Biotechnology and Pest Resistance: An Economic Assessment of Refuges

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Abstract

Biologists now engineer transgenic crop varieties that express proteins that are toxic to a variety of common agricultural pests. These transgenic crops offer farmers a new tool for effectively managing pests that reduce yields and increase production costs. However, the concern over pest resistance to these toxins has prompted the EPA to require resistance management plans. Seed companies have focused on a high-dose refuge plan where farmers are required to plant a constant proportion of cropland in refuge in order to maintain a susceptible pest population. Currently, entomologists recommend 20 to 40% refuge. This paper develops an economic model of pest management with pest resistance to estimate the constant proportion of refuge that maximizes farm income over a fixed planning horizon. Results indicate that there is a clear economic tradeoff between the pest control and population management benefits afforded by a transgenic variety and the resistance management benefits and savings in production costs afforded by refuge. Under certain circumstances a 20 to 40% refuge is economically sensible. However, the optimal proportion of refuge is sensitive to a number of uncertain biological factors: the initial frequency of resistant pests, and the survival rate of resistant and susceptible pests. Additionally, we find that when the pest population and resistance develop slowly, the economic losses of a suboptimal proportion of refuge are relatively small; however, the biological consequences in terms of pest susceptibility are very large.

I. Introduction

Biologists now engineer transgenic crop varieties that express proteins that are toxic to a variety of common agricultural pests. These transgenic crops offer farmers a new tool for effectively managing pests that reduce yields and increase production costs. Mason et. al. (1996) indicates that the cost to U.S. farmers of the European Corn borer alone is over one billion dollars annually. However, with all the excitement over the potential agricultural benefits of transgenics, there are also concerns. Both laboratory and field pests have exhibited an ability to develop a resistance to toxins produced by these varieties (Hama, et. al., 1992; Tabashnik, et. al., 1992; Martinez-Ramirez, et. al., 1995; and Tabashnik, et. al., 1995). Evidence suggests resistance is genetic which implies that the wide spread use of transgenics will result in increased selection pressure and the development of a resistant pest population. Once a largely resistant pest population emerges, transgenics will no longer effectively control the targeted pests, thus diminishing the value of the expressed toxins for future pest management.

The Environmental Protection Agency (EPA) has addressed concerns over pest resistance by conditionally approving transgenics with the proviso that seed companies develop effective resistance management plans. In response, seed companies have focused attention on a high-dose refuge management strategy. There are two important components to this plan. First, crops express high levels of toxins with the goal of killing all of the targeted pests. Second, farmers plant a portion of their cropland in refuge, areas where the expressed toxin is not used for pest control. These refuges allow pests susceptible to the toxin to thrive and mate with pests that are resistant. By establishing refuges for susceptible pests, selection pressure is reduced slowing the proliferation of resistant pests.

Pest resistance, or alternatively pest susceptibility, can be viewed as a traditional nonrenewable common property resource (Hueth and Regev, 1974; Regev, Gutierrez, and Feder, 1976; Regev, Shalit, and Gutierrez 1983). Susceptible pests are valuable because they can be controlled using a transgenic crop variety. However, exploiting this value reduces the proportion of susceptible pests in the population. Therefore, the use of a transgenic will eventually lead to a largely resistant pest population for which the transgenic has little value. If a single farmer has the exclusive rights to this resource, a socially optimal management strategy will result. Hotelling's rule implies that this optimal management strategy will result in the farmer extracting the value of susceptible pests at a rate equal to the interest rate. However, if multiple farmers compete for the use of this resource, then there are strategic incentives to exhaust pest susceptibility faster than is socially optimal. Therefore, the EPA's attempts to encourage resistance management can be justified to prevent too rapid a buildup of resistant pests.

Currently some entomologists recommend that farmers plant 20 to 40 percent of their cropland in refuge under a high-dose refuge management plan (Bessin, 1995; Hutchinson, 1996). The agreement between the EPA and Monsanto covering Monsanto's YieldGard® protein requires 5% refuge if farmers do not apply pesticides on refuge acreage to control corn borers and 20% if pesticides are applied. Clearly, there is disagreement about the optimal proportion of refuge.

Even if there were agreement about the recommended proportion of refuge, unless such a recommendation results in the value of pest susceptibility increasing at the rate of interest, it will not result in a first-best or optimal management strategy. However, choosing the size of refuge carefully can result in a second-best (and potentially more practical) policy. This paper determines the conditions under which continuously planting 20 to 40 percent refuge represents an optimal second-best policy for controlling Bt resistance in the European Corn Borer, a major agricultural pest in corn. We then determine what size of refuge maximizes the net present value of crop production over a fixed planning horizon, and estimate the value of the Bt technology under an optimal second-best resistance management policy.

Our results indicate that there is a clear economic tradeoff between the pest control and population management benefits of a transgenic variety, and the resistance management benefits afforded by refuge. Under certain circumstances a 20 to 40 percent refuge is economically sensible. However, the optimal proportion of refuge is sensitive to a number of uncertain biological factors: the initial frequency of resistant pests, and the survival rate of resistant and susceptible pests. Additionally, we find that when the pest population and resistance develops slowly, the economic losses of a suboptimal proportion of refuge are relatively small; however, the biological consequences in terms of pest susceptibility are very large.

II. The Model

The model we develop builds on Taylor and Headley (1975). Suppose there is a single pest afflicting an agricultural production region. Following Onstad and Gould (1997) and Roush and Osmond (1996), we assume the pest population is characterized by the Hardy-Weinberg principle where resistance is conferred by a single recessive allele that is not sex linked. The fundamental assumptions embodied in the Hardy-Weinberg principle include (i) the pest is a diploid, (ii) reproduction is sexual, (iii) pest generations do not overlap, (iv) mating is random, (v) the pest population is large, (vi) migration is negligible, (vii) mutation is negligible, and (viii) natural selection other than that resulting from the use of a transgenic does not effect the locus under consideration (Hartl, 1988). R denotes the resistance conferring allele, and S denotes all other possible alleles occurring at the resistance locus. Therefore, pests can be one of three possible genotypes: a resistant homozygote— possessing a pair of the resistant alleles, RR; a heterozygote— possessing a single resistant allele, RS or SR; or a susceptible homozygote— possessing no resistant alleles, SS. Define N_g as the total pest population in generation g measured as the number of pests per plant. Define R_g as the frequency of the R allele in generation g. The Hardy-Weinberg principle implies that there will be $R_g^2 N_g$ resistant homozygotes, $(1 - R_g)^2 N_g$ susceptible homozygotes, and $2R_g(1 - R_g)N_g$ heterozygotes in generation g.[1]

The agricultural production region is planted in a single annual crop but there are two possible crop varieties.[2] The first variety is a refuge crop where pest survival rates are normal. The second variety is a transgenic genetically engineered to be toxic to pests possessing at least a single S allele. The proportion of susceptible homozygotes that survive in the transgenic is ρ_{SS}, while the proportion of heterozygotes that survive is ρ_{RS} where ρ_{SS} and ρ_{RS} lie on the unit interval. If the high-dose strategy is completely effective, $\rho_{SS} = 0$ and $\rho_{RS} = 0$. Let ϕ be the proportion of acreage planted in refuge, while

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[1] Note that the Hardy-Weinberg principle gives the expected gene frequencies in equilibrium. For the purpose of the analysis presented here, we assume that pest population moves immediately to equilibrium such that the Hardy-Weinberg frequencies are always satisfied. An interesting question beyond the scope of this paper is the effect of the rate of transition to the Hardy-Weinberg frequencies.

[2] The model is easily generalized to include additional crops.

1 - ϕ is the proportion of transgenic. Therefore, we assume that a fixed proportion of refuge is planted in each time period. We also assume that the spatial arrangement of the refuge crop is selected optimally.[3]

Without pest pressure, the expected yield per acre for both crops is Y. However, actual yields are lower depending on the extent of pest pressure. The extent of pest pressure depends on the number of pests infecting each plant per year, the time at which the plant is infected, and a number of other environmental factors that may stress the plant during the growing season. Since many insect pests can produce multiple generations in a single cropping year, we define $D_i(N^i_t)$ as the proportion of yield loss for the ith crop where N^i_t is a measure of the number of pests per plant for each generation of pests in year t, $i = 0$ for refuge, and $i = 1$ for the transgenic. N^i_t is a vector of G pest populations where G is the number of generations of pests annually. $D_i(N^i_t)$ lies on the unit interval and is non-decreasing in each of the elements of N^i_t. Therefore, the average yield per acre at harvest for the ith variety in year t is $y^i_t = Y(1 - D_i(N^i_t))$. Our specification of pest damages implicitly assumes that pests distribute uniformly over the production region.[4]

The number of pests per plant in the ith crop in the $g + 1$ generation depends on the population of pests and the frequency of the resistant allele in generation g, and the fecundity of the pests and proportion of crop acreage planted in refuge. The proportion of pest that survive each generation is equal to the proportion of pests on refuge acreage plus the proportion of resistant homozygotes, heterozygotes, and susceptible homozygotes that survive on transgenic acreage:

$$z_{t+g} = \phi + (1-\phi)\left[R_{t+g}{}^2 + \rho_{SS}\left(1 - R_{t+g}\right)^2 + \rho_{RS}2R_{t+g}\left(1 - R_{t+g}\right)\right] \qquad (1)$$

where g now denotes the generation of pests with $g = 0$ at time t. The population of pests in generation $t + g + 1$ is

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[3] The optimal spatial arrangement of the refuge crop is an interesting question in itself, but it is also beyond the scope of our analysis. Onstad and Gould (1997) consider the optimal spatial arrangement of refuge and find that separate plots of refuge result in slower resistance development when compared to mixing refuge and non-refuge varieties on a single plot

[4] Many pests including the European corn borer exhibit clumping; but we abstract from this spatial variation in order to focus on the population genetics of Bt. resistance.

$$
\begin{aligned}
N_{t+g+1} &= N\left(z_{t+g} N_{t+g}\right) \\
&= N\left(\phi, N_{t+g}, R_{t+g}\right)
\end{aligned} \tag{2}
$$

Equation (2) states that next generation's pest population depends on the number of pests that survive this generation and implicitly assumes that reproductive rates are not affected by the composition of the pest population between resistant and susceptible pests. The next generation of pests may be increasing or decreasing in the surviving pest population depending on the amount of intraspecific competition.

The change in the frequency of resistant alleles from $t + g$ to $t + g + 1$ given ϕ is

$$
\begin{aligned}
R_{t+g+1} &= \frac{2R_{t+g}^{2} + \phi 2R_{t+g}\left(1 - R_{t+g}\right) + (1-\phi)\rho_{RS} 2R_{t+g}\left(1 - R_{t+g}\right)}{2z_{t+g}} \\
&= R\left(\phi, R_{t+g}\right)
\end{aligned} \tag{3}
$$

The numerator of equation (3) measures the number of R alleles contributed to the next generation of pests by surviving resistant homozygotes and heterozygotes. The denominator measures the total number of alleles contributed to the next generation from all surviving pests. Therefore, $N^0_t = [N_t, \ldots, N_{t+G}]$ and $N^1_t = [(R_t^2 + \rho_{SS}(1 - R_t)^2 + \rho_{RS} 2R_t(1 - R_t))N_t, \ldots, (R_{t+G-1}^2 + \rho_{SS}(1 - R_{t+G-1})^2 + \rho_{RS} 2R_{t+G-1}(1 - R_{t+G-1}))N_{t+G-1}]$ since all pest survive in refuge fields while only a proportion of susceptible homozygotes and heterozygotes survive in transgenic fields.

Given the average price per yield, P, and the production costs per acre for the ith crop, C^i, the expected profit per acre at time t is

$$
\pi_t(\phi) = \phi\left[PY\left(1 - D_0\left(N_t^0\right)\right) - C^0\right] + (1-\phi)\left[PY\left(1 - D_1\left(N_t^1\right)\right) - C^1\right], \tag{4}
$$

where the damage functions translate pest numbers at different times of the growing season into an end-of-season damage level.

The first term in equation (4) is the profit per acre of refuge multiplied by the proportion of refuge planted. The second term is the profit per acre of transgenic multiplied by the proportion on transgenic planted. Therefore, the objective is

$$
\underset{\phi}{Max} \sum_{t=0}^{T-1} \delta^t \pi_t(\phi) \tag{5}
$$

subject to equations (2), and (3) for $t = \{1,\ldots,T-1\}$, $g = \{1,\ldots,G\}$, $0 \leq \phi \leq 1$, the initial pest population, N_0, and proportion of resistant alleles, R_0, where T is the length of the planning horizon and δ is the discount rate. To focus on pest control and population and resistance management within the planning horizon, we assume that the discounted salvage value of cropland beyond the planning horizon is negligible.

A better understanding of the factors determining the optimal size of refuge can be obtained by assuming a single generation of pests. Differentiating equation (5) with respect to ϕ yields the first-order condition

$$\begin{aligned}
&\sum_{t=0}^{T-1} \delta^t PY\left[D_0(N_t^0) - D_1(N_t^1)\right] + \\
&\sum_{t=0}^{T-2} \delta^t PY\left[(1-\phi)\frac{\partial D_1}{\partial N_{t+1}^1}\frac{\partial N_{t+1}^1}{\partial N_t}\frac{\partial N_t}{\partial \phi} + \phi\frac{\partial D_0}{\partial N_{t+1}^0}\frac{\partial N_{t+1}^0}{\partial N_t}\frac{\partial N_t}{\partial \phi}\right] = \\
&\sum_{t=0}^{T-1} \delta^t (C^1 - C^0) + \sum_{t=0}^{T-2} \delta^t PY(1-\phi)\frac{\partial D_1}{\partial N_{t+1}^1}\frac{\partial N_{t+1}^1}{\partial R_t}\frac{\partial R_t}{\partial \phi}.
\end{aligned} \tag{6}$$

Equation (6) says to plant refuge until the marginal cost of another acre of refuge equals the marginal benefit from that last acre. There are two components of marginal cost from planting more refuge and less transgenic. The first component is the increased damage from corn borers in a given year, holding the corn borer population constant. The first term on the left-hand side of equation (6) is the discounted sum of the increased damage over the planning horizon. The increased damage is always greater than zero as long as there are susceptible corn borers in the population.

The second component of the marginal cost of another acre of refuge arises from the increased damage in future years due to increased future corn borers populations. More refuge today means greater corn borer pressure in the future. A higher population increases damage on both refuge and the transgenic crop as shown by the second term on the left-hand side of equation (6). The increased damage in future years is discounted and summed over the entire planning horizon.

The right-hand side of equation (6) measures the marginal benefits of an additional acre of refuge. There are two components of marginal benefit as well. The first is the direct benefit of not having to pay the premium charged for the transgenic crop. This saving, $C^1 - C^0$, is discounted and summed over the entire planning horizon.

The second component of the marginal benefit arises from the slowdown in the rate that corn borer resistance builds up. More refuge means a decrease in the proportion of future corn borers that are resistant to the transgenic crop. Fewer resistant corn borers translates into decreased corn borer damage. The benefits from resistance management accrue in this model only to the acreage on which the transgenic crop is grown. These benefits are also discounted and summed over the planning horizon.

In summary, the optimal (constant) proportion of refuge is where the discounted stream of benefits from another acre of refuge in terms of cost savings and better resistance management, equal the discounted stream of costs from that additional acre from increased pest damage and higher future pest populations. The next two sections present estimates of the optimal proportion of refuge using Bt corn for control of European corn borer for a base case scenario (Section III) and for alternative assumptions about key biological and economic parameters that affect the optimal refuge (Section IV).

III. The Optimal Proportion of Refuge for Bt Corn

Bt corn expresses one of several forms of a protein found in the soil bacterium *Bacillus thuringiensis*. This protein is toxic to the European corn borer (ECB), a significant corn pest. Depending on the premium charged for Bt seed corn, substitution of Bt corn for other pesticides results in little increase in production costs, and in some instances may even reduce production costs. However, relatively few farmers currently use pesticides for controlling the ECB because of high scouting and application costs and low pesticide efficacies. The high efficacy of Bt corn presents an opportunity for farmers to effectively control the ECB increasing yields with a marginal increase in production costs. However, resistance threatens to diminish the value of Bt corn to farmers. In compliance with the EPA's provisions for resistance management, seed companies offer Bt corn under the condition that farmers plant a portion of acreage in refuge. If no ECB pesticides are applied to the refuge, then 5% is deemed sufficient. If pesticides other than Bt are applied, then 20% refuge is required.

We determine numerically the optimal proportion of refuge for a high-dose refuge management plan assuming no pesticides are applied to the refuge. To implement our model, we need information on corn borer damage, corn borer population dynamics, price, production costs, yields, the planning horizon, and the discount rate. Since much of the information needed to determine the optimal size refuge is uncertain, we conduct a sensitivity analysis to understand which biological and economic parameters have the greatest impact on the optimal proportion of refuge.

The ECB can produce as many as four, and as few as one generation annually. Southern, warmer climates tend to experience three or four generations, while more temperate northern climates generally face one or two generations. However, throughout most of the Corn Belt, two generations is normal (Mason et. al., 1996).[5]

Damage estimates for the ECB vary depending on a variety of environmental and management factors. For instance, damages will be higher when corn is stressed by drought and in early or late-planted corn. Depending on a plant's stage of development, estimates indicate that the marginal yield loss per pest per plant ranges from 2 to 6% on average (Mason et. al., 1996). Since our interest is in evaluating the seasonal damage of the ECB over a broad production region, we assume

$$D_t\left(N_t^{\prime}\right)=\sum_{g=0}^{G-1} d_g N_{t+g} \tag{7}$$

where d_g is the constant marginal proportion of yield loss per pest. Based on Mason et. al. (1996) we set $d_g = 0.04$, as a rough estimate of the average marginal yield loss per pest.

We adopt the population model developed by Onstad (1988) following Onstad and Gould's (1997a,b) studies of Bt resistance in the ECB. Onstad's population model is designed to predict the temporal and spatial dynamics for two generations of ECB in single-season field level studies or multiple season regional analysis. Because entomologists generally report season average yield losses per pest per plant and we assume that pests are uniformly distributed, we simplify Onstad's population model to focus on the average number of surviving fifth instar larvae from one generation to the next.[6] We then use the number of surviving fifth instars to predict the average marginal yield loss per plant. Specifically, we assume that 89% of surviving fifth instars enter and

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[5] In some areas, farmers can face two different strains of European corn borer. For instance, a farmer may face both a single generation population and a two generation population. While we will not consider these areas, our model can be extended to incorporate multiple populations with different generational attributes.

[6] We simplify Onstad's model in the sense that we do not consider the temporal or spatial variation in the pest population.

survive pupation; 8.1% of over-wintering pupae survive; the population contains an equal number of males and females; fertility is 95%; 95% of eggs hatch and survive to become first instars; 35% of first instars survive; 61% of second instars survive; third instar survival is density dependent such that

$$I_{4th} = \begin{cases} 0.48, & for\ I_{3rd} \leq 10.1 \\ 0.48 \cdot \dfrac{3.96 \cdot I_{3rd} - 3.96 \cdot 10.1 + 200}{21.0 \cdot I_{3rd} - 21.0 \cdot 10.1 + 200}, & for\ I_{3rd} > 10.1 \end{cases} \tag{8}$$

where I_{3rd} and I_{4th} are the number of third and forth instars; 44% of the forth instars survive; and 81% of fifth instars survive. To complete our population dynamics, we assume that female moths lay an average of 2 egg masses a night for 10 nights, and that the average number of eggs per mass is 15 for first generation moths and 30 for the second generation (Mason et. al., 1996). These assumptions result in two distinct inverted V growth functions, one for each generation. The implied carrying capacity for the first generation is 1.77, while that for the second is 2.81. We also assume that the pest population starts in equilibrium at the carrying capacity.

Gould et. al. (1995) found the frequencies of resistant alleles to Bt toxins in the tabacco budworm to be of the order of magnitude of one in a thousand. Subsequently, Onstad and Gould (1997) use this value in their studies of Bt resistance in the ECB. We also adopt an initial frequency of resistance alleles of one in a thousand.

The survival rates of susceptible homozygotes and heterozygotes is very uncertain since Bt varieties are new and until recently, have not been available for widespread production. Roush and Osmond (1996) considers heterozygote survival rates ranging from 0.50 to 0.005 assuming that all susceptible homozygotes are destroyed. However, the authors offer their skepticism for heterozygote survival rates close to 0.0. Onstad and Gould (1997b) start with a completely effective high-dose strategy, a survival rate of 0.0 for both susceptible homozygotes and heterozygotes, and then allow the heterozygote survival rate to increase to 0.001 and 0.01. Sharing Roush and Osmond's skepticism, we initially assume a homozygote survival rate is 0.0, and a heterozygote survival rate of 0.05. Later we consider the sensitivity of our results as the heterozygote survival rate varies between 0.0 and 1.0.

We use National Agricultural Statistical Service (NASS) and Economic Research Service (ERS) data to calculate reasonable economic parameter values for the real price of corn, the pest free yield, and production costs. The real price of corn, \$2.35, was calculated using NASS monthly average corn prices in the U.S. from 1991 to 1996 deflated to 1992 price levels. The average U.S. yield reported by NASS from 1991 to 1996 was 120 bushels per acre. Assuming an average annual ECB yield loss of 6.4% (Calvin, 1996) implies an average annual ECB pest free yield of about 128 bushels per acre. Excluding returns to management, the average production costs for refuge corn, \$185, was calculated using 1995 ERS corn budgets deflated to 1992 dollars using NASS price indices. Transgenic production costs are assumed to be \$5.00 higher since Bt seed corn is expected to sell for a \$3.00 to \$10.00 dollar per acre premium.[7] We assume a real discount rate of 4%. Finally, we choose a planning horizon of 25 years. The values for our initial parameters are summarized in Table 1.

The optimal proportion of refuge given our initial parameters is 0.26 resulting in an annualized net income of \$111 per acre (Table 2). If only refuge is planted the annualized income per acre is \$61 implying that the value of the Bt technology under an optimal high-dose refuge management plan is an annualized \$50 an acre, or a discounted present value of \$820 an acre over the 25 year planning horizon. Planting Bt corn exclusively yields an annualized income of \$81 an acre such that the value of an optimal resistance management plan is an annualized \$30 an acre, or a discounted \$496 over the 25 year planning horizon. Therefore, planting Bt corn exclusively reduces the value of the technology by 60 percent.

Figures 1 illustrates how the proportion of refuge affects the annual average pest population over the 25 year planning horizon. Planting too little refuge results in excellent ECB control early in the planning horizon. However, resistance builds rapidly and the pest population recovers to its initial level faster. For example, with no refuge, resistance builds up within 2 years and the population recovers within 15 (Table 2). For

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[7] If Bt corn is substituted for chemical control cost, then it is possible that a farmer could see no change or even a small decrease in production costs. However, Calvin (1996) and others indicate that only a small percentage of corn is actually chemically treated for the European Corn borer due to high costs, and relatively poor efficacy.

the optimal proportion of refuge, resistance is delayed for 21 years and the population does not recover during the planning horizon. Therefore, planting no refuge results in a higher average ECB population and a lower annualized income. Planting too much refuge provides excellent ECB control throughout the planning horizon, but this high level of control is experienced primarily on Bt fields. Refuge fields experience higher ECB pressure resulting in a higher average population. At the extreme, when only refuge is planted resistance never develops, but the population remains at its initial level.

The results in Table 2 and Figure 1 illustrate the tradeoff between early population management and late population management obtained through resistance management. By planting less refuge, better population control is obtained in earlier years, less in later years. More refuge reduces population control in earlier years, but improves the future control of pests by controlling resistance. Equation (6) indicates that the optimal size refuge equates the marginal cost from diminshed pest control with the marginal benefit of cost savings and better resistance management.

IV. Sensitivity Analysis

Our base case presents strong economic support for the use of refuges and suggests that a 20 to 40% refuge is not unreasonable. However, our results are specific to our initial parameters. To obtain a better understanding of the factors influencing the optimal size of refuge, we now consider the sensitivity of our results to alternative biological and economic factors.

Sensitivity to Biological Factors

Figure 2 shows the optimal proportion of refuge for one to four generations of ECB as the survival rate of heterozygotes increases from 0.0 to 1.0 holding all other parameters constant. For the third and forth generations of ECBs, we assume the same population dynamics as those used for the second generation of pests. For a single generation of ECBs, we assume the same population dynamics as those used for first generation of ECBs. The optimal proportion of refuge is invariant at 1.0 for a single generation of ECB due to the high overwintering mortality and the premium charged for Bt corn. The high overwintering mortality naturally diminishes the population over time so the additional control afforded by Bt corn is not worth the annual $5 per acre premium over a 25 year planning horizon. For two generations, the optimal proportion of refuge increases in steps, while for three and four generations, it increases rapidly and reaches a plateau. For all generations a low heterozygote survival rate results in readily controlled pest populations and a lack of resistance buildup. However, as the heterozygote survival rate increases, resistance and population growth quickly become a problem. For high heterozygote survival rates, the plateaus are due to a rapid population recovery that diminishes the value of additional resistance management obtained through increasing the proportion of refuge.

Two additional results from Figure 2 require further explanation. First, the optimal proportion of refuge may be higher or lower for more generations annually. This result is attributable to the tradeoff between population and resistance management. As the heterozygote survival rate increases, resistance develops faster when there are more generations annually; however, the population also recovers faster. Therefore, whether the optimal refuge is higher or lower as the number of generations increase depends on whether the development of resistance is relatively faster or slower than the recovery of the ECB population.

Second, while the optimal size of refuge is generally increasing for two to four generations, the increase is not continuous and smooth. Most notably for two generations and a heterozygote survival rate between 0.16 and 0.54, the optimal proportion of refuge bounces up and down. Further investigation reveals that this result is attributable to an objective function that is scalloped due to the piecewise linear nature of the growth function adopted from Onstad (1988). These scallops result in discontinuous jumps in the optimal proportion of refuge as a particular parameter increases or decreases.

Figure 3 shows the optimal proportion of refuge for one to four generations of ECB as the initial frequency of the resistant allele increases from 0.0001 to 0.01. As before, the optimal size of refuge is invariant at 1.0 for a single generation. For two to four generations, the optimal refuge tends to increase because resistance develops faster making resistance management more important. The increase is less pronounced for two generations due to the overwintering of second generation pupae, and the low fecundity of first generation moths.

The optimal proportion of refuge is generally decreasing in the initial pest population for two generations of ECB in order to reduce early yield losses (Figure 4). For three and four generations, the optimal proportion of refuge is insensitive to the initial population because of the growth rate and carrying capacity of the population tend to be more important determinants of pest pressure. When there is a single generation of ECB, the optimal size refuge is frozen at 1.0 until the initial pest population becomes large enough to recover the Bt seed corn premium. Therefore, even with a high overwintering mortality, if there is a high initial ECB population, it is optimal to invest in Bt corn to more rapidly reduce the naturally declining ECB population.

Sensitivity to Economic Factors

The optimal proportion of refuge generally increases with the length of the planning horizon (Figure 5). The reason for the increase is that a longer planning horizon puts more weight on the ability to control ECB in future periods. Thus the benefits of resistance management are given greater value. For a single generation, the pest control benefits of increased yields outweigh the additional cost of Bt corn when the planning horizon is short. For a longer planning horizon, the additional pest control benefits are reduced by a high overwintering mortality, which reduces the value of Bt corn and makes planting only refuge optimal. For three and four generations, the optimal proportion of refuge increases at a diminishing rate due to a quick recovery of the ECB population that reduces the value of Bt for resistance management. For two generations, a slower recovery of the ECB population makes Bt corn more valuable resulting in a slower increase in the proportion of refuge.

Increasing Bt production costs increases or has little or no effect on the optimal proportion of refuge (Figure 6). For a single generation, very low production costs are required to justify the additional expense. The optimal proportion of refuge increases with two generations as higher production costs diminish the value of Bt corn. For three and four generations, the quick recovery of the ECB population and high control benefits of Bt corn result in almost no change in the optimal proportion of refuge.

Increasing the marginal yield loss per pest per plant increases the value of pest control (Figure 7). The optimal proportion of refuge exhibits large decreases for a single generation once the additional damages are sufficient to recover the Bt premium and for two generations in general since the ECB population and resistance are slow to develop. For the more rapid population recovery and development of resistance that occurs with three and four generations, the optimal proportion of refuge declines slowly once damage is appreciably greater than zero.

Finally, the optimal proportion of refuge is relatively insensitive to the price of corn and decreasing in the discount rate. Increasing the price of corn increases the value of higher Bt corn yields and population and resistance management but has no effect on the added production costs of Bt corn. This results in no change or a small decrease in the optimal proportion of refuge as the relative value of ECB control increases. Increasing the discount rate increase the value of current production while decreasing the value of future production. The optimal size refuge decreases in order to capture more pest control benefits earlier in the planning horizon.

The optimal size of refuge balances the marginal cost of pest damage against the marginal benefits of lower seed costs and improved resistance management. The greater the proportion of refuge, the larger the pest population and the lower annual income in earlier years. However, more refuge slows the development of resistance and the recovery rate of the pest population, which leads to higher annual income in the future. The pest population tends to recover more rapidly when there are more generations of pest per year, when the initial frequency of resistant alleles is higher, and heterozygote survival rate is higher. The faster the ECB population recovers, the lower the benefits of resistance management and the higher the benefits of pest control and population management.

V. Policy Implications

Entomologists and other scientists argue that 20 to 40% refuge is necessary to control resistance. Currently, seed companies are requiring 5 to 20% refuge depending on whether or not ECB pesticides other than Bt are applied to the refuge. Under our initial assumptions, 26% refuge is optimal, but our results are sensitive to a number of important biological factors for which there is currently little information available to guide policy. We now explore the economic and biological consequences of a policy that requires too little or too much refuge.

Figure 8 presents annualized farm income and Figure 9 presents the final proportion of resistant alleles as the proportion of refuge increases from 0.0 to 1.0 for one to four generations of ECB and our initial parameters. For a single generation, annualized income is insensitive to the proportion of refuge since the pest population is naturally decreasing and Bt corn only serves to speed this decrease. Therefore, too little or too much refuge will have little economic impact. However, the final proportion of resistant pests is very sensitive to the proportion of refuge. Below 18% refuge, a wholly resistant pest population develops by the end of the planning horizon. Above 30% refuge results in little increase in the proportion of resistant pests.

High overwintering mortality and low fecundity of second-generation moths results in an ECB population that is increasing but readily controlled with Bt corn when there are two generations annually. The objective function is particularly flat when the proportion of refuge falls between about 0.1 and 0.4, but noticeably decreases below 0.1 and above 0.4. Therefore, the economic consequences of planting too little or too much refuge are negligible between about 10 to 40% refuge. However, below 35% refuge, a wholly resistant ECB population develops within the planning horizon, while above 50% refuge, there is little increase in the resistant ECB population.

The more rapid development of resistance and the faster recovery of the ECB population result in more noticeable economic losses from a suboptimal proportion of refuge when there are three or four generations of ECB. Additionally, a wholly resistant ECB population develops within the planning horizon with less than 45% refuge for three generations and less than 50% refuge with four generations. Maintaining a high level of susceptibility requires nearly 60% refuge for three generations and 70% for four generations.

Comparing annualized income and the final proportion of resistance for one to four generations of ECB highlights two important results with significant policy implications. First, when the pest population grows more rapidly and resistance develops faster, the economic losses of a suboptimal proportion of refuge are more pronounced. Second, even when the economic losses of a suboptimal proportion of refuge are small, the biological consequences of a resistant pest population are large.

We have purposefully focused on the value of pest susceptibility for agricultural production, and ignored any other economic value of maintaining susceptibility to Bt in the ECB gene pool because of our inability to quantify such benefits. However, our results indicate that maintaining a susceptible pest population has a greater negative impact on farm income when the growth of the pest population and the development of resistance are faster. Therefore, when the heterozygote survival rate, and the initial frequency of resistant alleles is higher, when there are more generations of pests annually, and when the planning horizon is longer, resistance management plans that aim to maintain pest susceptibility will result in a more significant loss of farm income.

VI. Conclusions

Genetically engineered crops add a new weapon to a farmer's pest control arsenal. However, the potential for pest resistance and the common property nature of pest management threaten to diminish the value of this new weapon. Thus, resistance management plans can potentially improve the economic returns to genetically engineered crops. One resistance management plan currently receiving attention is based on a high-dose refuge strategy where crops are genetically engineered to express high levels of toxins and farmers are expected to plant a portion of their crop acreage in refuge. Entomologists and other scientists recommend that 20 to 40% of crop acreage be planted in refuge.

The purpose of this paper was to develop a model to evaluate the optimal size of refuge when Bt corn is planted to control the European corn borer and to evaluate the value of Bt corn under a high-dose refuge management plan. While the optimal size of refuge is sensitive to a host of important biological and economic factors, under certain circumstances the current recommendations can be justified. We also find that the economic losses of a suboptimal refuge are more pronounced when the pest population recovers rapidly and resistance develops faster. While the economic consequences of a subopitmal refuge may be small for slow population growth and resistance development, the biological consequences in terms of lost pest susceptibility can still be large.

The number of genetically engineered crops available for production will almost certainly increase in the foreseeable future and pest resistance will likely pose a substantial obstacle to deriving the full economic benefit from these new crops.

Therefore, pest resistance management will become increasingly important. A high-dose refuge management plan has the potential to improve the economic returns to genetically engineered crops. However, the success of this type of plan depends on cooperation between the EPA, seed companies, and farmers. Future research needs to evaluate the potential benefits of a high-dose refuge management plan as compared to other potential resistance management plans, and needs to determine what incentives are necessary to facilitate these plans. Additionally, economists must work with entomologists and other scientists to improve models of resistance management and to obtain the biological information necessary to implement these models.

Table 1: Initial parameters.

Parameter Name	Symbol	Initial Value	Range for Sensitivity Analysis
Biological Parameters			
Generations of Pests Per Cropping Season	G	2	1-4
Survival Rate of Susceptible Homozygotes	ρ_{SS}	0.00	
Survival Rate of Heterozygotes	ρ_{RS}	0.05	0.0-1.0
Initial Pest Population (Pests Per Plant)	N_0	1.77	0.1-5.0
Initial Frequency of Resistant Alleles	R_0	0.001	0.00001-0.01
Economic Parameters			
Planning Horizon (Years)	T	25	1-50
Interest Rate	$(1 + \delta) / \delta$	0.04	0.0-0.2
Price of Corn Per Bushel	P	\$2.35	\$1.75-\$3.50
Pest Free Yield (Bushels Per Acre)	Y	128	
Production Cost for Refuge Crop (Per Acre)	C^0	\$185	
Production Cost for Bt Crop (Per Acre)	C^1	\$190	\$185-\$277.50
Constant Marginal Yield Loss (Pests Per Plant)	d_g	0.04	0.002-0.10

Table 2: Comparison of alternative pest control strategies using Bt. corn and refuges for the initial parameters.

	Pest Control Strategy		
	Optimal Refuge ($\phi = 0.2648$)	No Refuge ($\phi = 0.0$)	Only Refuge ($\phi = 1.0$)
Annualized Farm Income (Per Acre)	\$111	\$81	\$61
Average Annual Frequency of Resistant Pests (Pest Per Plant)	0.33	0.97	0.001
Final Frequency of Resistant Alleles (Pest Per Plant)	1.0	1.0	0.001
Average Annual Pest Population (Pest Per Plant)	0.047	3.01	4.57
Final Pest Population (Pest Per Plant)	+0.0[a]	1.77	1.77
Year Frequency of Resistant Alleles Exceeds 0.001	21	2	
Year Pest Population Recovers to Original Size		15	0

[a] The final pest population per plant is very small, but positive.

Figure 1. The effect of the proportion of refuge on the average annual pest population.

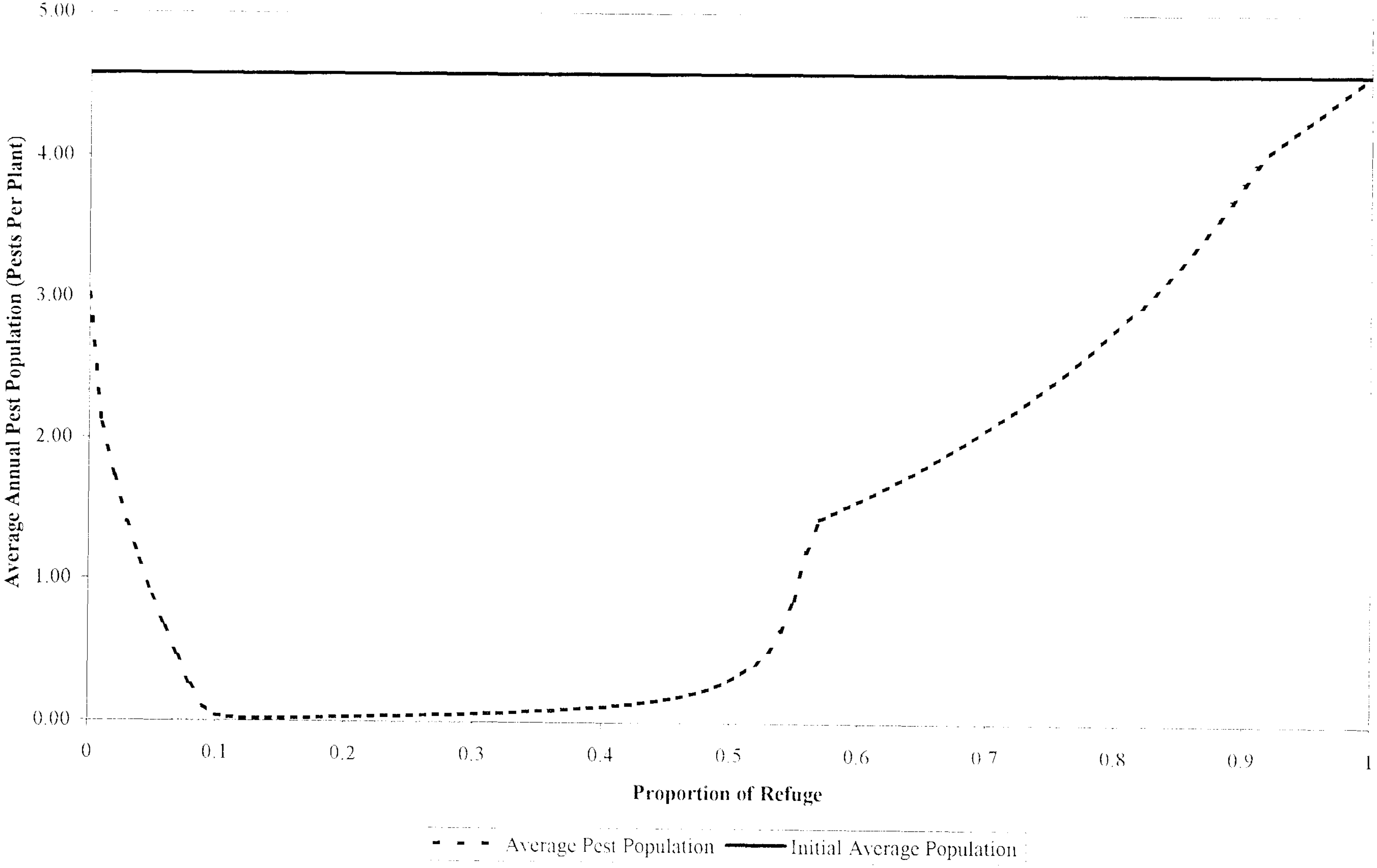


Figure 2. The effect of the heterozygote survival rate on the optimal proportion of refuge.

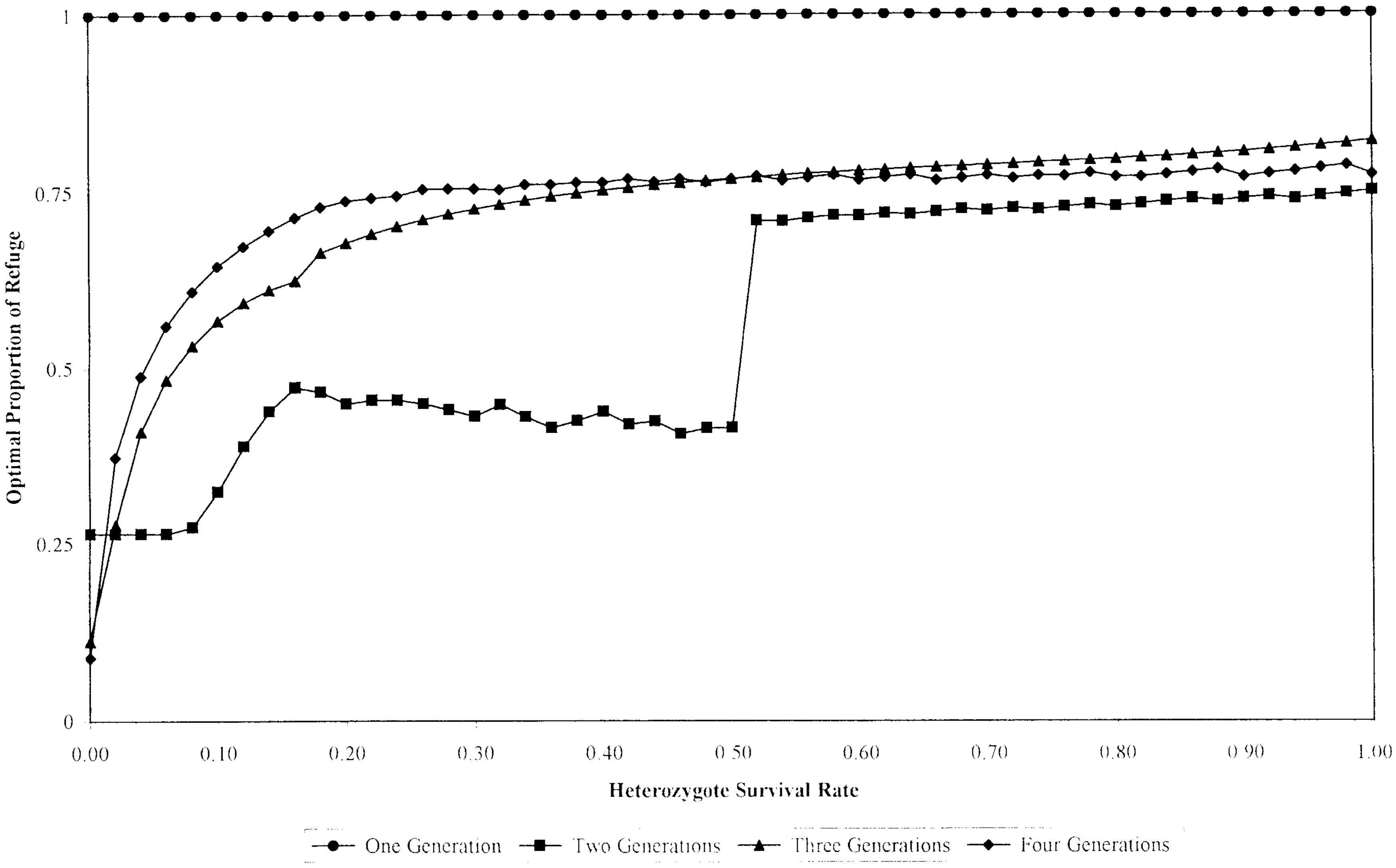


Figure 3. The effect of the initial frequency of resistant alleles on the optimal proportion of refuge.

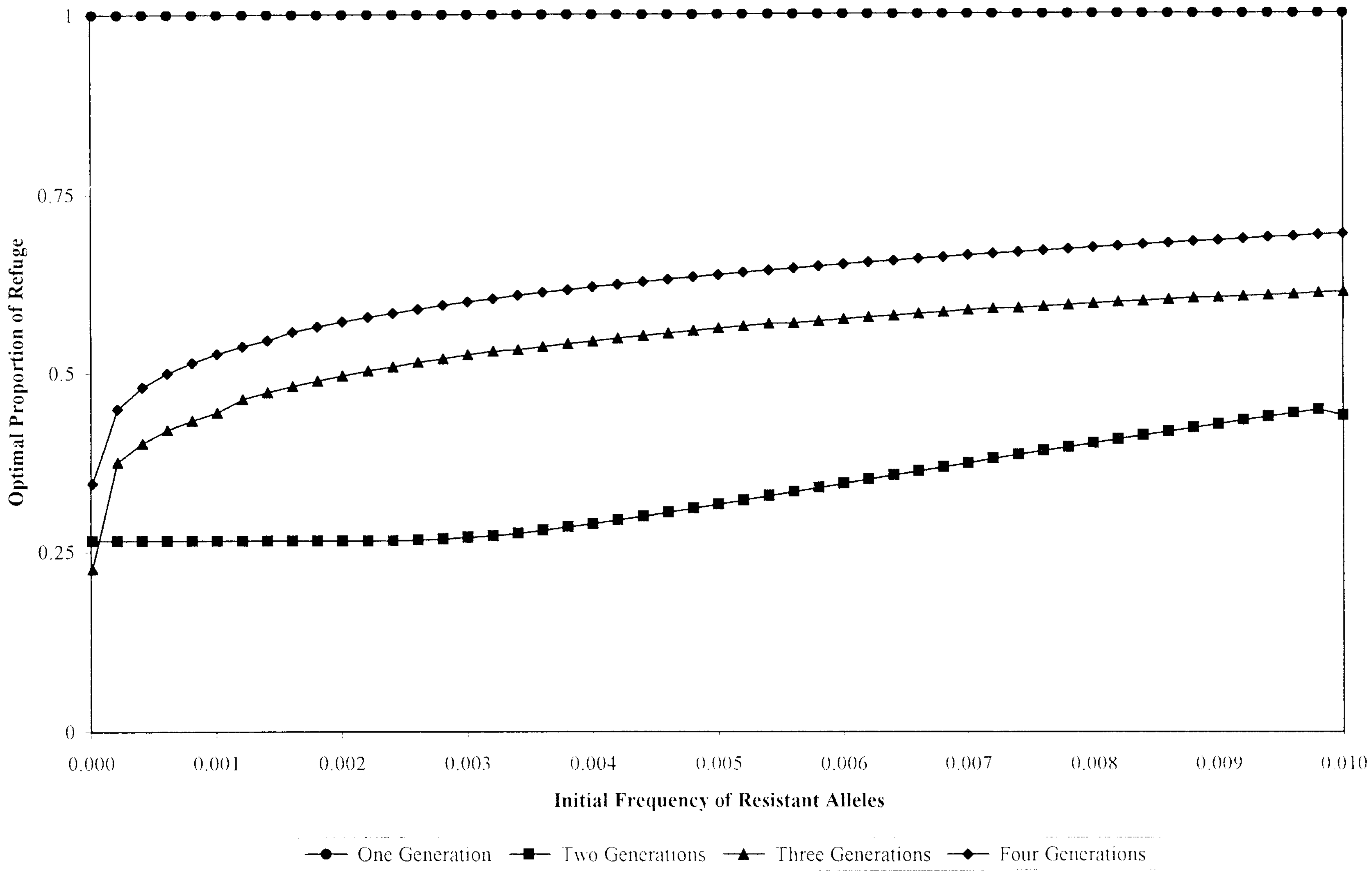


Figure 4. The effect of the initial pest population on the optimal proportion of refuge.

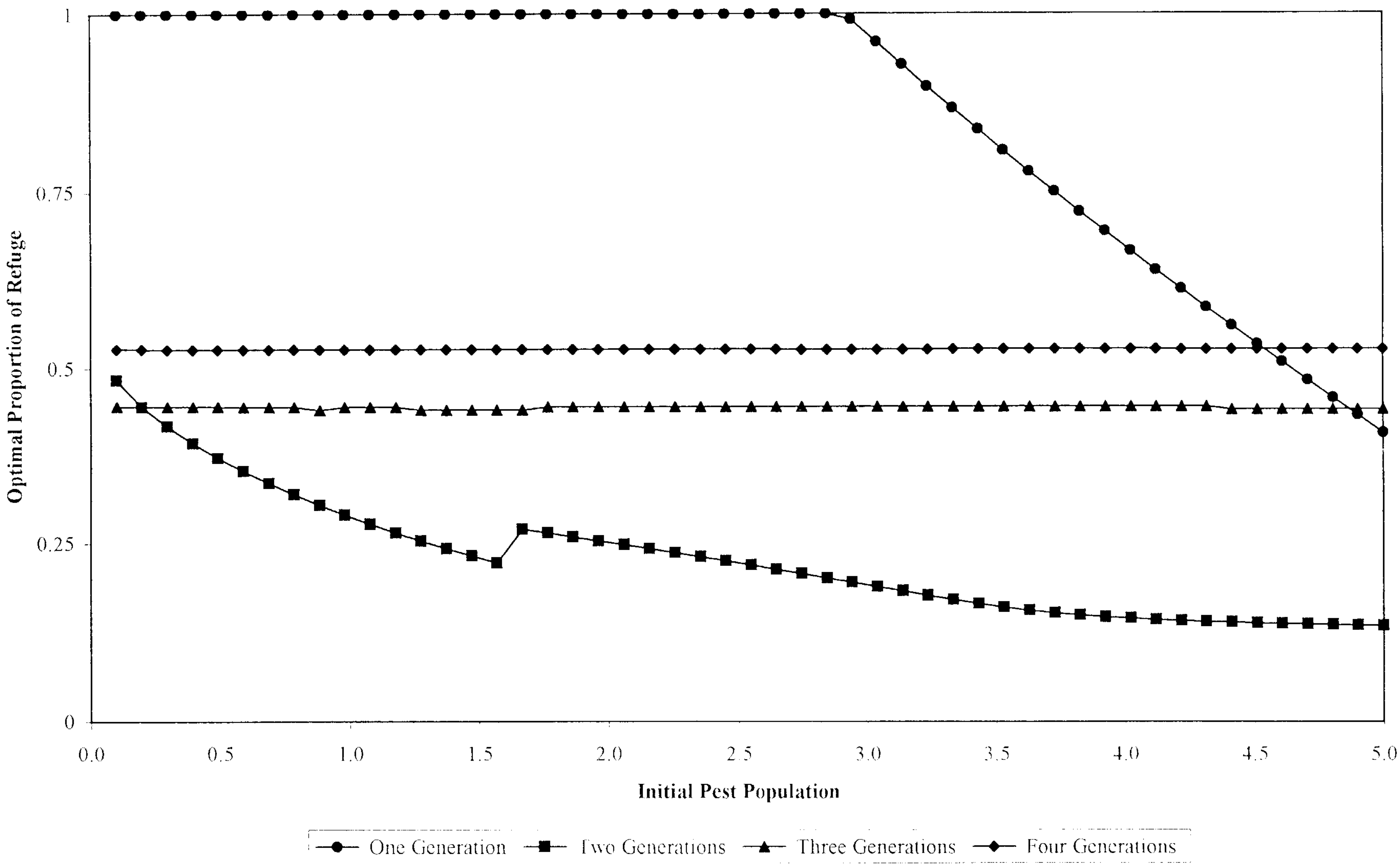


Figure 5. The effect of the length of the planning horizon on the optimal proportion of refuge.

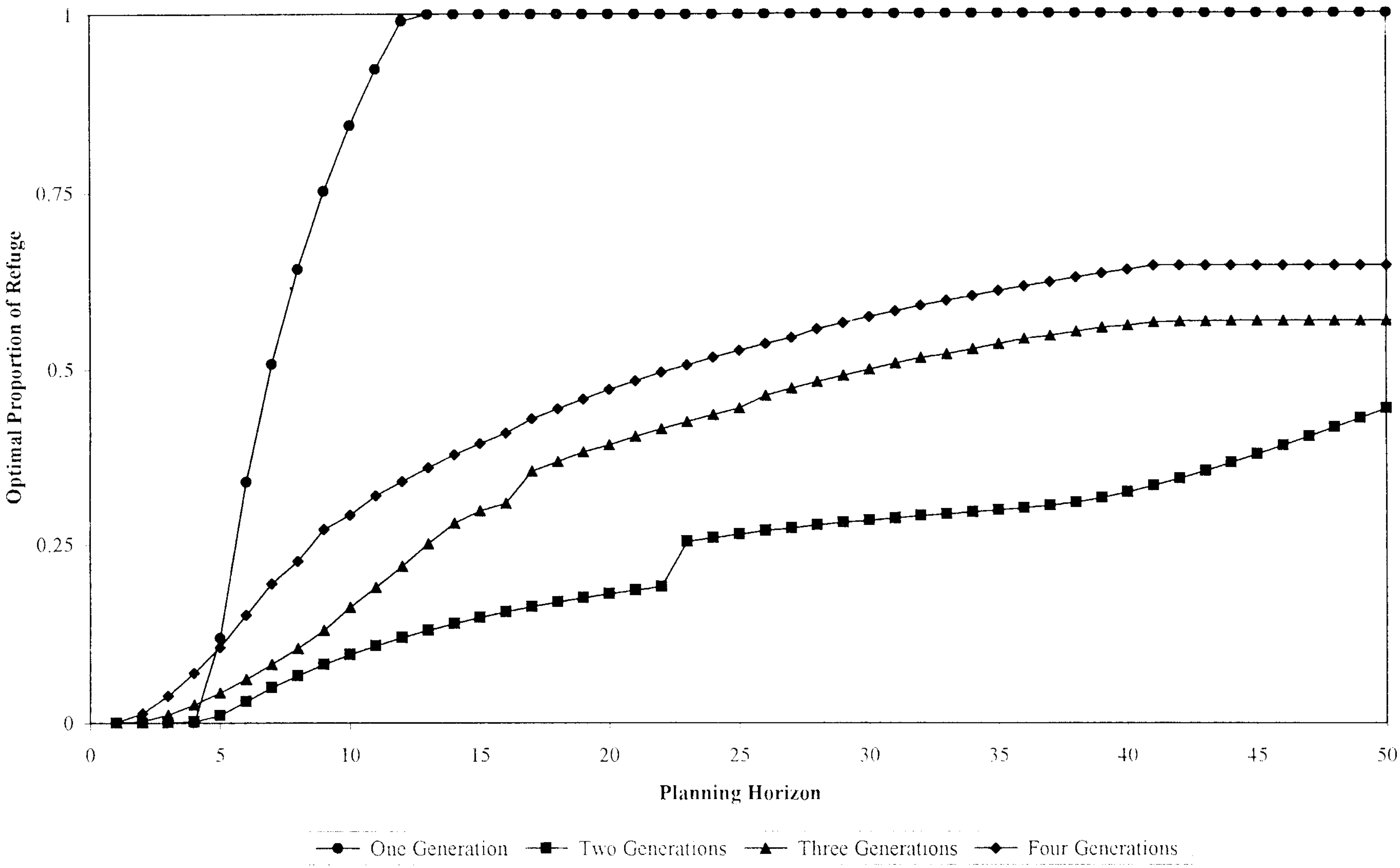


Figure 6. The effect of higher transgenic production costs on the optimal proportion of refuge.

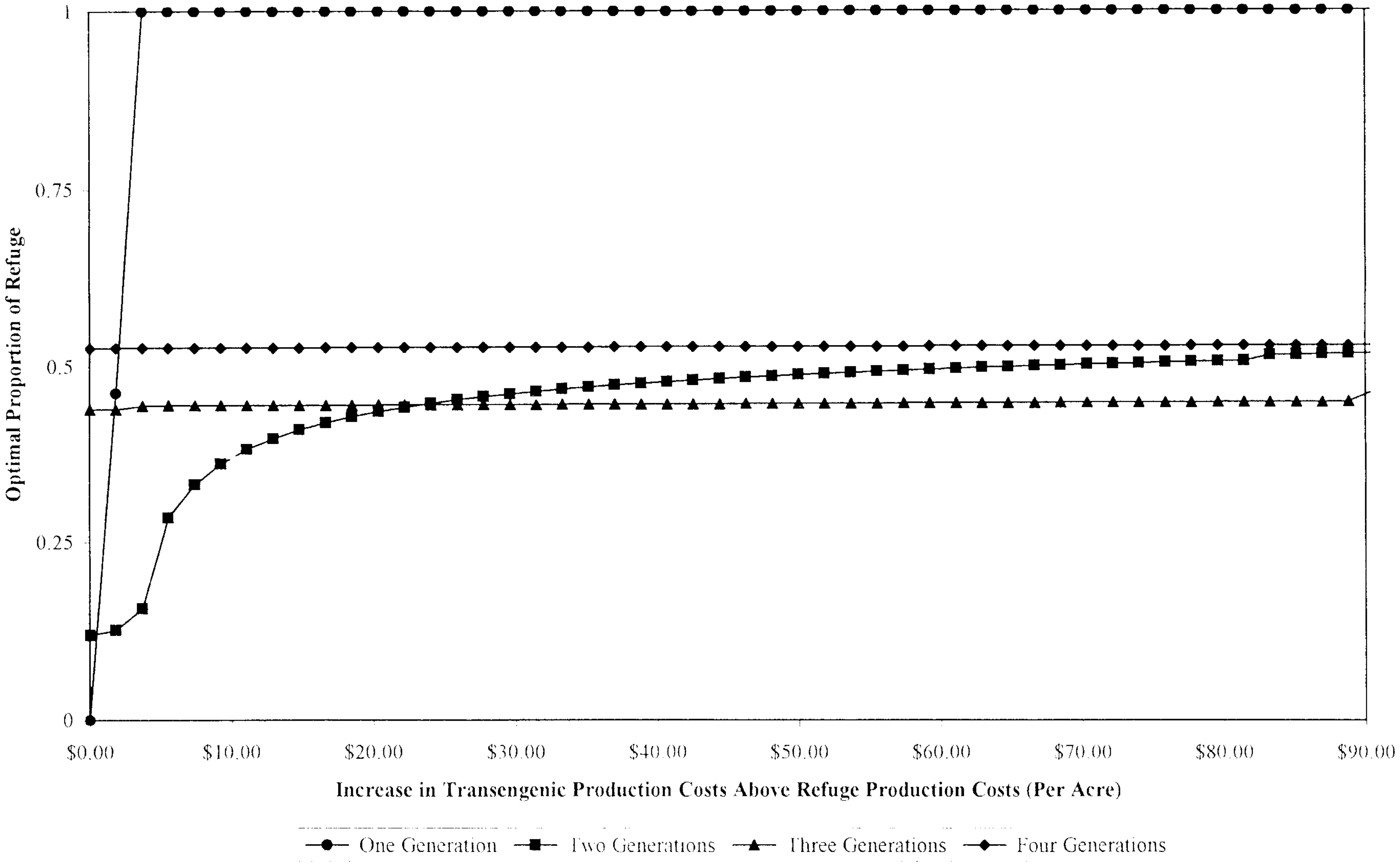


Figure 7. The effect of the marginal yield loss on the optimal proportion of refuge.

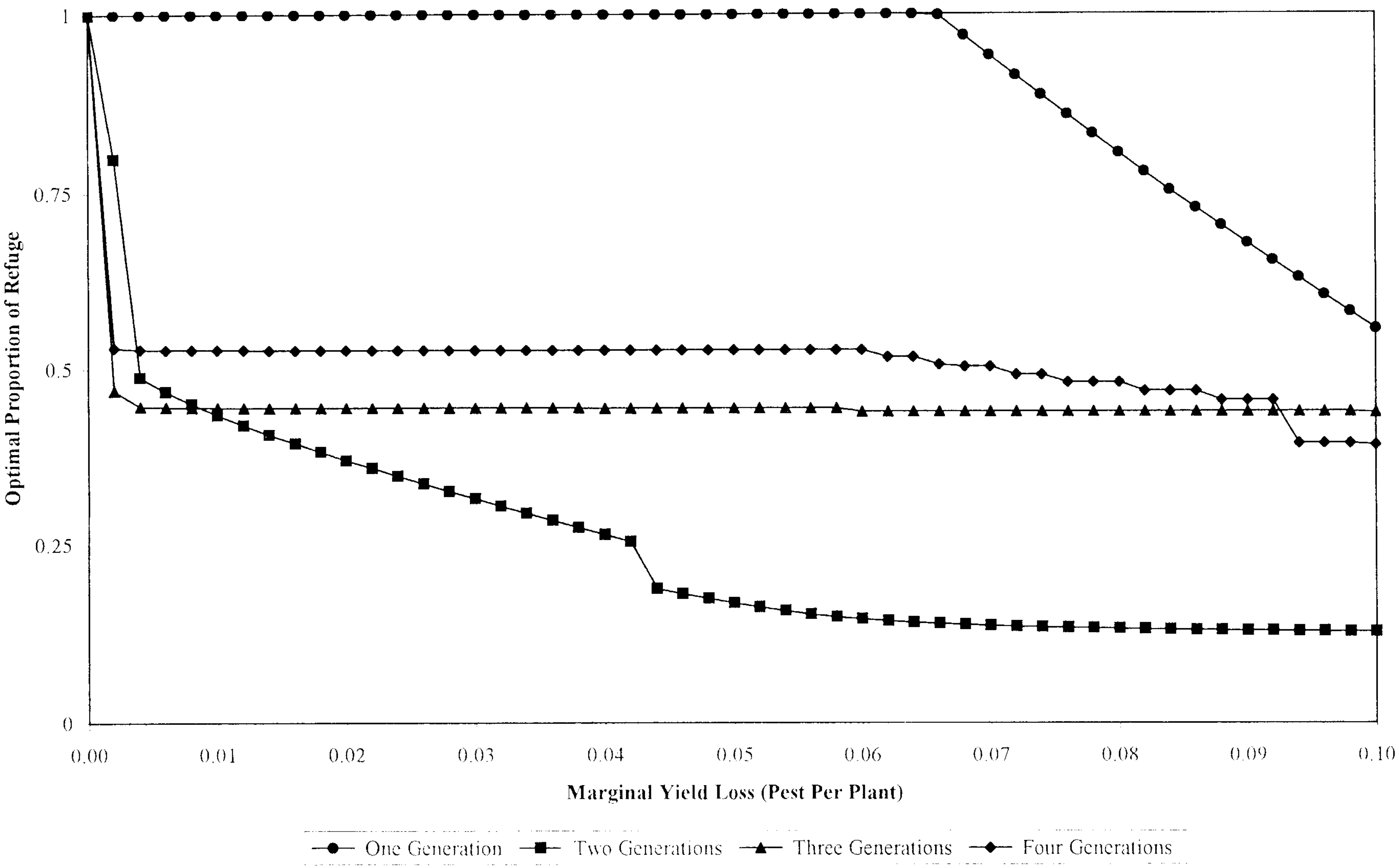


Figure 8: Effect of the proportion of refuge on annualized income.

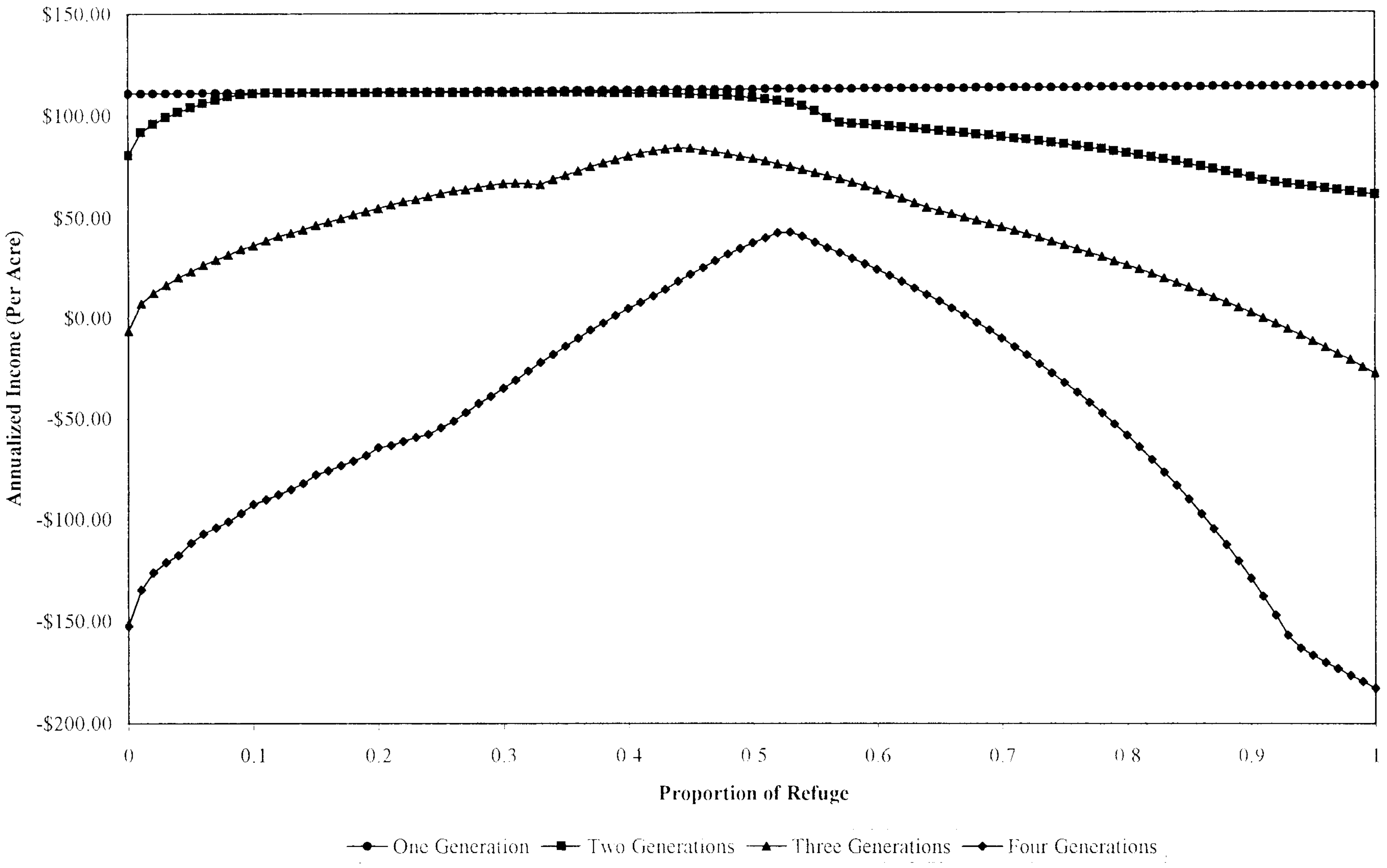
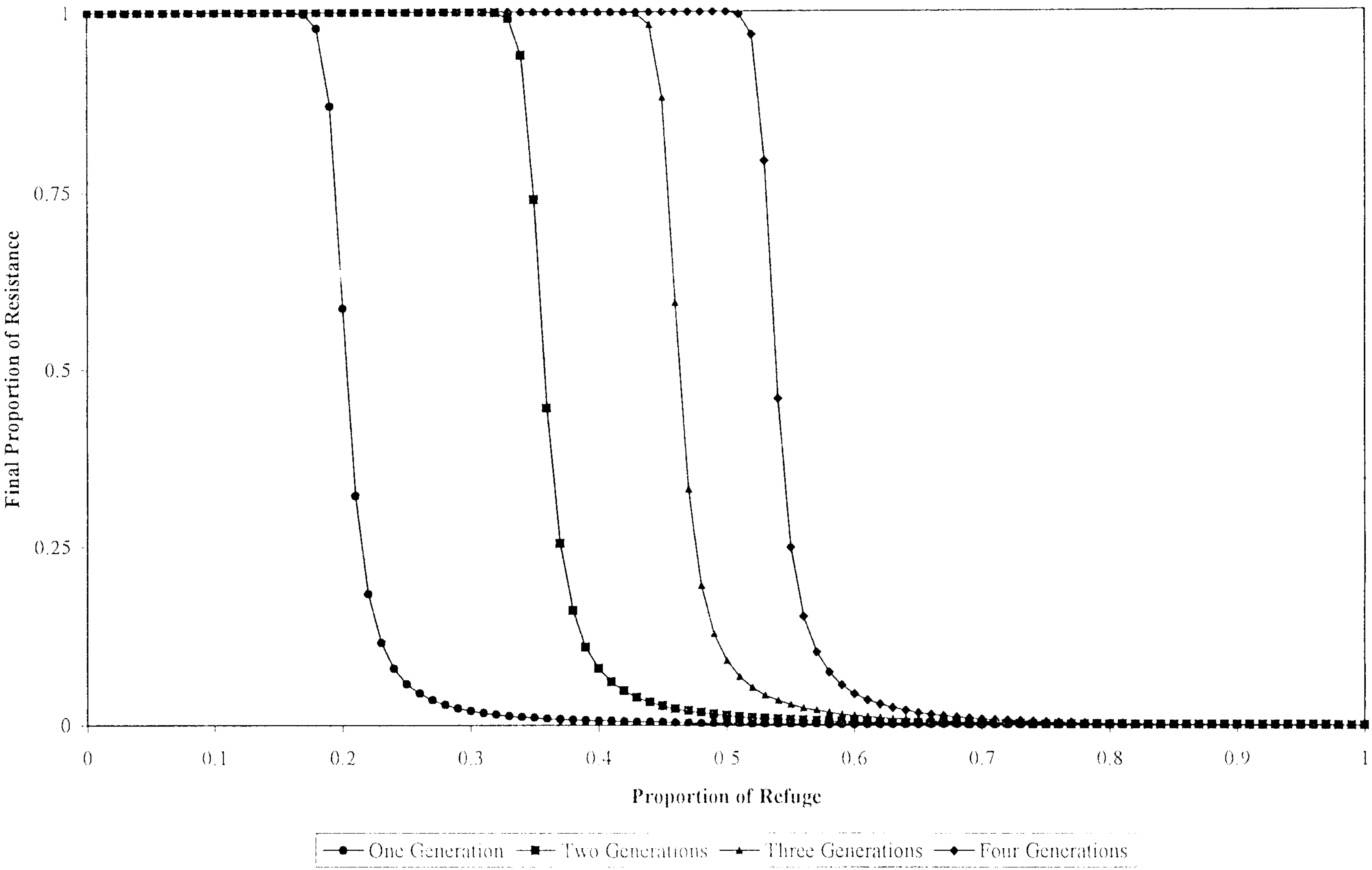


Figure 9. Effect of the proportion of refuge on the final proportion of resistant alleles.



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