-quality moths. Refuge plants should also have large cover abundance in areas where Bt maize is planted. While wild host plants may suffice in IRM strategies for polyphagous pests, this is not the case with stenophagous pests. This review discusses data of ecological studies and stem borer surveys conducted over the past decade and shows that wild host plants are unsuitable for development and survival of sufficient numbers of stem borer individuals. These grasses rather act as dead-end-trap plants and do not comply with refuge requirements of producing 500 susceptible individuals for every one resistant individual that survives on Bt maize.

Key words: *Busseola fusca*, *Chilo partellus*, grass, refuge, stem borer

Genetically modified (GM) Bt maize expressing Cry proteins constitute an important stem borer management tool (Kruger et al. 2009, 2012a; De Groote et al. 2011) and provides convenient and cost effective options for mitigating yield losses and other constraints faced by small farmers (Gouse et al. 2005, Hellmich et al. 2008, De Groote et al. 2011, Brookes and Barfoot 2014, Azadi et al. 2015). Diverse lepidopteran pests attack maize in Africa, and maize production is threatened by new invasive pests, such as *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) (IITA 2016) and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae), which have potential to spread throughout the continent (Yonow et al. 2016). Economically important indigenous stem borer species known to attack maize on the continent are *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae), *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), and *Eldana saccharina* Walker (Lepidoptera: Pyralidae) (Kfir et al. 2002). In North Africa, *Sesamia cretica* Lederer (Lepidoptera: Noctuidae) is the most important stem borer species (El-Shazly et al. 2013). Bt maize has been evaluated against all of these species (Table 1), with results showing varying levels of control (Van Rensburg 1999, Tefera et al. 2016). While South Africa and Egypt are the only two countries on the continent where Bt maize has been approved, it is expected that Bt maize will be released in several African countries within the next several years (Tumusiime et al. 2007, Mabaya et al. 2015).

Insecticidal traits in GM maize hold many benefits for African small-scale maize producers for whom chemical control and labor costs associated with control is beyond their financial means. Reduced insecticide use has been reported on Bt maize in commercial farming systems (Pilcher et al. 2002; Hofs et al. 2006; Naranjo 2009; Kruger et al. 2009, 2012a; Raybould and Quemada 2010; Brookes and Barfoot 2014). Reduced pest status of stem borers was reported throughout South Africa since the release of Bt maize in 1998 (Gouse et al. 2005, Kruger et al. 2012a). Additional benefits such as reduced incidence of ear rot (Flett and Van Rensburg 1992, Munkvold et al. 1997, Schulthess et al. 2002), and lower rates of *Fusarium* spp. infections and mycotoxins produced by ear rot fungi associated with borer damage, may also result from reduced lepidopteran pest damage to maize (Munkvold et al. 1997, Bowers et al. 2014). Bt maize may therefore, under certain environmental conditions, also be considered the first line of defense against grain-infecting fungi, which is exacerbated by stem borer damage to plants (Gressel et al. 2004).

Table 1. African maize stem borer species evaluated for susceptibility to Cry proteins

Species	Proteins	Source
Busseola fusca	Cry1Ab	Van Rensburg 1999, Kotey et al. 2017, Mugo et al. 2011, Tefera et al. 2016
	Cry1Ba	Mugo et al. 2011
	Cry1.105+Cry2Ab2	Kotey et al. 2017
Sesamia calamistis	Cry1Ab	Van Wyk et al. 2009, Van den Berg and Van Wyk 2007, Obonyo et al. 2008
	Cry1Ba	Mugo et al. 2011
	Cry1.105+Cry2Ab2	Venter 2015
Sesamia cretica	Cry1Ab	El-Shazly et al. 2013
Eldana saccharina	Cry1Ab	Keeping et al. 2007. Venter 2015
	Cry1Ba	Tende et al. 2010, Mugo et al. 2011
	Cry1.105+Cry2Ab2	Venter 2015
Chilo partellus	Cry1Ab	Van Rensburg 1999; Tende et al. 2005, 2010; Mugo et al. 2011; Tefera et al. 2016; Obonyo et al. 2008
	Cry1Ba	Mugo et al. 2011; Tende et al. 2005, 2010
	Cry1.105+Cry2Ab2	Venter 2015

For Bt maize technology to remain effective and for its benefits to be available to farmers over the long term, this technology needs to be managed in such a way that target pests do not evolve resistance (Brookes and Barfoot 2014). Since the first deployment of Bt crops, there has been concern regarding resistance development of target pests (Tabashnik 1994, Gould 1998, MacIntosh 2009).

In this paper, evidence of wild host plant diversity, abundance, and suitability as refugia for stem borers is reviewed and discussed in terms of insect resistance management (IRM) in the African context. While the focus is on the African maize stem borer, *Busseola fusca* reference is also made to other economically important stem borer species. *Busseola fusca* has already evolved resistance to Cry1Ab Bt maize in South Africa (Van Rensburg 2007; Kruger et al. 2009, 2011), and resistant populations occur throughout the maize-producing regions of the country (Van den Berg et al. 2013, Campagne et al. 2016).

IRM in Africa is faced by unique challenges provided by farming practices of small holder farmers who should derive benefit from this technology (MacIntosh 2009, Assefa and Van den Berg 2010, Raybould and Quemada 2010, Van den Berg et al. 2013). While industrial agriculture generally utilize largely crop monocultures across very large regions with few wild or uncultivated areas, environments in Africa support a wide diversity of crops on small plots, or crops intermixed with wild areas within the landscape. In Africa, cereal crops are usually grown in small fields (<1.5 ha; Schulthess et al. 1997, Gouse et al. 2006, Tumusiime et al. 2007, Aheto et al. 2013, Bøhn et al. 2016), surrounded by grasses that could potentially host lepidopteran stem borers (Mailafiya et al. 2011, Midega et al. 2014). IRM strategies that are effective in large monoculture production systems in North America are unlikely to be appropriate for the small, more diverse agricultural systems of south-east Asia or Africa (MacIntosh 2009). The risk of Bt resistance evolution is high in areas where grower compliance to refuge requirements may be poor such as in developing countries with developing infrastructure, and where enforcing of stewardship programs is problematic (Carroll et al. 2012). IRM strategies, especially planting of refuges, may be difficult to implement in a small holder farmer context (Carroll et al. 2012) and implementation thereof provides a huge challenge to small farmers and subsequently to stewardship of the technology in the African context (Assefa and Van den Berg 2010, Azadi et al. 2015). The design of any IRM strategy should therefore consider constraints imposed by the nature of different agricultural systems (Forrester 1990) and be appropriate for African farmers' practices and contexts (Scoones and Thompson 2011).

Insect Resistance Management

The goal of IRM is to delay or prevent the evolution of resistance (Andow 2008). The high dose–refuge strategy is the most widely used approach to delay resistance evolution (Gould 1998, Glaser and Matten 2003, Gryspeirt and Grégoire 2012, Tabashnik et al. 2013). This IRM strategy relies on two equally important measures: high-dose expression of the Bt toxin in the plant to kill all susceptible individuals; and the presence of an appropriate refuge (Glaser and Matten 2003) to produce sufficient numbers of high quality susceptible individuals within close proximity to the cropping area, where resistance selection pressure is exerted on the target pest species. The purpose of the high dose of Bt toxin is therefore to kill as many individuals of the target pest as possible, in particular heterozygous genotypes that carry one resistance allele (RS types), whereas the purpose of the refuge is to allow a sufficient number of homozygous susceptible (SS types) pest individuals to survive on that particular crop (Renner 1999, Gould 2000, USEPA 2001) or in the crop environment (Andow 2008).

The key assumptions of this IRM strategy (Andow 2008, Bourguet 2004, Carriére et al. 2010, Gryspeirt and Grégoire 2012, Tabashnik et al. 2013) are that: 1) plant tissue must be sufficiently toxic that any resistance allele in the target population is functionally recessive, 2) resistance genes are initially rare, and 3) there is random mating between resistant and susceptible adults, the latter which is produced in the refuge in sufficient numbers, at the same time that moths emerge from Bt fields.

Challenges to resistance management of especially *B. fusca* are provided by the deployment of low-dose events against this species. Since the high-dose requirement is not met for *B. fusca* in currently available Cry 1Ab maize events (Van Rensburg 1999, Campagne et al. 2016), an important assumption is violated. The latter, together with a lack of appropriate refuges or noncompliance, may contribute to rapid resistance evolution of this pest in particular.

A refuge is defined as a habitat in which the target pest can maintain a viable population in the presence of Bt fields, where there is no additional selection for resistance to Bt toxins and pest insects occur at the same time as in the Bt fields (Ives and Andow 2002, Bourguet 2004, Gryspeirt and Grégoire 2012). An appropriate or acceptable refuge is therefore based on the common premise that adequate numbers of nonselected insects are produced in close proximity to Bt crops to ensure that resistant insects will rarely mate with each other (USEPA 1998). Consequently, rare resistant moths that develop on Bt maize, instead of mating with each other, mate with the overwhelming number of susceptible moths from the refuge (Tabashnik and Croft 1982, Gould 1998).

Refuge designs can take on several forms (Glaser and Matten 2003), for example, either planting of a structured refuge (deliberately planted in association with the Bt crop) in close proximity to the crop, or unstructured refugia (naturally present as part of the cropping system) in the form of non-Bt maize fields, mixtures of Bt and non-Bt seed, or wild host plants of the particular pest species. Structured refuges include all suitable non-Bt host plants for a target pest that are "planted and managed" by people (USEPA 2001). It is therefore essential that refuges, whether they consist of plantings of non-Bt maize, wild hosts, or alternative host crops, should serve the intended purpose of refuge plantings, i.e., providing sufficient numbers of susceptible offspring to mate with resistant survivors. Furthermore, it is important that the design, placement, and size of the structured refuge should be based on knowledge of pest biology (Roush 1997, USEPA 2001, Siegfried and Hellmich 2012). The effectiveness of any refuge depends on its size and spatial arrangement relative to the Bt crop, the behavioral characteristics of the pest, and management requirements (Bates et al. 2005, Gryspeirt and Grégoire 2012, Detiloff et al. 2016).

The importance of appropriate refugia in delaying resistance evolution has been pointed out by several authors (Bourguet 2004, Siegfried and Hellmich 2012, Tabashnik et al. 2013). The current refuge requirements in the case of structured refugia for Bt maize in Africa are similar to those in the United States. These are either a 20% refuge planted to non-Bt maize which may be sprayed with insecticides, or a 5% refuge area that may not be sprayed (Gould 2000, Shelton et al. 2000, USEPA 2001, Van den Berg et al. 2013). Poor compliance to refugia requirements has been highlighted as the major contributor to resistance evolution, especially for the African maize stem borer, *B. fusca* (Kruger et al. 2009, 2011, Tabashnik et al. 2013). What makes IRM strategies against this pest even more challenging is that it is not only inherently more resistant to the Bt toxin (Tabashnik et al. 2009), but the inheritance of resistance is also not recessive (Campagne et al. 2013). Since implementation of a structured refuge strategy is expected to be complicated in small farming environments (Carroll et al. 2012, Van den Berg et al. 2013), any source of pests, such as wild host plants, where pest individuals are not subjected to selection pressure by Bt maize, would contribute to delaying resistance evolution.

Importance of Grasses in Stem Borer Ecology

Lepidopteran stem borer larvae feed inside stems of many species of monocotyledonous plants which belong to the Poaceae, Cyperaceae, and Typhaceae families (Le Ru et al. 2006a). The importance of wild host plants, mostly thick-stemmed grasses, in the ecology of lepidopteran pests of maize has been discussed extensively over the past 60 yr, with several surveys that catalogued the diversity of *Busseola* spp., *Sesamia* spp., *Chilo* spp., and *E. saccharina* throughout Africa (Ingram 1958; Nye 1960; Atkinson 1980; Conlong 2000; Haile and Hofsvang 2001; Mazodze and Conlong 2003; Ong'amo et al. 2006, 2013; Moolman et al. 2014).

Some authors considered wild host species to be the source of stem borer infestations in crops and that these wild hosts were important in sustaining pest populations (Ingram 1958; Nye 1960; Bowden 1976; Seshu Reddy 1982, 1983, 1985, 1990, 1998; Nwanze and Mueller 1989; Verma and Singh 1989; Minja 1990; Harris and Nwanze 1992). This continuous erroneous reporting on the importance of wild hosts over the years created the perception that stem borers were present in high numbers in wild host plants, that these plants were abundant, and that they could serve as refugia for stem borers and be part of an IRM strategy for Bt maize.

The use of unstructured refugia and wild host plants as refuges is not approved as an IRM strategy for African stem borers, but it is often suggested as a possible solution (Head 2004; Mulaa et al. 2007, 2011; Tefera et al. 2016). Several for the grass species that act as stem borer hosts are also utilized as forage crops throughout sub-Saharan Africa and have in the past been considered as good options to serve as refuge crops. It has been suggested that wild unmanaged grasses as well as forage grasses, which are of agricultural value, be cultivated with the specific aim of being a refuge for maize stem borers (Kanya et al. 2005, Mugo et al. 2005, Mulaa et al. 2011). The presence of these cultivated host plants and natural refuges in some areas of East Africa has been considered sufficient to not require the additional planting of refugia for stem borers (Mugo et al. 2005, Mulaa et al. 2011).

Recent studies from East and Southern Africa have, however, started questioning the contribution that wild host plants could make as reservoirs for stem borer pest infestation (Le Ru et al. 2006a,b; Mailafiya et al. 2011; Moolman 2011). While these plants may have the characteristics of refuge crops in that they are hosts, are cultivated in association with maize fields, and are managed by humans (USEPA 2001), the fact that they do not produce sufficient numbers of high-quality moths make them unsuitable as refuge crops. This poor suitability of wild grasses as a refuge for lepidopteran stem borers became evident from field studies conducted throughout Africa over the past decade.

Desired Characteristics of Refuge Plants

Important requisites for a refuge to be effective can be summarized as follows: 1) it should produce sufficient numbers of moths, 2) moths should be of high quality, 3) the refuge must be present in sufficiently large numbers (cover abundance) in a particular geographical area, and 4) moths should emerge at the same time that moths emerge from the Bt crop, otherwise the purpose of the refuge is defeated.

Carrying Capacity of Wild Hosts

The suitability of any host plant to serve as refuge is determined by its carrying capacity, which is in turn influenced by its host status (whether it allows survival of large numbers of high-quality individuals) and abundance in particular geographical areas. For a refuge to be effective, USEPA (2001) indicated that it should produce 500 susceptible adults for every adult emerging from a Bt plant in the transgenic crop area (assuming a resistance allele frequency of 5×10^{-2}). This requirement is, however, not met by any wild host plants or forage crops that are known hosts of stem borers in Africa.

Planting crop cultivars that result in poor pest survival, the application of chemical control measures in a refuge, or unsuitable wild host plants that act as unstructured refugia, evidently result in reduction of the effective size of refugia (Gould 1998). The plant species in a refuge, whether it is a cultivated crop (including a managed forage grass species) (Hokkanen 1991) or a wild host, should therefore be highly suitable for pest development. To a certain extent, the characteristics of an ideal trap crop, i.e., a highly preferred oviposition host and suitable for pest development, are also those that would make for a particular plant species to be a good refuge plant.

While wild and forage grasses may be attractive for stem borer oviposition, they are unfortunately poor hosts, as indicated below.

Poor Host Status of Grasses

No studies have previously been conducted on the actual number of stem borer moths emerging (carrying capacity) from refuge plantings of Bt maize and no empirical evidence exists to indicate that the 5% or 20% refuge options allow for sufficient numbers of susceptible moths to emerge. Similarly, no information exists on the carrying capacity of the two most common host grass species (Napier grass—*Pennisetum purpureum* and wild sorghum—*Sorghum arundinaceum*) that are suggested as refuges for stem borers.

Although no information exists on the moth carrying capacity of maize, indications of numbers of moths that may emerge from a certain unit area do however exit for sugar cane and sorghum. The potential moth production capacity of a crop can be illustrated through the use of a stem borer moth production index, such as that used by Bessin et al. (1990) in sugarcane and Van den Berg (1997) for grain sorghum. The moth production index estimates the number of moths that could emerge from a specific cultivar of the crop and can indicate if it suppresses pest numbers compared with other cultivars. This index is a product of the number of moth exit holes per stalk and the number of stalks per hectare, and is expressed as the number of moths that emerge from the crop per hectare over a season. Bessin et al. (1990) showed that up to 77,000 moths of the sugarcane borer, *Diatraea saccharalis* F. (Lepidoptera: Pyralidae), can emerge from a sugarcane field with a plant stand of 3,000 per hectare, after larvae have completed their life cycle on the crop. Van den Berg and Van der Westhuizen (1998) showed that a highly resistant sorghum cultivar produced only 40,000 *B. fusca* moths per hectare compared with a susceptible cultivar that produced 113,000 moths per hectare over a growing season, at a plant stand of 50,000 per hectare.

On wild host plants, stem borer densities do not reach the levels observed in crops, mostly as a result of low survival of young instars (Nye 1960, Shanower et al. 1993, Schulthess et al. 1997, Gounou and Schultess 2004). Compared to maize and sorghum, thick-stemmed grasses, owing to certain antibiosis or antixenosis characteristics, are poor hosts of stem borers and have low carrying capacity. In many cases, these grasses are dead-end-trap crops. For example, marked preference for oviposition of *B. fusca* and *C. partellus* moths has been reported on *P. purpureum* but it is a very poor larval host for these species (Khan et al. 1997; Ofomata et al. 2000; Van den Berg et al. 2001; Ndemah et al. 2002; Rebe et al. 2004a,b; Mohamed et al. 2004; Khan et al. 2006, 2007; Van den Berg 2006; Van den Berg et al. 2006). In Eritrea, Haile and Hofsvang (2002) also reported that although *B. fusca* preferred certain grass species to maize for oviposition, larval survival on these grasses were very low. No survival of *C. partellus* has been observed on the grass *Hyparrhenia tamba* (Rebe et al. 2004b) and other *Hyparrhenia* species which are attacked by stem borers (Haile and Hofsvang 2001, Matama-Kauma et al. 2008). Similarly, in West Africa, Kaufmann (1983) observed no survival of *B. fusca*, *S. calamistis*, or *E. saccharina* on *Pennisetum purpureum* and *Panicum maximum*.

Poor host status of grasses was also reported by Shanower et al. (1993) who observed <10% larval survival on wild host plants as opposed to 20–30% on cultivated crops. Chabi-Olaye et al. (2006) recorded <7% survival of *B. fusca*, *S. calamistis*, and *E. saccharina* on five common wild host grass species in West Africa. Shanower et al. (1993) reported <10% larval survival of *S. calamistis* and *E. saccharina* on the grasses, *Andropogon* sp., *Panicum maximum*, *Pennisetum purpureum*, *Pennisetum polystachion*, and *Sorghum arundinaceum*, compared with between 19 and 30% survival on maize. Atachi et al. (2005) reported 0.05% survival of *E. saccharina* as well as reduced fecundity on a common grass host species, *S. arundinaceum*, compared with 10% survival on maize.

Incidence of Stem Borer Infestation in Grasses

Further evidence of the poor host status and low carrying capacity of grasses for stem borers is provided by data on larval abundance in grasses under natural conditions. For example, the number of *B. fusca* larvae collected made up 0, 0.25, and 3.90% of the total number of stem borer larvae collected in grasses in the low, mid, and high-altitude zones of Kenya, respectively (Ong'amo et al. 2006). To increase the likelihood of finding stem borer larvae in wild grasses, biased sampling is usually used instead of random sampling such as in maize fields (Ong'amo et al. 2006, Moolman et al. 2014). Extremely low incidences of stem borer larvae in wild hosts was reported by Moolman (2011) who reported that only 0.0067% of stems of the most common wild host plant species showed signs of borer infestation. The total number of stems inspected for damage in the latter study was estimated at 14,000,000 on a total of 125 hectares, over a period of 2 yr.

In a 2-yr survey in different agro-ecological zones in Kenya, Mailafiya et al. (2011) reported that *B. fusca* was virtually absent from wild hosts and that it was only found in *S. arundinaceum*. In surveys during which a total of 24,674 larvae were collected from wild host plants in eight countries in East Africa (Le Ru et al. 2006a), the proportion of larvae made up by *B. fusca* was below 1.6% except for collections from Eritrea and Ethiopia. Haile and Hofsvang (2002) showed significantly lower numbers of *B. fusca* pupae in wild grass species compared with maize and sorghum in Eritrea. Similarly, Ndemah et al. (2007) described the exceedingly low densities of stem borers in grasses in Cameroon. A 5-yr field survey in South Africa, following a biased sampling strategy, yielded only 4,413 stem borer larvae from 66 wild host plant species (Moolman et al. 2014). Of these, 1.9% were *B. fusca*, 1.7% were *C. partellus*, and 0.2% were *E. saccharina*. In Mozambique, surveys between 2008 and 2011 yielded no *B. fusca* from wild host plants, and from a total of 1,920 larvae collected from 30 plant species, only two were *S. calamistis* and 68 were *C. partellus*. The latter study in Mozambique also showed very low abundance of stem borers in wild host plants, with only 99 larvae of *C. orichalcociliellus* collected from three host plants over a 2-yr sampling period (Moolman et al. 2014). During the same period, only 86 *C. partellus* individuals were collected from five species of grasses and two individuals of *S. calamistis* were collected from sugar cane.

Only 0.06% of the total number of stem borers collected in wild host plants, during country-wide surveys in South Africa between 2005 to 2010, were found to be economically important species (*B. fusca*, *C. partellus*, and *S. calamistis*; Moolman et al. 2014). In surveys conducted by Ong'amo et al. (2006) across agro-ecological zones in Kenya, 189,600 stems were checked and only 14.7% of the borer population in these found to be *B. fusca*. Much lower borer densities on wild hosts than cultivated crops have also been reported by Nye (1960), Schulthess et al. (1997), and Ndemah et al. (2002) in West Africa.

Quality of Moths Emerging From Refuges

The presence of high-quality insects that perform competitively in the field are critical to the success of area-wide integrated pest management programs (Calkins and Parker 2005, Boersma and

Carpenter 2016). It is furthermore important that the emergence of moths from crop fields and refuges is synchronized to allow for random mating (Gryspeirt and Grégoire 2012). Since stem borer larval feeding in the whorls of plants occurs during the early stages of colonization of wild host plants, larval antixenosis and antibiosis at this stage may prevent successful colonization of wild grasses (Rebe et al. 2004a). Mulaa et al. (2007) reported lower weights of borer larvae reared on different grass species compared with maize, for *B. fusca*, *S. calamistis*, *E. saccharina*, and *C. partellus* as well as reduced fecundity of species. Reduced fecundity of *E. saccharina* moths originating from larvae that fed on grasses was also reported by Shanower et al. (1993) and Atachi et al. (2005). Positive correlations between moth size and fecundity for *C. partellus* (Berger 1989), *B. fusca* (Kruger et al. 2012b, Kaufmann 1983), and *E. saccharina* (Kaufmann 1983) were also reported after feeding on different host plants. Differential survival, growth and development periods on different grass species compared with maize were also reported for *C. partellus* (Mohamed et al. 2004), *C. orichalcociliellus* (Ofomata et al. 2000), and *B. fusca* (Khan et al. 2007).

Any factor, for example, slower larval development in grasses, that result in disruption of synchronization in moth emergence between the Bt crop and refuge will have adverse effects on IRM, as assortative mating may lead to increased incidence of resistant individuals in pest populations (Gryspeirt and Grégoire 2012). Campagne et al. (2016) showed that together with nonrecessive resistance, any deviations from random mating of *B. fusca* can significantly increase the rate of resistance evolution.

Geographical Distribution and Land Cover Abundance of Wild Host Plants

To be sufficient as a refuge, areas of wild host plants should be sufficiently large and situated inside the geographical areas where the Bt maize crop is cultivated. If refuges are too small, it will not contribute to significant delays in resistance development (Gould 1998, Tyutyunov et al. 2008).

Studies conducted in East Africa provide valuable information regarding the occurrence and abundance of wild host plants. Several studies indicated that the cover abundance of host plants is very low and that thick-stemmed grasses are not abundant enough to serve its purpose as refuges in IRM strategies. At one site in Western Kenya, wild host plants and maize covered 11% and 50%, respectively, of the surveyed area, whereas at another site, 27% of the surface cover was under maize and 13% under wild host plant species during the cropping season (Otieno et al. 2008). Furthermore, while *C. partellus* was found in the natural habitat surrounding cereal fields at very low densities, *B. fusca* was absent (Otieno et al. 2008). The cover abundance of the wild hosts of *C. partellus* varied between 0.01 to 3.6% among different vegetation classes, whereas *P. maximum* dominated the host plant community in different vegetation types with the highest cover abundance of 3.56%. The cover abundance of other stem borer hosts such as *P. purpureum* and *R. cochinchinensis* ranged between 0.12 and 0.49% (Otieno et al. 2008). The latter study also did not record *B. fusca* from wild host plants sampled in natural habitats in some eco-regions. In Uganda, Matama-Kauma et al. (2008) also showed a very low surface cover (0.5%) of *S. arundinaceum*, the most important host plant of *B. fusca* in that country.

In a study of the diversity and abundance of stem borers in cropping as well as off seasons, in grassland and Forest Woodland systems in Kenya, Otieno et al. (2008) recorded *B. fusca* on only two host plant species, *P. purpureum* and *Setaria magaphylla*, which collectively made up a mean percentage cover abundance of 0.26% during the cropping season. Although *C. partellus* has a higher number of wild host plants than *B. fusca*, the total percentage cover abundance for all the wild hosts combined was 1.2% during the cropping season (Otieno et al. 2008). In a survey specifically aimed at assessing the cover abundance of wild hosts in the high rainfall regions of Kenya where Bt maize will most likely be introduced first, Kanya et al. (2005) showed that although 14 wild host plant species occurred in the region, cover abundance was low (<10%), and that wild hosts would not sustain sufficient numbers of moths as required for an IRM strategy to be effective.

Host Plants of *Busseola* Species

Improved taxonomical expertise using morphological and molecular tools allowed accurate identification of stem borers collected from wild host plants over recent times (Otieno et al. 2008; Mailafiya et al. 2011; Le Ru et al. 2006a,b; Ong'amo et al. 2006, 2013; Moolman et al. 2014). From these surveys of 197 plant species in 15 African countries, Calatayud et al. (2014) reported *B. fusca* to occur on only seven species: *Sorghum arundinaceum*, *Setaria megaphylla*, *Pennisetum purpureum*, *Panicum maximum*, *Cymbopogon nardus*, *Cymbopogon giganteus*, and *Arundo donax*.

Interestingly, several other *Busseola* species were recorded during these surveys. *Busseola phaia* and *B. segeta* have been reported as pests of maize in certain areas of Kenya and Tanzania, respectively, whereas *Busseola nairobica* has been reported to be frequent in grasses around maize fields in parts of Kenya (Calatayud et al. 2014). *Busseola fusca* was also recently recorded from sugar cane (*Saccharum officinarum*) (Assefa et al. 2015) in South Africa.

Host Exploitation Strategies

Careful consideration of the host exploitation strategy (monophagous vs. polyphagous) as well as the actual importance and presence of wild hosts at a regional scale should be done during development of IRM strategies for different pests. This is especially important in the African context where it has been a long-held belief that wild host plants are the source of stem borer infestations in crop fields and that it could therefore contribute to IRM. Wild host surveys conducted in Cameroon over a period of 2 yr also indicated that, in terms of feeding strategy, the majority of stem borer species are either monophagous or oligophagous (Ong'amo et al. 2014), confirming reports by Le Ru et al. (2006a) that different stem borer species in general have specialized to feed on a diverse range of host plants, but that individual species have limited hosts.

IRM strategies for polyphagous pest species may include wild host plants and other host crops that could serve as part of a larger refuge. For such pests, refuges may be composed of cultivated nontransgenic crop plants or perhaps any other host plants, including weedy species that can support significant population sizes of the target insect pest species (USEPA 2001).

For example, the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae), is highly polyphagous and infests many herbaceous wild or cultivated plant species in proximity to Bt crops (Gould 1998). For a highly polyphagous pest such as *Helicoverpa armigera* (Lepidoptera: Noctuidae), the possibility of using other crops as refuges for Bt cotton seems viable. A study of the population dynamics of *H. armigera* in China showed that other crops can be used as a refuge for *H. armigera* in Bt cotton-growing areas (Ye et al. 2015). This was also done with *Heliothis* spp. infesting Bt cotton in the United States, or other crop species refuges such as tobacco for Bt cotton in United States, and pigeon pea for Bt cotton in Australia (Andow 2008). Indigenous plants and weedy hosts of *H. armigera* were also indicated to provide appropriate refuges in Bt cotton production areas in South Africa (Green et al. 2003). The legume pod borer, *Maruca vitrata* (Lepidoptera: Crambidae), the target pest of Bt cowpea in West Africa, is a polyphagous pest of grain legumes that has a wide distribution throughout tropical and subtropical regions worldwide (Agunbiade et al. 2014). The reservoirs of *M. vitrata* maintained on alternative host plants can contribute to IRM by sustaining individuals that have not been subjected to selection pressure on Bt cowpea (Onstad et al. 2012).

IRM in the African Context

The information above indicates that wild host plants will not contribute significantly to an IRM strategy in terms of the refuges it provides for stem borers in a Bt maize cropping environment. Stem borer populations in such refuges will most likely not sustain and repopulate themselves through a high net reproductive rate (Caprio et al. 2009) since, as shown above, larval survival in grasses is low and survivors are of poor quality and moth emergence from the Bt maize crop and wild host plants may not be synchronized. Wild host production of specific moth species in most cases is therefore likely to be low to nonexistent and unpredictable.

The challenges to IRM with Bt maize in Africa should be addressed through the development of robust refuge systems that take into account the entire cropping system, not just a single crop and pest. Current IRM strategies and reliance on wild host plants as refuge in most of the developing world is not appropriate to small farming systems. Previous experience has shown that compliance to requirements of structured refuge approaches will be low, necessitating novel approaches to address this problem.

It is therefore necessary to have a new look at integrated pest management strategies that may serve to reduce selection pressure for resistance evolution. The value of trap crops such as forage grasses, which have low carrying capacity and suppressive effects on stem borer populations, has been indicated before but their possible value has not been considered before in development of IRM strategies.

To be accepted by farmers, IRM strategies must be compatible with the existing cropping systems and normal farming practices. If other crops are planted as refugia, these must be economically viable, socially acceptable, and easy to implement by those making the management decisions at the farm level (Mulaa et al. 2011). To delay resistance evolution, novel IRM strategies that are appropriate for use in small-scale agriculture are needed.

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