Optimal Control of Pest Resistance to Transgenic Crop Varieties

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Abstract

Transgenic corn varieties entered the market in 1996. These plant varieties carry a gene from the soil bacterium *Bacillus thuringiensis kurstaki*, Bt, that makes the plant produce a toxin deadly to the pest insect European Corn Borer (ECB) *Ostrinia nubilalis (Hübner)*. Since ECB may build up genetic resistance to this toxin, the growers of transgenic corn varieties are required to plant a portion of their field (refuge) with regular corn. This requirement is expected to prolong the efficiency of Bt corn in combating the ECB because some non-resistant pests can survive in the refuge, and thereby dilute the build-up of resistance in the overall pest population. A fixed refuge size of 20 percent is the currently recommended "rule-of-thumb" by the Environmental Protection Agency (EPA). Past work has searched for an economically-optimal refuge size utilizing discrete-time simulation approaches in which refuge size is treated as an exogenous parameter whose optimal value is found through numerical iteration. The objective of this work is to fine-tune parametric refuge specifications by formulating a bioeconomic model capable of endogenously determining the optimal trajectory of refuge sizes over time via an analytical optimal-control rule. The model will provide novel comparative statics/dynamics results demonstrating the sensitivity of the optimal trajectory to important economic and biological parameters.

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I. Statement of Problem

Crop varieties have been genetically altered to produce toxins that make them highly poisonous to herbivorous pest insects. One such toxin is the Bt[1] protein expressed in transgenic varieties of corn, potatoes, soybeans and cotton. Since their introduction in 1996, Bt crop varieties have been widely adopted. A major concern is that the targeted pest species (e.g., the European Corn Borer (ECB) *Ostrinia nubilalis*) will build up irreversible genetic resistance to the Bt toxin (EPA). Consequently, the effectiveness of Bt in combating pests is reduced over time (Purdue News).

To delay the build-up of resistance, farmers are required to grow regular (non-transgenic) crop varieties on a fixed percentage (refuge) of their fields along with their new transgenic varieties (Weiss). Currently, growers of Bt corn varieties are required to set aside 20 percent of their field[2] to refuge (Andersen). The biologic rationale is that the refuge allows for some susceptible insects to survive. This slows down the development of resistance in the overall pest population, thereby prolonging the efficacy of the Bt crop varieties. However, the refuge requirement imposes financial costs on growers of Bt corn, since the yield loss in the refuge is larger than on Bt corn. Moreover, allowing pest insects to survive in the refuge may lead to

[1] Bt is short for a gene found in the soil bacterium *Bacillus thuringiensis kurstaki*. Corn plants with the Bt gene will express so-called Cry-proteins, deadly to the larvae of the corn pest insect ECB (Hyde, Martin, Preckel, and Edwards).

[2] A refuge size of 50 percent is required in areas where Bt corn and Bt cotton are grown together (Andersen).

larger future pest populations, and hence more serious pest infestations. Economically optimal refuge sizes should strike an intertemporal balance between these costs and the benefits of extended pest susceptibility to Bt crops.

Pioneering work in formulating economically-optimal refuge sizes follows a discrete-time simulation approach to accommodate relatively complex assumptions regarding the population genetics of resistance build-up (Onstad and Guse; Hurley et al. 1997, 1999). Refuge size is treated as an exogenous parameter. The optimization procedure iterates over a range of refuge sizes to find the value optimizing the annualized value of crop production in the refuge and transgenic portions of the field.

II. Objectives

Our goal is to develop a theoretical model capable of providing an analytical understanding of the dynamics of the problem. We aim to fine-tune parametric refuge specifications by formulating a bioeconomic model capable of endogenously determining the optimal trajectory of refuge sizes over time via an analytical optimal-control rule. There are two significant payoffs to this approach. First, the model will be able to generate novel comparative static/dynamic results showing how optimal refuge sizes respond over time to changes in underlying bioeconomic parameters. This will significantly advance the bioeconomic theoretical underpinnings of the refuge size decision. Second, the model is capable of investigating a wider range of management possibilities. For example, instead of setting aside the same refuge size every year, farmers may find it optimal under various circumstances to initially establish large refuges followed by smaller sizes or vice-versa. The model sheds light on when such strategies can be expected to be optimal.

III. Methodology

We formulated a crop production model that links optimal annual refuge sizes to their long-run impacts on the build-up of pest resistance to a transgenic crop variety. The model is composed of two interrelated components and accounts for both the pest population numbers and genetic make-up. The "crop-production" component is a discrete optimal control specification of a representative producer's annual crop production problem, where the producer maximizes the Net-Present-Value (NPV) of production. The "population-genetics" component is a difference equation that measures the growth in the frequency of a resistant allele, and hence the growth in the frequency of pests genetically resistant to the plant toxin. The model is calibrated for a representative Bt corn producer using parameter values available from a number of past studies (Onstad, Onstad and Gould; Onstad and Guse; Hurley et al. 1997, 1999).

The crop-production and population-genetics components operate in tandem. The crop-production component generates a trajectory of optimal refuge sizes via an analytical optimal-control rule. This information is conveyed to the population-genetics component because the optimal refuge size enters the difference equation that measures the growth of the resistant allele frequency as a parameter. In the other direction, the frequency of the resistant allele in the pest population indirectly determines the optimal refuge size in the crop-production component. This is because the resistant allele frequency affects both the growth of the pest population and the amount of yield loss from the transgenic crop. The sequencing of the information exchange between the two components is complicated because each operates on a different time scale. The optimal refuge size is an annual planting decision, while the genetic composition of the pest population is a multi-annual process (Gould 1986, 1991). A fully-integrated analytical/numerical solution, compatible with both time frames, is possible with application of “slow-manifold” theory (Wasow).

We assume that the pest population genetics follow a single-locus, 2-allele, diploid[3] specification (Hurley et al. 1997, 1999; Onstad and Gould; Onstad and Guse). When the conditions for the Hardy-Weinberg Law hold, the gene frequencies of a population remain at steady-state levels through time. The Hardy-Weinberg Law requires that the population is large and randomly mating, that there is no mutation or migration, and that there is no selection (Falconer and Mackay). Except for the requirement of no selection, we will assume that all the other conditions for the Hardy Weinberg Law hold. In this way we can isolate the effect of selection. Similar to Hurley et al. (1997) we make the simplifying assumption that the pest population is uniformly spread out on the representative producer’s field. Finally, we assume in our model that the pest population exhibits logistic growth. According to Mason (pp.184), the logistic population model implies “that population growth always is limited in a finite environment.” By assuming logistic growth, the model pest population growth will not explode when the pest population is allowed to grow freely, for instance, when there are large refuge portions with no pesticide control. In some models, survival has been taken to be density independent in models if the ECB populations were assumed to remain small within the time horizon set for the model, due to, for instance, constantly large transgenic portions (Onstad and Guse; Onstad and Gould). However, in studies of natural, uncontrolled and agricultural Lepidoptorous pest populations, a logistic growth type model fit the population data well

[3]Diploid; For each locus on a chromosome, there are two genes that are identical in size, shape, and except for allelic differences, in genetic composition (Weaver and Hendrick, p. 478; Lincoln, Boxhall, and Clark, p 87)

(Mason; Chilcutt and Tabashnik; Fantanou et al.).

IV. Population-Genetics Component

Under the genetic assumptions made for this model, a pest can be either homozygous resistant, homozygous susceptible, or heterozygous. For a homozygous resistant pest, both alleles at the locus for resistance to the plant toxin are of the resistant type; for a pest that is homozygous susceptible to the plant toxin, the alleles at this locus are both of the susceptible type. A pest that is heterozygous at this locus has a combination of one resistant allele and one susceptible allele at this locus.

An individual's viability and fertility combine to form the absolute selective value. Building on Roughgarden, we set the absolute selective value of a pest equal to one plus (1 +) the pest's contribution to population growth. We then derived the absolute selective value specific to each of the genotypes in the pest population. The sum of the absolute selective values of the genotypes multiplied with their respective genotype frequencies (which are determined by the gene frequencies) gives the absolute mean viability of the population. The absolute mean viability and the increase in absolute mean viability for a marginal increase in the frequency of resistant alleles are needed to describe the growth of the resistant allele in terms of a difference equation (Roughgarden). This growth equation represents the population-genetics component of the model. Given the frequency of resistant alleles, the pest population numbers and the refuge size in season t, the population-genetics component can be used to compute the frequency of the resistant allele in season $t+1$. This gene frequency enters the crop-production component of the model.

V. Crop-Production Component

The crop-production component is the optimization problem of one representative producer of the transgenic crop. The optimization problem is set up as an optimal control problem in discrete time (Clark). The producer maximizes the net present value of annual profits from the transgenic crop and the refuge crop subject to the pest population dynamics. The difference equation describing the discrete pest population dynamics in our model is given by Roughgarden. This equation implies that the pest population in time period $t+1$ is a multiple of the pest population in time period t, where the multiplier is the absolute mean viability of the pest at time t.

In a time period, the grower's profit is the sum of the profit in the transgenic portion and in the refuge portion of the field. The existence of the pest in the field reduces the grower's profit by causing crop yield loss. Yield loss is assumed to be proportional to the number of pests per plant in the profit function (Hurley et al. 1997, 1999; Hyde et al.; Onstad and Gould; Onstad and Guse). In the refuge, the proportional yield loss is assumed to be the same for all pest genotypes. However, the proportional yield loss caused by pests on the transgenic crop is only caused by resistant and, to some extent, heterozygous pests. Therefore, for the yield loss in the transgenic portion, we derive a mean proportional yield loss that depends on the frequencies of the different genotypes. In summary, the crop-production component consists of the individual grower's profit function, the growth equation for the pest population, the initial conditions, and the constraints on the parameters.

The producer chooses the proportion of refuge crop to grow in order to maximize the net present value of annual profits subject to the pest population dynamics in every season t. In the crop-production component, the pest population is the state variable and the gene frequency of resistant alleles found from the population-genetics component is taken to be a parameter. The optimal refuge size found in the crop-production component enters the population-genetics component as a parameter. If a small refuge rather than a large refuge size is optimal, then the result is faster growth in resistant alleles in the pest population. Hence, the crop-production component and the population-genetics component are connected by the optimal refuge sizes and the frequencies of the resistant allele.

VI. Optimal Solution to the Model

The slow multi-annual dynamics of the population genetics component are coordinated with the fast annual dynamics of the crop-production component via Tihonov's theorem (Wasow). The two model components adjust toward their respective equilibrium value. These adjustments stop when each component reaches its equilibrium. Planting the transgenic crop puts selection pressure on the pest population and the frequency of resistant alleles will increase until its maximum value of one (1) is reached. For any one trajectory of the resistant alleles, we have corresponding trajectories of pest population sizes and refuge sizes. Using our model, we can derive comparative static and dynamic results that show how changes in biological and economical parameters affect the optimal trajectory of refuge sizes.

VII. Conclusion

Transgenic crop varieties have been genetically modified to be toxic to certain pest insects. When growing transgenic crops, these pest insects may build up genetic resistance that is irreversible. By setting aside a portion of the field to regular crops (refuge), the build up of resistance may be slowed down. We developed a bioeconomic model that can be solved endogenously for the optimal refuge sizes in the form of an optimal control rule. The model captures the economics, the population dynamics, and the genetic processes of the problem. We calibrated our model for Bt corn and the European Corn Borer and found the optimal trajectory of refuge sizes for the chosen set of parameter values. We also derived new comparative static/dynamic results.

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