

An Economic Optimization Model of Pesticide Resistance: Alfalfa and Egyptian Alfalfa Weevil—an Example¹

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ABSTRACT

Environ. Entomol. 8: 101-107 (1979)

The incorporation of pesticide resistance into a realistic economic optimization model of the interaction of Egyptian alfalfa weevil populations (EAW = *Hypera brunneipennis* (Boh.)) and alfalfa (*Medicago sativa* (L.)) is described. The model has 4 components: the population dynamics of the weevil; the dynamics of the crop; pesticide induced mortality; and the evolution of resistance in the weevil population. The paper presents the optimal within season and long-term pesticide spraying patterns after resistance develops for 2 cases: with and without information on the developments of resistance.

List of Symbols

(by order of their appearance)

EAW	= Egyptian alfalfa weevil.
$x = (x_1, \dots, x_t, \dots)$	= a vector of pesticide applications (lb/acre) at time periods 1, . . . , t, . . . within the growing season.
$b(x)$	= benefits as function of the pesticide applications.
$C(x)$	= costs of pesticide applications.
$f(x)$	= a set of biological constraints.
ξ_j	= parameters of the biological constraints.
I	= net rate of infestation of adult weevils immigrating into the alfalfa field per 56 D° (numbers/acre/time).
a, t	= age and time for the plant population.
a', t'	= age and time for the weevil population is implied (i.e., a different threshold for development).
$L(t, a)$	= leaf mass density, as a function of time and age.
$\mu_L(\cdot)$	= leaf mortality function.
$S(t, a)$	= stems' density function.
$\mu_S(\cdot)$	= stems' mortality function.
$R(t, a)$	= roots' mass density function.
$\mu_R(\cdot)$	= roots' mortality function.
$N(t, a)$	= pest number density function
$\mu_N(\cdot)$	= pests' mortality function.
V_t	= the amount of leaf tissue consumed by the pest population.
ψ	= leaf wound healing loss rate due to V.
L^*	= the total leaf mass susceptible to weevil attack.
L^*/V	= the weevil population leaf supply/demand ratio.

$\Gamma_{t,t+j}$	= $g(L_t^*/V_t, \text{age})$ starvation survivorship functions of larvae from time t to time t+j.
W	= frequency of the resistance gene.
α_j (j = 1, 2, 3)	= kill parameters for the adult pest of the pesticide with respect to genotypes, while δ_j are those for larvae.
$W_{A,t}$	= frequency of the resistance gene in the adult pest.
$\beta(n)$	= the fitness of resistant weevils during generation n.
γ_1, γ_2	= parameters of plant leaf growth.
$\kappa(x_t, W_t)$	= pesticide "kill function"—the proportion of pests surviving an application of x_t when their resistance gene frequency is W_t .
$\gamma_{3,t}$	= fecundity parameters.
$N_{z,t}$	= number of larvae that become pupae at time t (and later emerge as young adults).
η_1, γ_4	= weevil starvation parameters.
ϕ_i	= consumption rate factors (parameters) of ith instar larvae.
$W_{z,t}$	= frequency of resistance gene in the pupal population.
$K_l(x_t, W_t)$	= larval survivorship from pesticides.
δ_l	= kill parameter for $K_l(x_t, W_t)$.

Considerable progress has been made in recent years on the development of realistic simulation and optimization models of various crop systems. Ruesink (1976) reviews much of that work.

This paper explains from a biologist's point of view the formulation of an economic optimization model of the interaction of Egyptian alfalfa populations (EAW = *Hypera brunneipennis* (Boh.)), and alfalfa (*Medicago sativa* (L.)) growth and development. The model also incorporates the development of pesticide resistance in the weevil population. The model has 4 components: (1) the population dynamics of the weevil, (2) the dynamics of the crop's growth, (3) the pesticide induced mortality, and (4) the resultant evolution of resistance in the weevil population. Pest control optimization models have been developed by Regev et al. (1976a) for this species, and Shoemaker (1976) for the true alfalfa weevil, *H. postica* (Boh.). Some theoretical implications of the development of resistance in pest populations are de-

¹ Received for publication Nov. 8, 1977.

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⁵ This publication was supported in whole or in part by the National Science Foundation and the Environmental Protection Agency, through a grant (NSF DEB-75-04223) to the University of California. The findings, opinions and recommendations expressed herein are those of the author(s) and not necessarily those of the University of California, the National Science Foundation or the Environmental Protection Agency.

scribed by Taylor and Headley (1975), Comins (1976), Regev et al. (1976b) and later by Georghiou and Taylor (1977).

While resistance has not developed in the Egyptian alfalfa weevil, it has developed in *H. postica* in Armenia (Mardzhangan et al. 1969) and the potential exists for similar development here. More important, pesticide resistance is a general problem, and the methods outlined here have considerable application to other pest (insects, fungi, bacteria, weeds, etc.) problems.

The Optimization Problem

The economic problem is defined by maximizing an objective function (profit) subject to the biological constraints.

This can be written as

$$\max \{B(x) - C(x)\} \quad (1)$$

subject to:

$$\begin{aligned} f_j(x) &\leq \xi_j, j = 1, \dots, J \\ x &\geq 0 \end{aligned} \quad (2)$$

where B and C are the benefits and cost functions, respectively, x is a vector of pesticide controls, f_j represent the set of biological interactions described below, and ξ_j is a set of parameters of the biological system. By choosing appropriate quantities of pesticide, the farmer attempts to maximize his within season profit. However, because resistance develops as a result of overexposure to insecticides (i.e., the effectiveness of the pesticides decreases from season to season), the farmer's long run profits can be expected to decrease (see Luck et al. 1977). The economic model examines the long run implications of pesticide resistance by solving a series of single-season problems. The single-season problems were solved using a non-linear programming algorithm (G.R.G.)⁶. The constraints in the optimization problems are put in the form of difference equations (see below) which describe the dynamics of the biological system (plant-pest-pesticide)⁷.

Phenology of the Weevil and Alfalfa

Fig. 1 describes the basic phenology of the EAW and alfalfa during fall, winter, and spring (see Gutierrez et al. 1976 for complete details). After the onset of cool weather (temperatures below 5.5°C) in the fall (time = t_0), the adult weevils begin their migration back into the alfalfa fields. The rate of infestation (I) can be computed from temperatures during this period and from early season estimates of adult numbers in the field. The maximum number of weevils which will arrive in the field can be estimated from I and from the fact that most of the weevils are in the field by t_{max} . The adults die at a temperature dependent rate and are not greatly influenced by natural enemies or adverse weather experienced in California. Larvae from eggs deposited after time t_0 hatch after time $t_0 + b$ (i.e., the last frost) and are able to begin their larval development.

The alfalfa plant begins its spring development soon after the last frost ($t_0 + b$) and grows ca. 550D° > 5.5°C (-day degrees) at which time it is harvested (t_h). The descriptive model for the alfalfa-EAW interaction is presented below in its continuous form, and those seeking complete details should see Gutierrez et al. (1976), Gutierrez and Wang (1976) and Wang et al. (1977) as the models are much too detailed to review here. The brief description presented here merely depicts the form of the models (e.g., age structure).

Plant parts

$$\frac{\partial L}{\partial t} + \frac{\partial L}{\partial a} = -\mu_L(N, \dots) L(t, a) \quad (3)$$

$$\frac{\partial S}{\partial t} + \frac{\partial S}{\partial a} = -\mu_S(\cdot) S(t, a) \quad (4)$$

$$\frac{\partial R}{\partial t} + \frac{\partial R}{\partial a} = -\mu_R(\cdot) R(t, a) \quad (5)$$

Weevil

$$\frac{\partial N}{\partial t'} + \frac{\partial N}{\partial a'} = -\mu_N(L, \dots) N(t', a') + I_N \quad (6)$$

$L(t, a)$, $S(t, a)$ and $R(t, a)$ are mass density functions for leaves, stems and root tissues, while $N(t', a')$ is number density functions for the weevil population. Each of these equations requires a set of initial conditions for age structure. Also note that $\mu_L(\cdot)$, $\mu_S(\cdot)$, $\mu_R(\cdot)$ and $\mu_N(\cdot)$ are the complex mortality functions, where $\mu_L(\cdot)$ includes N and $\mu_N(\cdot)$ includes L (i.e., the numbers and age structure of weevil affects L , and vice versa). I_N is a net immigration rate for adult weevils (see Christensen et al. 1974, Gutierrez et al. 1976) emerging from or going into diapause. The plant part models are coupled via a metabolic pool model which determines the growth rate of each part, while the weevil model couples to the leaf model and hence to the other models via the reduced photosynthate production and growth.

Resistance to Insecticides

A pesticide mortality function estimated from field experiments by W. Cothran, C. G. Summers, and J. B. Christensen (Univ. of Calif.) on nonresistant weevils is used in this work (see Regev et al. 1976a), while the rate of pesticide-induced mortality on resistant weevils is assumed (see Appendix 1).

For convenience, it is assumed that the resistance mechanism to the toxicant is known and is controlled by a single gene. Many cases of resistance to pesticides of this nature are known (Brown 1967, Georghiou 1972), though cases of cross-resistance to members of a family of pesticides are becoming more common (Luck et al. 1977). In these cases, many genes may be involved rendering this problem too complex to analyze at this point in time. The analysis is thus restricted to the simple one-gene case or groups of genes which are linked and acting as one supergene. The population is assumed sufficiently large so that random mating and all other criteria for simple Mendelian inheritance are met. At the popu-

⁶ G.R.G. is a computer code using the reduced gradient method to solve non-linear programming problems. The code was developed by J. Abadie, (Electricité de France).

⁷ See Appendix I for parameter estimates not given in the text.

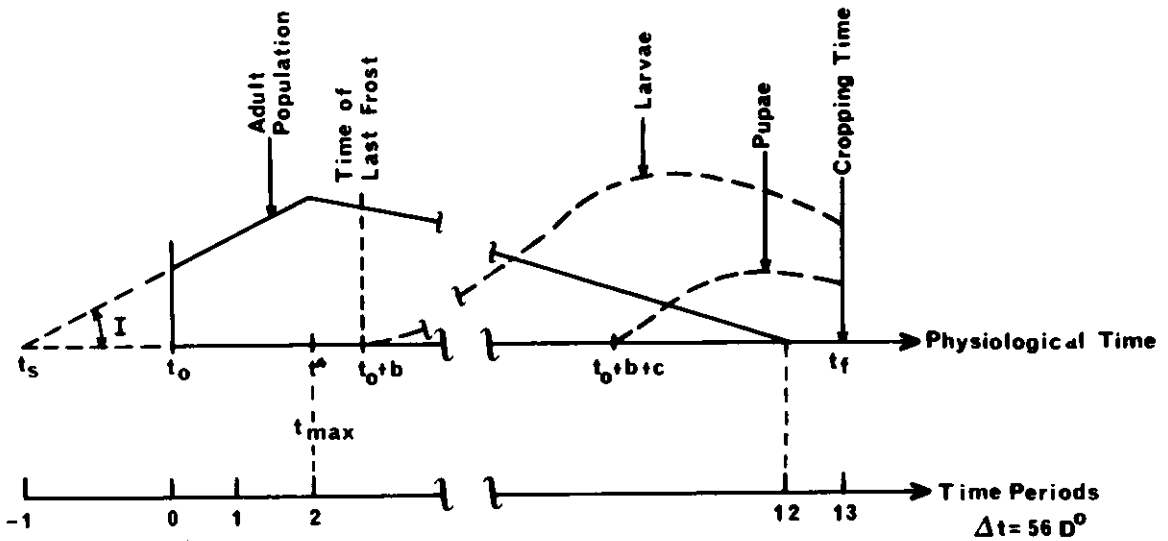


FIG. 1.—The phenology of the Egyptian alfalfa weevil in California. Time t_s is the beginning of the adult migration, I is the rate of infestation which equal zero at t^* , t_0 is the time after which eggs deposited survive the last frost and hatch at $t_0 + b$, while $t_0 + b + c$ is the time when the 1st pupae appear in the population.

lation level, it is important to know the frequency of the resistant (W) and susceptible ($1-W$) genes in the population, hence the well-known Hardy-Weinberg law is used to describe the changes in gene frequencies. The sum of the 2 gene frequencies at any time t is equal to 1, and the genotype frequencies equal $W^2 + 2W(1-W) + (1-W)^2 = 1$ (see Crow and Kimura 1970).

Optimization Model for EAW and Alfalfa

Simulation models (at least complex ones) have proven unsatisfactory for optimization work because very large numbers of runs are required to solve even simple problems, and because they usually lack analytical structure. The complex simulation model (Gutierrez et al. 1976) was used to assemble and simplify the relevant relationships inherent in the complex system and once simplified, the understanding was used to develop a realistic distillate for optimization purposes. The field data and the simulation model reported by Gutierrez et al. (1976) were used to judge the accuracy of the simpler version of the model. The simpler version of the model captures the dominant features of the biology and meets the core limitation of the computer and the differentiability conditions needed by the G.R.G. program. Time is measured in physiological day degrees above the base of 5.5°C for both the plant and the weevil. This simplification does not create undue difficulties because the time scales are correlated. The time unit (Δt) is 56 day-degrees (see Fig. 1).

The Plant

As noted above, the simulation model for the plant is both age and time dependent, but here a very simple time dependent model for the plant growth and development is used in the optimization problem.

$$L_t = (L_{t-\Delta t})(1 + \gamma_1) + \gamma_2 \tag{7}$$

where L_t is grams of leaf dry matter per sq. ft. and γ_1 and γ_2 are parameters estimated by least-squares from field dry matter production data. The quantity $(1 + \gamma_1)$ is the production rate of new photosynthate during Δt , while γ_2 is a component of growth which comes from the reserves.

Coupling the plant with the insect model has 2 components accounting for the increments (1) of leaf tissues consumed by the pests (V_t), and (2) wound healing losses which are a fraction (ψ) of the leaf tissue consumed during Δt . Hence, the effects of feeding can be incorporated as follows:

$$L_t = (L_{t-\Delta t} - (1 + \psi)V_t)(1 + \gamma_1) + \gamma_2. \tag{8}$$

The Weevil Model

The rate (I) of adult weevil infestation is given per 56 day degrees (i.e., Δt), and reaches a peak at time $t = 2$ (c.f. Fig. 1). All of the adult weevils will die by time 12 (560 day degrees) after peak infestation ($t = t_2$). A linear approximation from field data is assumed, so that without pest control, the number of adult weevils per acre ($N_{A,t+1}$) after t_2 is given by

$$N_{A,t+1} = N_{A,t} \left(1 - \frac{1}{12-t} \right)$$

The survivorship rate from pesticide applications $\kappa(x, W)$ depends on the amount of pesticides used per acre (x_t), as well as the frequency of the resistant gene (W_t), in the following way:

$$\kappa(x_t, W_t) = W_t^2 e^{-\alpha_1 x_t} + 2W_t(1-W_t)e^{-\alpha_2 x_t} + (1-W_t)^2 e^{-\alpha_3 x_t} \tag{9}$$

where W_t^2 is the proportion of resistant homozygous weevils, $(1-W_t)^2$ the proportion of susceptible homozygous weevils and $2W_t(1-W_t)$ the proportion of heterozygous weevils.

The α_i ($i = 1, 2, 3$) are the kill parameters for the 3 phenotypes such that $\alpha_1 < \alpha_2 < \alpha_3$. Thus the motion equations for the adult weevils are:

$$N_{A,1} = I, \text{ and } N_{A,2} = N_{A,1} \kappa(x_1, W_1) + I$$

$$N_{A,t+1} = N_{A,t} \cdot \kappa(x_t, W_t) \cdot (1 - 1/(12-t)) \text{ for } t=2, \dots, 11. \quad (10)$$

The frequency of the resistance gene (W_t) in the adult weevil population is affected by the amount of pesticides used in the preceding time period in the following way:

$$W_{t+1} = W_t^2 e^{-\alpha_1 x_t} + W_t (1 - W_t) e^{-\alpha_2 x_t} \frac{N_{A,t}}{N_{A,t+1}} \times \left(1 - \frac{1}{12-t}\right) \quad t = 2, \dots, 11. \quad (11)$$

The adult population prior to $t=2$ is given by a similar equation, but $(1 + W)$ replaces $(1 - 1/(12-t))$, which corrects for new immigrants. The genotypes of the new generation are described in a later section.

Immature Stages

The numbers of larvae are of little interest to us other than to enable us to calculate the rate of leaf consumption at any time t . This relationship is developed in a later section. Pupae require 6 time periods (~ 336 degree days = D°) to develop from the time of oviposition, hence we first find them in the population at time $t = 7$. The number of pupae depends on the number of larvae which survive severe food shortage, as well as the total amount of pesticides sprayed during the larval period ($220 D^\circ$). It is assumed that egg and pupal survival are not affected by the pest control policy nor by natural environmental factors, and thus every pupa emerges as a young adult which leaves the field. As we shall see this assumption makes little difference to the results because the optimal spray policy is not directed towards pupae, and the eggs are protected within plant tissues. Thus, the number of larvae that become pupae ($N_{z,t}$) at time t is given by:

$$N_{z,t+6} = \gamma_{3,t} \cdot N_{A,t+1} \cdot K\ell \left(\sum_{j=t+3}^{t+6} x_j, W_{t+1} \right) \cdot \Gamma_{1+2,t+5} \quad (12)$$

where

$\gamma_{3,t}$ is a fecundity parameter.

$K\ell(x_j, W_t)$ is the survivorship rate from pesticide applications on larvae.

$$K\ell(x_t, W_t) = \beta W_t^2 e^{-\delta_1 x_t} + 2W_t \times (1 - W_t) e^{-\delta_2 x_t} + (1 - W_t)^2 e^{-\delta_3 x_t}$$

δ_1 are the kill parameters for larvae.

β is a fraction of homozygous resistant larvae which will die prematurely because the resistance gene

is not well integrated into the gene pool (i.e., fitness).

and

$\Gamma_{1+2,t+5}$ are starvation survivorship functions depending upon the supply/demand ratios throughout all the larvae stages, i , in the following way.

$$\Gamma_{1+2,t+5} = \prod_{i=2}^5 (1 - \eta_i e^{-\gamma_4 (L^*/V)^2 t + 1}) \quad (13)$$

where

η_i are the age dependent starvation scalars (i.e., 1st instar die at a faster rate than older larvae).

L^*/V is the ratio of the supply of leaves in the crop to that demanded by the weevil population during Δt .

and

γ_4 is the starvation parameter (see Appendix).

The consumption of leaf tissue per time period by the larvae (V_t) is the direct damage to crop. This consumption is calculated on the basis of the number of larvae in each i^{th} instar stage $N_{e,i,t}$, multiplied by their consumption rate (ϕ^i):

$$V_t = \sum_{i=1}^4 N_{e,i,t} \cdot \phi^i \quad t = 3, \dots, 12 \quad (14)$$

In the computer program, the number of larvae of each i^{th} instar was not computed directly, since this would require 24 more equations. Instead the consumption rates were calculated via the number of adult weevils, oviposition rate, starvation survivorship of the larvae and pesticide application.⁸

The genetic composition of the surviving pupal population is calculated for time periods 7-12 when pupae are found. The frequency of the resistance gene in the pupal population may be calculated as follows:

$$W_{z,t+6} = \left(\beta W_{t+1}^2 e^{-\delta_1 \sum_{j=t+3}^{t+6} x_j} + W_{t+1} (1 - W_{t+1}) e^{-\delta_2 \sum_{j=t+3}^{t+6} x_j} \right) \Gamma_{1+2,t+5} \cdot \gamma_{3,t} \cdot \frac{N_{A,t+1}}{N_{z,t+6}}, \quad t = 1, \dots, 6 \quad (15)$$

The frequency of the resistant gene in the pupal population ($W_{z,t}$) is necessary to calculate the resistant gene frequency of the adult population which will immigrate to the field in the next season. In some computer analyses, the fitness (β) of the resistant homozygous larvae was increased with successive seasons (i.e., $[.7 \leq \beta(n) \leq 1]$).

Optimization Results and Discussion

If growers are to maximize their profits with regards to pest control, they must decide not only if it is economic to control them, but when and what quantity of

* The actual equations for V_t are very cumbersome but were necessary to maintain the number of equations within the computer limits. They do not add to the understanding of the model, and therefore were not reproduced here. Interested readers can obtain them from one of the authors.

pesticide should be applied. Simulation models are not suitable for evaluating this kind of problem, because even the simpler problem of optimizing the timing of pesticide applications (i.e., zero or some constant amount) over the 12 periods in this problem would require 2^{12} computer simulations (Shoemaker 1976). This fact clearly demonstrates the advantage of the optimization program.

In this problem, the alfalfa hay crop is given from equation (8) by L_t —the leaf mass at harvest (t_t). The revenue function $f(L_t)$ is defined as price multiplied by crop, but the price is adjusted for quality which decreases as the leaf/stem ratio decreases (i.e., as defoliation increases). The revenue $f(L_t)$ is thus written as $f[L_t(x_1, \dots, x_{12})] = B(x)$ as in equation (1). The cost function is simply the pesticide price multiplied by the amount of pesticide used. The price of pesticides increases with time to include the additional costs which frequently accrue from induced secondary pest outbreaks of mites and lepidopterous pests as a result of pesticide use late in the season (Regev et al. 1976a, Luck et al. 1977).

This section considers 2 policies which farmers may use to control the pest, and examines the effects of these policies on the development of resistance, pesticide use, profit, and infestation rates.

Case 1

The grower uses the *standard* optimal pesticide application schedule recommended for the area.—In this case, the timing and quantity of pesticides are assumed to be the optimal policy as determined for a single season when pesticide resistance was not present in the population (c.f. Regev et al. 1976a). Table 1 presents this policy. Because starvation effects on the weevil population were ignored by Regev et al. (1976a) but are included here, the total pesticides applied are slightly lower. In Case 1 the quantity of pesticides is applied each year at the “optimal” (standard) time without regard to the development of resistance. The grower assumes that the infestation rates are high and damaging, when in fact

Table 1.—The timing and amounts of pesticides applied in the standard policy.

Time periods	1	2	3	4	5-12	Total
Pesticides applied in ounces per acre	8.72	14.67	0	3.72	0	27.11

they are a function of the previous season’s survival (assumed 2.25% of the adults produced the previous year). The model also assumes that this is a standard policy for some effective region (i.e., the San Joaquin Valley).

Formally, the problem is stated as $\text{Max } \Pi(x)$, subject to equations (9), (10) and (12), with

$$W_0 = W_t = .01 \text{ and } I_0 = 2.15.$$

The results show that applying the same policy season after season causes a rapid increase in the development of resistance (Table 2, Fig. 2). In fact, after 4 seasons, the resistance gene has a frequency of 0.95, but because of low populations, it requires at least 3 seasons to rebuild its populations and reduce profits to \$75.00/acre.

Case 2

The *informed* single season optimal policy.—In Case 2, the grower knows not only the level of resistance, but

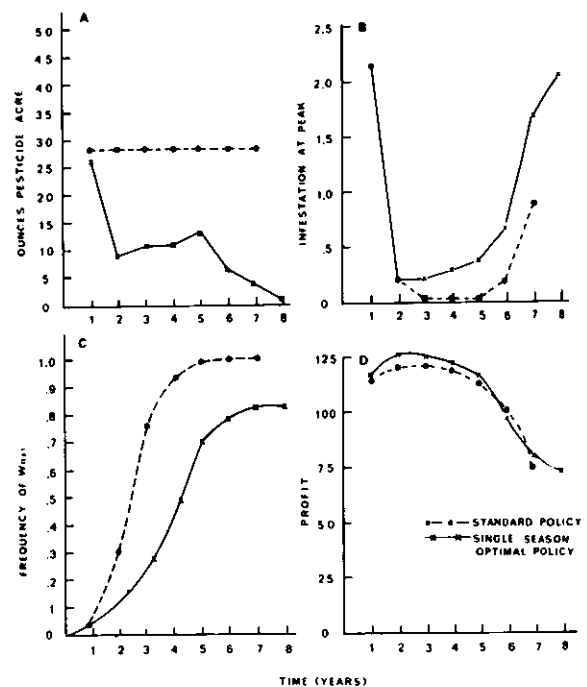


FIG. 2.—A comparison of paths for (A) pesticide use, (B) infestation (C) the frequency of the resistance gene and (D) profit for the standard and single season optimization policies (see text for complete details).

Table 2.—Evolution of the crop system after repeated applications of the standard policy.

Season	1	2	3	4	5	6	7
Total oz. of pesticides	27.11	27.11	27.11	27.11	27.11	27.11	27.11
Initial W_0	0.01 ⁿ	0.061	0.305	0.756	0.958	0.994	0.999
Final W	0.061	0.305	0.756	0.958	0.994	0.999	0.999
Initial peak density	2.15	0.2	0.03	0.02	0.05	0.22	0.91
Pests leaving	8.92	1.37	0.91	2.44	9.64	40.84	83.95
g/ft ² of leaf mass	15.82	16.20	16.23	16.17	15.87	14.60	11.67
Profit/acre	116.30	120.04	120.07	120.05	116.88	103.56	75.64

also the initial density of the pest at the beginning of each season. (N.B. In practice these parameters could be assessed, though with some difficulty.) This policy is also myopic in that it ignores the long-term implications of resistance.

Formally, the optimization problem is

$$\text{Max } \Pi(x) = B(x) - C(x)$$

subject to equations (9), (10), (11), (12), and (15), and

$$I_{t_2} = 2.15$$

at peak infestation. The control variables in this problem are the within season pesticide application (timing and quantity). The optimal solution to the problem depends upon 2 initial conditions, (i) the frequency of the resistance gene ($W_0 = 0.01$), and (ii) the adults' infestation rate during the autumn period. As in Case 1, 2.25% of the adults leaving the field at the end of the season (n) return the next season I_{n+1} . The sequence of these solutions is given in Table 3 and compared to Case 1 in Fig. 2.

The results show that the quantity of pesticides applied is initially high, but decreases as a result of the low rates of infestation. They begin to increase again after the 3rd season because the pesticides are less effective (i.e., the frequency of $W_3 = 0.697$). The rate of increase of resistance here is slower than in Case 1, but the levels of infestation are higher. This realistic example supports common contention that overexposure to pesticides not only decreases profit more rapidly, but also speeds up the development of resistance. In Case 1, the level of resistance gene after 3 years is 0.95, while in Case 2 it is only 0.82 after 7 seasons. Also note that in both cases the optimal application time for pesticides is before time period 3, which is contrary to the current practice of spraying during periods 6-8 (see also Regev et al. 1976a). The latter solution also conflicts with current practices, wherein the dosage rate is increased until the material is ineffective, the farmer is bankrupt, or some alternate technology is implemented.

While policy 1 uses more pesticides than policy 2 and hence increases environmental damage, the same relative profit is achieved after a 7-yr period. Undoubtedly, the amount of pesticide used would be lower under both policies, especially the 1st one, if environmental costs would be included as part of the cost function (see Regev et al. 1976a). The reduction would be most noticeable in the profit during years 2-8.

The paths for resistance development are very similar. Neither policy does much by way of managing resistance development; the optimal policy merely delays the rate of resistance development. Once resistance is high, the infesting populations grow geometrically and profits decline dramatically. Using a purely theoretical Lotka-Volterra simulation model, Georghiou and Taylor (1977) show that resistance develops slowest when the population is diluted with immigrants, fitness of resistant individuals is low and susceptible individuals have a higher reproductive rate. The latter 2 parameters were examined in this realistic optimization model, and the conclusions were generally the same. It is apparent that a dilution of the population with susceptible migrants would have a similar effect. The contribution of this paper is that it arrives at these conclusions based upon a realistic model of a specific parasite-host interaction.

Neither of the above policies is optimal, since they are myopic single-season solutions which ignore the long-term (multi-season) implications of resistance and infestation development. The long-term optimal solution to this problem is quite complex, and technically difficult to accomplish. A computer program capable of quickly evaluating this problem has been developed, but this work will be reported elsewhere (Regev et al. In press) simply because it is too complex to report in a paper of reasonable length. A preliminary report was given in Regev et al. (1976b).

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Table 3.—The results of single-season optimization problems over an 8-yr time period showing the evolution of various parameters.

	Time Periods	Years							
		I	II	III	IV	V	VI	VII	VIII
Within season pesticide applications	1	7.06	0.00	4.85	5.23	6.06	4.22	3.48	0
	2	11.56	8.22	5.41	5.85	6.71	2.77	0	0
	3	0	0	0	0	0	0	0	0
	4	4.45	1.5	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	6	3.06	0	0.54	0.56	0.64	0	0	1.32
	7-12	0	0	0	0	0	0	0	0
Total x (pesticides)		26.14	9.72	10.80	11.64	13.41	6.99	3.48	1.32
Initial W_0		0.010	0.067	0.132	0.258	0.457	0.674	0.789	0.82
Final W		0.067	0.132	0.258	0.457	0.697	0.789	0.82	0.82
Initial I at peak		2.15	0.205	0.237	0.269	0.368	0.674	1.71	2.06
Pest leaving per sq/ft		9.13	10.57	11.98	16.44	30.10	76.57	92.17	94.98
Leaf mass g/ft ²		15.82	15.80	15.76	15.57	15.02	12.73	10.35	9.73
Profit \$/acre		116.87	126.42	125.40	122.98	116.05	97.38	78.29	74.53

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Appendix I. Parameter Estimation

1. *Alfalfa Prices.* Data concerning the effects of defoliation are difficult to obtain as the actual values may vary widely, depending upon market supply/demand considerations (V. E. Marble, Univ. of Calif. alfalfa specialist). The assumed price (P) per ton of alfalfa is highly conservative and is computed on the basis of the amount of leaf matter present at the harvest

$$P = U + 4.2014L + .2035L^2$$

where

$0 \leq L \leq 16$ = the leaf mass in grams per ft² (i.e., our simulation unit)

U = 15.1253 which is the price assumed paid for completely defoliated alfalfa (L = 0).

2. *Pesticide Costs.* The basic costs for pesticides (C) is 0.6 dollars per ounce to time period 6, after which its price increases by the rate t/10 dollars.

3. Pesticide kill function parameters for homozygous resistant, heterozygous and susceptible individuals, respectively.

a) adults $\alpha_1 = 0$, $\alpha_2 = 0.095$ and $X_3 = 0.19$

b) larvae $\delta_1 = 0$, $\delta_2 = 0.14$ and $\delta_3 = 0.28$

4. In the optimization model, fitness (β) of homozygous resistant larvae compared to homozygous susceptible larvae.

$$\beta = 0.9$$

5. Starvation parameters for larvae feeding on defoliated alfalfa.

a) age dependent effects for larvae $i = 2, \dots, 4$ periods of age $N_2 = 0.15$, $N_3 = 0.3$, $N_4 = 0.45$, $N_5 = 1.0$.

Note that young larvae are more strongly affected by defoliation than are older larvae.

b) The parameter $\gamma_4 = 0.005$ was estimated from the simulation to meet the criteria that 85-90 adults max emerged/square foot of alfalfa during the 1973-74 season at Davis, CA (see Gutierrez et al. 1976).