Physiologically based demographics of Bt cotton–pest interactions I. Pink bollworm resistance, refuge and risk

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Abstract

Transgenic cotton expressing the genes for the production of protoxin of the bacterium *Bacillus thuringiensis* (Bt) is used to control lepidopterous pests. Among the most successful applications is for control pink bollworm (*Pectinophora gossypiella* Saunders (i.e. PBW)) in irrigated cotton of the southwestern United States. A major threat to this technology is the development of resistance commonly assumed recessive, autosomal and controlled by a single diallelic gene.

A physiologically based, distributed maturation time demographic model of Bt cotton and 10 of its major pests is developed. Here we used the model to examine the population dynamics and resistance development in pink bollworm as modified by weather and spatial and temporal refuges. The dynamics of the other pest species are reviewed in the second paper of this series.

The economics of Bt cotton for control of PBW in southern California is put in the context of the historical overuse of pesticides and the alternative short season cotton technology. The analysis posits that in the short run, the Bt cotton may be risk reducing and economic, but in the longer term it may be risk increasing.
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Keywords: Demographic model; Bt cotton; Pink bollworm; Resistance; Refuges; Risk

1. Introduction

Susceptibility to pesticides in target agricultural pest populations is a valuable natural resource in agriculture that must be managed carefully to keep the efficacy of a pesticide as long as possible, especially if the pesticide is environmentally friendly and if replacement options are more damaging. The incorporation of genes for the production of Bt toxin from the bacterium *Bacillus thuringiensis* by transgenic crops is thought to be an environmentally friendly innovation (Luttrell and Herzog, 1994). Cottons expressing the Cry1Ac δ-endotoxin (i.e. Bt toxin) have given good control of pink bollworm (*Pectinophora gossypiella*

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Saunders) and tobacco budworm (*Heliothis viresens* (F.)) (Williams, 2000), but variable control of other pest species is occurring (Luttrell et al., 1999). In 1999, about 8 million ha in the United States were planted to Bt cotton (USDA, 2000), and pressure is growing to introduce it worldwide (USDA-FAS, 2000; Pray et al., 2000; Qaim and Zilberman, 2003).

To examine the impact of Bt toxin on population growth and resistance in pests of cotton requires the development of holistic models (Parker et al., 2000; Stark and Banks, 2003). The models presented here and in a related paper (Gutierrez et al., 2005) realistically captures the field biology of Bt cotton and of its 10 herbivore pests [pink bollworm (PBW), tobacco budworm (TBW), bollworm (BW, *H. zea* (Broddie)), fall armyworm (FAW, *Spodoptera fugiperda* (J.E. Smith)), beet armyworm (BAW, *Spodoptera exigua* (Hübner)), cabbage looper (CL, *Trichoplusia ni* (Hübner)), soybean looper (SBL, *Psuedoplusia includens* (Walker)), plant bugs (LY, *Lygus* spp., Heteroptera), whitefly (WF, Homoptera), cotton bollweevil (*Anthonomus grandis* Boh.)].[1] Here we model the population dynamics and possible development of resistance in pink bollworm to Bt toxin, while the biology and dynamics of the other pest species in Bt cotton and the references for both papers are found in the second paper of this series (Gutierrez et al., 2005).

There is a well-known trade-off between simple models amenable to mathematical analysis and more complex and realistic models that seek to capture the subtleties of the biological interactions. Mills and Getz (1996) reviewed population dynamics models and emphasized the importance of bottom-up effects, especially of plant effects on higher trophic levels, effects that are critical in the analyses of transgenic crops used in pest control. Despite knowing little about movement and migration of cotton pests (Fitt et al., 1995; Peck et al., 1999; Tang et al., 2001), simple theoretical models have been developed to assess strategies for delaying resistance to Bt toxin (e.g. Mallet and Porter, 1992; Tabashnik, 1994; Caprio, 1998; Onstad

and Gould, 1998; Vacher et al., 2003, 2004; Linacre and Thompson, 2004). Although simplified and omitted plant dynamics, the models have heuristic value giving general insights into the effects of refuge size and spatial heterogeneity on Bt resistance management.

Ru et al. (2002) developed an age-structure simulation model for bollworm (*Helicoverpa armigera* (Hubner)) that included the effect on pest dynamics and resistance of declining Bt toxin levels with plant age but did not include plant dynamics. The analysis questions the utility of the Bt refuge strategy in cotton in China.

Our model of Bt cotton and its pests differs from prior models in several ways: it is a physiologically based; it has age (mass) structured distributed maturation times demographics; the same models for resource acquisition and allocation are used across species, be they plant or animal (Gutierrez, 1996); species-specific supply/demand ratios govern much of the temporal dynamics; pest dynamics modules are integrated in the system and may be implemented singly or in combination using Boolean variables; the biology of Bt cotton includes the decline in toxin levels with plant and subunit age; the lethal and sub-lethal effects of Bt toxin concentrations on pests and their vital rates are included; there is feed back between pest attack and plant compensation; the model includes pest time varying preferences for plant sub units; insecticides of varying toxicity may be included; observed weather is used to drive the dynamics of the system (see Appendix A).

1.1. Review of transgenic Bt cotton

B. thuringiensis (Bt) based insecticides are examples of low-impact pesticides that have been used since the 1950s without significant development of resistance in target pests (Federici, 1999). These microbial Bt preparations are highly sensitive to light and heat and decay rapidly after being applied in the field, while Bt protoxin in transgenic cotton is continuously produced and it is quite stable. Susceptible pests feeding on Bt cotton tissues activate the protoxin in their gut killing susceptible individuals (Ostlie et al., 1997). Constant presence of Bt protoxin (hereafter toxin) in transgenic plants and the planting of Bt crops on a broad scale is thought to make the development of resistance more likely (Gould, 1997, 1998; Mellon and Rissler,

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[1] The cotton bollweevil has historically been a primary pest of cotton in the southern United States (and elsewhere in the Americas), but it is currently controlled by pheromone-based technologies. It is not susceptible to the Bt toxin and hence was not included in the analysis. Whiteflies are also thought to be immune to the toxin and are not reviewed.