

Incorporating natural enemies in an economic threshold for dynamically optimal pest management

Wei Zhang^{a,*}, Scott M. Swinton^b

^a Environment and Production Technology Division, International Food Policy Research Institute (IFPRI), 2033 K Street NW, Washington, DC 20006, USA

^b Department of Agricultural, Food, and Resource Economics, 202 Agriculture Hall, Michigan State University, East Lansing, MI 48824-1039, USA

ARTICLE INFO

Article history:

Received 24 July 2008

Received in revised form 24 January 2009

Accepted 30 January 2009

Available online 13 March 2009

Keywords:

Biological control

Ecosystem services

Pest regulation service

Natural enemies

Dynamic optimization

Economic threshold

Soybean aphid

ABSTRACT

The control of pests by their natural enemies represents an important regulating ecosystem service that helps maintain the stability of crop ecosystems. These services, however, are often ignored in pest management decision making. In addition, the use of broad-spectrum insecticides can damage the populations of natural enemies, reducing the cost-effectiveness of insecticide investment if unaccounted for in treatment decisions.

The existing literature on modeling of biological control of insect pests has generally focused on simulations of the population dynamics of pest and natural enemy species and the processes underlying pest control. But agriculture is a managed ecosystem where predator–prey relationships are heavily influenced by human managers. In modeling managerial choices, this study develops an intra-seasonal dynamic bio-economic optimization model for insecticide-based pest management that explicitly takes into account both the biological control effect of natural enemies on pest density and the nontarget mortality effect of insecticides on the level of natural pest control supplied. The model captures predator–prey interactions, linking them to crop growth and yield damage functions, which in turn are evaluated in a dynamic optimization framework. We introduce a new decision rule for judicious insecticide decisions using a natural enemy-adjusted economic threshold. This threshold represents the pest population density at which insecticide control becomes optimal in spite of the opportunity cost of injury to natural enemies of the target pest. Using field data from Michigan, the model is applied to the case of soybean aphid (*Aphis glycines*, Matsumura), a recent invasive pest of soybean (*Glycine max*), whose management is of both economic and environmental importance to the North Central region of the United States. As illustrated by the numerical examples, such natural enemy-adjusted threshold is likely to lead to fewer recommendations for insecticide use than naïve models that ignore natural enemies, resulting in less insecticide use, while maintaining profitability for farmers that rely on chemical pest control methods.

The bioeconomic model developed in this study can be used to conduct a wide variety of analyses such as identifying dynamically optimal spray strategies and estimating the implied economic value of natural control services. Furthermore, with the incorporation of inter-year carry-over factors, such as overwintering of pests and natural enemies, the current model can contribute to building multi-year models for studying long-term pest management.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The control of pests by their natural enemies represents an important ecosystem service that suppresses pest population growth and has the potential to mitigate pest control costs and crop yield loss in agricultural ecosystems (Naylor and Ehrlich, 1997; Losey and Vaughan, 2006; Costamagna et al., 2007a). In addition to the well-documented human health and environmental risks of applying broad-spectrum insecticides (Naylor and Ehrlich, 1997;

Thomas, 1999), another unwanted consequence is the decimation of ambient populations of natural enemies along with the biological control services they provide. In the long run, loss of natural enemies can exacerbate existing pest problems or even trigger the emergence of new pests (Calkins, 1983; Naylor and Ehrlich, 1997; Krishna et al., 2003). Such unintended effects reduce the cost-effectiveness of insecticides if unaccounted for in treatment decisions, creating an “opportunity cost” to producers in terms of foregone natural control services that would have been provided by existing natural enemies if no pesticides had been used.

Bioeconomic modeling of the behavior of ecological communities has the advantages of quantitatively describing biological processes and interactions and predicting their response to man-

* Corresponding author. Tel.: +1 202 862 5626.

E-mail addresses: w.zhang@cgiar.org, zhangwe9@gmail.com (W. Zhang).

agement decisions (King et al., 1993). As such, it is an important tool for improving management by making explicit inefficiencies (e.g., from unwarranted or untimely input use) and costs of unintended feedbacks (such as loss of beneficial insects to broad-spectrum insecticides). This study develops an intra-seasonal dynamic bioeconomic optimization model that explicitly integrates the population dynamics of ambient natural enemies into pest management decision making. We offer a new treatment decision rule: the natural enemy-adjusted economic threshold (NEET). The NEET is defined as the pest population density threshold at which insecticide control becomes optimal in spite of the opportunity cost of injury to natural enemies of the target pest. Using recent field data from Michigan, the model is applied to the case of soybean aphid (*Aphis glycines*, Matsumura) (SBA), the most significant invasive insect threat to soybean (*Glycine max*) production in North America (Ragsdale et al., 2007).

The remainder of the paper begins with a review of existing approaches to pest management modeling. We then present a dynamic bioeconomic optimization model for the NEET, parameterized for the case of SBA. Parameter estimation and model validation are followed by numerical examples to illustrate how the model works. Sensitivity analysis is performed to examine the uncertainty in parameter values and assumptions. Finally, we highlight contributions of the model, identify limitations and suggest future research directions.

2. Models of pest management

The existing models of pest management threshold decision rules have been developed on two fronts by biologists and by economists. This study extends the literature to integrating natural enemies into a dynamic optimization economic decision model by offering a new threshold decision rule concept of NEET.

The threshold approach to pest population control was pioneered by entomologists Stern et al. (1959) as a quantitative approach to integrated pest management. The pest population threshold models define the economic injury level (EIL) as the pest population density at which the benefit of control measures justifies the associated cost. Because there are time lags between when scouting reports show profitability-threatening pest levels and when fields can be sprayed, the economic threshold (ET) for pest control occurs at the lower population density when action must be taken to prevent an increasing pest population from reaching the EIL (Pedigo et al., 1986). The traditional pest population threshold models are based on pest abundance, but recent improvements develop a dynamic ET that moves up or down with changes in biological mortality caused by natural enemies during the period between ET determination and EIL realization (Musser et al., 2006). However, the pest population threshold models are limited by a static EIL-determination framework that (1) lacks a dynamically optimal decision guide when multiple treatments are needed, (2) omits natural control services, and (3) ignores the nontarget mortality effect of broad-spectrum insecticides on natural enemies.

Separate from the pest population threshold models pioneered by entomologists, economists introduced models that integrated the concept of marginality. Headley (1972) redefined the ET as the optimal (net-return-maximizing) pest population density where the marginal value product of damage control equals the marginal cost of control. Hall and Norgaard (1973) later improved Headley's framework by developing a more general model that considers the optimal timing and quantity of a single insecticide application. Like the pest population threshold models, these profitability threshold models are essentially static, as illustrated below for a net-return-maximizing producer, because current period control decisions do not affect future opportunities (Kamien and Schwartz, 1981; Bor,

1995):

$$\begin{aligned} \max_x \quad & [p \cdot y - c(x)] \\ \text{s.t.} \quad & y = f(y^0, S) \\ & S = g(x, S_0) \end{aligned}$$

where p is the output price, y^0 is the pest-free historical yield level, and harvest yield y is a function of y^0 and pest population density S . Pest population density is in turn determined by initial population density S_0 and control action x , whose cost is evaluated by cost function $c(x)$. The optimal control action is achieved where the marginal value of avoided yield loss equals the marginal input cost of pest control.

Because rapidly reproducing pest populations can often recover from insecticide spraying and again pose threats to profitability, multiple treatments may be required, and hence a model that incorporates dynamic aspects of pest management into threshold development is needed (e.g., Talpaz and Borosh, 1974; Zacharias and Grube, 1986; Harper et al., 1994; Bor, 1995). Moreover, the role of natural enemies should also be included if the model is to predict pest populations accurately and the susceptibility of natural enemies to insecticides is needed to complete a model that incorporates a NEET.

Incorporating a time component t , the above static model can be transformed to a dynamic form with first order difference equations (i.e., causal links are expressed at the next time period). With the introduction of natural enemies (denoted by NE), the dynamic decision model is expanded to:

$$\begin{aligned} \max_{x_t} \quad & \left[p \cdot y_T - \sum_{t=1}^{T-2} c(x_t) \right] \\ \text{s.t.} \quad & y_{t+1} = f(y_t, S_t), \quad \text{and} \quad y_1 = y^0, \quad t = 1, \dots, T-1 \\ & S_{t+1} = g(x_t, S_t, NE_t), \quad t = 1, \dots, T-2 \\ & NE_{t+1} = h(x_t, S_t, NE_t), \quad t = 1, \dots, T-3 \end{aligned}$$

where y_{t+1} denotes the yield potential at period $t+1$, and harvest yield is evaluated at the terminal period $T(y_T)$.¹ The state variable y_{t+1} captures changes in yield potential that can be expected as translated from plant damage due to pest injury. The optimal control action in period $t(x_t)$ not only directly affects the pest density in the next period, S_{t+1} , but also indirectly affects subsequent pest density S_{t+2} through its impact on natural enemies in period $t+1$, NE_{t+1} . Hence, the profit-maximizing decision over the full time horizon entails spraying in period 1 only if the associated cost is no greater than the direct benefit of reduced pest damage adjusted for the loss of pest control by natural enemies. Depending on the relative magnitude of the biological interactions given the economic parameters, the inclusion of natural enemies can lead to less insecticide use, with potential social and environmental consequences.

Recent contributions to the ecological literature have modeled the biological control of insect pests. Developing detailed models of phenology, reproduction, dispersal, population and predation dynamics, Mills and Getz (1996), Bianchi and van der Werf (2004) and Bommarco et al. (2007) have produced biologically realistic simulations that enable evaluation of the pest suppression effect in a pest–predator system. These models contribute importantly to the theoretical basis for empirical studies of biological control by elucidating the interrelated population dynamics of pest and natural enemy species. Human pest control decisions are outside the scope of these models. Yet in a managed ecosystem like agriculture, human decisions about pesticide use are highly relevant to ecosystem structure, function and resultant services. Human decisions in

¹ Given the transition equations in the model, meaningful control action is to be carried out at least two periods prior to harvest in period T (i.e., $t = 1, \dots, T-2$ for x_t).

market-oriented working ecosystems are strongly driven by perceived profitability. However, perceptions of profitable pest control depend upon available information, which for farm managers currently omits a good grasp of how natural enemies affect current and future earnings.

Our model builds on past insect pest biological control models by linking ecological predator–prey models and crop plant growth with economic decision models in a dynamic optimization framework. The population dynamics of ambient natural enemies are explicitly modeled along with their suppressive effect on the pest population. The NEET decision rule incorporates the opportunity cost of losing these benefits due to insecticide sprays that can kill natural enemies. The NEET model is unique in incorporating multiple treatment opportunities and the effect of broad-spectrum insecticides on natural enemies into a dynamic optimization framework for threshold-based optimal pest management. This study's dynamic optimization framework factors in future control opportunities, which distinguishes this model from prior approaches that based control decisions on sequential sampling of pest and natural enemy populations (Nyrop et al., 1994; van der Werf et al., 1997).

3. Bioeconomic model of soybean aphid management

SBA is a recent invasive species that was first discovered in the North Central region of the United States in 2000. Within 4 years, it had spread to 21 states and south-central Canada (Landis et al., 2004). Not only is SBA capable of causing extensive damage to soybean yield with documented yield loss of up to 40% (DiFonzo and Hines, 2002), SBA outbreaks are also correlated with dramatic increases in virus incidence in vegetable crops (Thompson and German, 2003; RAMP, 2006). Since its invasion, SBA has prompted farmers to perform extensive spraying of soybean acreage, making it one of the key drivers of insecticide use in the region (Smith and Pike, 2002). For example, 42% of soybean acreage in Michigan and 30% in Minnesota were sprayed during the 2005 season, compared with less than 1% in the North Central region before SBA arrived (NASS, 2007).

Existing natural enemy communities play a key role in suppressing SBA populations in the North Central region of the United States (Fox et al., 2004; Landis et al., 2004; Costamagna and Landis, 2006; Costamagna et al., 2008). Natural enemies of SBA include 22 predator species (Rutledge et al., 2004), 6 parasitoid species (Kaiser et al., 2007), and several species of fungi that cause disease in aphids (Nielsen and Hajek, 2005). In particular, generalist predators (mainly ladybeetles, *Coccinellidae*) provide strong, season-long suppression, protecting soybean biomass and yield from SBA damage (Costamagna et al., 2007a). However, most insect natural enemies are susceptible to the major broad-spectrum insecticides used to treat SBA (C.D. DiFonzo, personal communication, 2006). Evidence from Iowa indicates that insecticides applied in the early season can actually result in greater SBA population later (O'Neal, 2007), undermining the cost-effectiveness of insecticide investment. While selective insecticides may reduce the risk on natural enemies, broad-spectrum insecticides have been shown to provide greater protection from SBA (O'Neal, 2007) and are likely to remain important options for farmers. The central question, therefore, is to choose the optimal level of broad-spectrum insecticide to conserve SBA natural enemies such that the economic benefit to the farmer outweighs the additional cost. Although agricultural insecticide recommendations for SBA control generally stress the need for assessing the presence of natural enemies before spraying (e.g., Smith and Pike, 2002; NCPMC, 2005), there has been no applicable decision guide that explicitly addresses conserving and capitalizing on the ecosystem service of pest regulation supplied by ambient natural enemies of SBA.

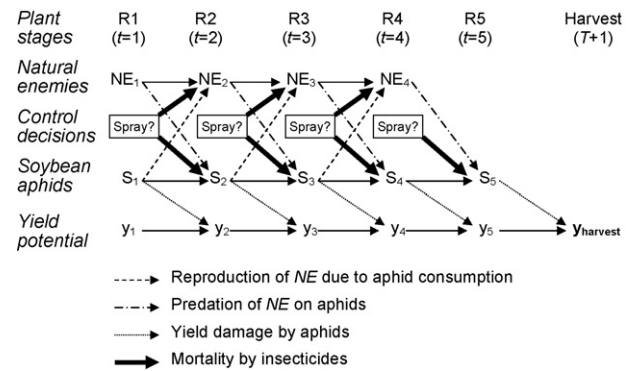


Fig. 1. Dynamics of soybean aphid pest control decisions based on natural enemy and aphid populations with resulting updating of crop yield expectations by soybean plant growth stage.

Applying the NEET concept, we develop an intra-seasonal dynamic bioeconomic optimization model for the optimal number and timing of insecticide applications to treat SBA, given a pre-determined dose, toxicity level and constant prices for crop and inputs. A stage-based, discrete dynamic framework is adopted (Fig. 1). Specifically, the system of soybean growth stages divides plant development into vegetative and reproductive stages (Pedersen, 2004) (Table 1). Our model focuses on the five early reproductive stages, R1 through R5, during which soybeans are most susceptible to SBA damage (Jameson-Jones, 2005). A final period ($T+1=6$) is included for harvest. The model assumes that a soybean producer maximizes the net returns over variable costs of SBA control, subject to the evolution of three sets of biological state variables over plant growth stages R1–R5. Those sets of state variables are (i) population dynamics of SBA, (ii) population dynamics of natural enemies, and (iii) crop yield response to surviving SBA pest density. The solution to this discrete dynamic optimization problem leads to an optimal sequence of control actions or the NEET decision rule. Although avoiding unnecessary insecticide use can potentially confer a wide range of social and environmental benefits, this model takes a narrower focus on farmers' private economic incentives for incorporating natural enemies in insecticide decisions. The model also does not account for such indirect benefits of SBA control as reduced incidence of viruses in vegetable crops.

Insecticide application decisions are modeled as binary choices at the standard application rate specified on the product label. Two reasons motivate this choice. First, pesticide manufacturers will only guarantee the efficacy of their products if applied at the recommended rates on the label. Second, few farmers have suitable data and time available to adjust pesticide rates to pest populations. Hence, we model the control decision in each stage as a binary choice, denoted by x_t ($x_t = 1$ for spray at fixed, label-recommended rates, and $x_t = 0$ for no spray at stage t). We assume that no more than one spray may occur in each stage and that the predicted yield

Table 1
Stages of soybean plant development.

Vegetative stages	Reproductive stages
VE (emergence)	R1 (beginning flowering)
VC (unrolled unifoliate leaves)	R2 (full flowering)
V1 (first trifoliate)	R3 (beginning pod)
V2 (second trifoliate)	R4 (full pod)
V3 (third trifoliate)	R5 (beginning seed)
V(n) (nth trifoliate)	R6 (full seed)
V6 (flowering will soon start)	R7 (beginning maturity)
	R8 (full maturity)

Source: Pedersen (2004).

upon reaching stage R5 is carried through to harvest so that SBA control is only meaningful during stages R1–R4. The growth of SBA population over the five reproductive stages of the soybean plant is given by

$$S_{t+1} = (S_t - k_{S,t} \cdot x_t \cdot S_t) + ng_t \cdot (S_t - k_{S,t} \cdot x_t \cdot S_t) - pr_t \cdot (NE_t - k_{NE,t} \cdot x_t \cdot NE_t) \quad (t = 1, 2, 3, 4) \quad (1)$$

where S_{t+1} denotes SBA density per plant at stage $t + 1$, NE_t denotes density of natural enemies per plant at stage t , $k_{S,t}$ and $k_{NE,t}$ represent mortality rates of SBA and natural enemies from insecticide application, respectively, ng_t denotes net growth rate of SBA population in the absence of insecticides, and pr_t is the aggregate predation rate per NE unit at stage t .

While a number of existing natural enemy communities jointly contribute to suppressing SBA population in soybeans (Fox and Landis, 2002), the role of generalist predators (mainly ladybeetles) is particularly important (Costamagna et al., 2007a) due to their high abundance in both number and overall suppression effectiveness (Costamagna et al., 2008). We therefore focus on the ladybeetle predators in our quantification of the natural enemy biological control effect by aggregating populations of major ladybeetle species and treating them as homogeneous in their control of the SBA population.

We adopt a dynamic Lotka–Volterra predator–prey model to describe changes in the population density of natural enemies over discrete time periods (Lotka, 1925; Volterra, 1926). Denoted by NE_{t+1} , the population density of natural enemies at stage $t + 1$ is given by

$$NE_{t+1} = (NE_t - k_{NE,t} \cdot x_t \cdot NE_t) + d_t \cdot (NE_t - k_{NE,t} \cdot x_t \cdot NE_t) + b_t \cdot (S_t - k_{S,t} \cdot x_t \cdot S_t) \cdot (NE_t - k_{NE,t} \cdot x_t \cdot NE_t) \quad (2)$$

($t = 1, 2, 3$)², where d_t (< 0) is the natural net decline rate that NE would suffer in the absence of prey and b_t (> 0) is interpreted as the reproduction rate of NE per prey encountered (Sharov, 1996, 1997, 1999).

Farmers often make sequential predictions on achievable yield over the course of the growing season based on perceptions of historical yield potential and pest damage. We introduce a conceptual model of yield–pest interaction that is consistent with the process of updating expectations of yield potential. We express the expected yield potential at stage $t + 1$ (denoted by $E_{t+1}[y]$) as a function of expected yield potential at the previous stage t ($E_t[y]$) and pest population density at t (S_t):

$$E_{t+1}[y] = f(E_t[y], S_t), \quad (t = 1, \dots, 5) \quad \text{and} \quad E_1[y] = \bar{y}_h, \quad (3)$$

where \bar{y}_h is the maximum (pest-free) potential yield or average historical yield upon which the season's first prediction is based. The actual yield at harvest, y_h , is assumed to be equal to yield potential evaluated at period $T + 1 = 6$ ("the final reward period"). In a nonlinear yield damage function of pest density, such as Cousens' (1985) rectangular hyperbolic model, a farmer's expectation of crop yield can be updated by replacing the parameter that represents the maximum potential yield with the fitted value of yield potential obtained in the previous period ($E_t[y]$) to render the following reformulated version of Cousens' model:

$$E_{t+1}[y] = E_t[y] \cdot \left(1 - \frac{\eta_t \cdot S_t}{1 + \eta_t \cdot S_t / \theta_t} \right) \quad (4)$$

² The natural enemy model is estimated for stages R1–R3 to predict population up to stage R4 ($NE_{t+1=4}$), which in turn affects SBA population in stage R5—the last stage in which SBA can cause damage to harvest yield in our model. Therefore, we do not need $t = 4$ for the natural enemy model.

where η_t denotes the proportion of yield lost per unit of pest density and θ_t denotes the maximum proportional yield loss to pest damage ($0 \leq \theta_t \leq 1$).

A soybean producer's objective function can be described as soybean revenue realized at harvest minus total SBA control cost:

$$\text{Max}_{\{x_t\}_{t=1}^T} \left[p \cdot y_h - \sum_{t=1}^T c(x_t) \right], \quad (t = 1, \dots, 5) \quad (5)$$

subject to Eqs. (1), (2) and (4), with S_1 , NE_1 , and $E_1[y]$ given. $\{x_t\}_{t=1}^T$ represents a sequence of control actions over the five time periods, p denotes output price, and $c(x_t)$ denotes control cost, including the cost of pest scouting to provide the basis for control decisions. The time value of money is ignored for this single-season optimization problem due to its short duration, i.e., there is no discounting of future values.

The profit-maximizing NEET decision rule can be applied to the SBA optimal management problem above by applying the method of dynamic programming (Bellman, 1957). Dynamic programming is a stage-wise search method that divides the optimization problem into sub-problems or decision stages that can be addressed sequentially, based on the principle that in an optimal sequence of decisions or choices, each subsequence must also be optimal (by Bellman's "principle of optimality"). The resulting optimal sequence of actions for the current discrete, finite time horizon problem prescribes the optimal number and timing of sprays based on the observed initial values of the three biological state variables.

4. Model estimation

4.1. Population of soybean aphid

To estimate the predation-free net growth rate of SBA population (ng_t), we adopt a meta-modeling approach by using simulated SBA growth data generated by a daily time-step model developed by Costamagna et al. (2007b). The model predicts SBA population growth under field conditions in the absence of natural suppression, based on Williams et al. (1999)'s discrete exponential population growth function. Specifically, SBA population density on day $day + 1$, denoted by a_{day+1} , is described as:

$$a_{day+1} = a_{day} \cdot e^{r_{day}} \quad (6)$$

where

$$r_{day} = r_{\max}(1 - C \cdot day) \quad (7)$$

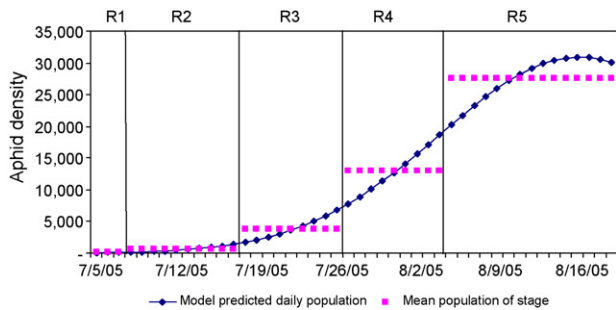
r_{day} is the intrinsic growth rate of SBA that decreases in time (day), and C is the reciprocal of the time to peak population. Starting at r_{\max} (the maximum intrinsic rate of increase) when $day = 0$ (when the population has its initial density), r_{day} decreases linearly until $r_{day} = 0$ when $day = 1/C$ (Costamagna et al., 2007b). Costamagna et al. (2007b) parameterize the model using data collected from predator exclusion cage experiments conducted in Michigan soybean fields between 2003 and 2005 and show that the model is robust against variability within and between experiments. The original model calibrates a maximum intrinsic growth rate (r_{\max}) of 0.40 (per day) for the initial infestation (Table 2). Field data from Michigan show that in 2005 soybean plants on average reached stage R1 about 2 weeks after the fields were colonized by aphids. Since we are interested in the SBA population during soybean reproductive stages R1–R5, we adjust the parameter value for maximum intrinsic growth rate to be 0.28, denoted by $r_{\max,adjusted}$, to account for the time lapse between the date of initial SBA infestation and the estimated date when plant enters stage R1 according to Eq. (7).

We first predict daily SBA population for the period of R1–R5 using the Costamagna et al. (2007b) model. Free of predation, the

Table 2

Soybean aphid population model parameters.

	Value of parameters
r_{\max}^a	0.40
C^a	0.02
$r_{\max, \text{adjusted}}^b$	0.28
Net population growth rate in stage R1 (ng_1)	5.29
ng_2	5.15
ng_3	2.35
ng_4	1.13

^a Parameters estimated by Costamagna et al. (2007b).^b Assuming a 2-week time lag between the date of initial infestation and the estimated date when plant enters stage R1.**Fig. 2.** Simulated predation-free daily soybean aphid density (aphids/plant) from Costamagna et al. (2007b) model.

SBA population increases rapidly and peaks in stage R5 before it starts to crash (Fig. 2). The simulated daily data are then combined with plant stage duration data from Fehr and Caviness (1977) to compute mean population density (\hat{S}_t) for each stage. The net SBA population growth rate per stage in the absence of natural suppression is given by

$$ng_t = \left(\frac{\hat{S}_{t+1}}{\hat{S}_t} \right) - 1 \quad (8)$$

The calculated net population growth rate is the highest during stage R1 at 5.29 (meaning that mean population density in R2 is about six times of that in R1) and drops to the lowest level of 1.13 in R4 (Table 2).

4.2. Population of natural enemies

To estimate the stage-specific net decline rate (d_t) and reproduction rate (b_t) for the natural enemy population model in Eq. (2), we use 2 years' of visual count data collected at Kellogg Biological Station Long-term Ecological Research site in Kalamazoo County of Michigan in 2003 and 2005 and perform ordinary least squares regression analysis on the following equation with robust standard errors obtained from the Huber/White estimator (Gould et al., 2006)³:

$$E[\Delta_{t+1}] = d_t \cdot NE_t + b_t \cdot (S_t \cdot NE_t) + \sum_{\omega=1} \xi_{\omega,t} \cdot Dummy_{\omega} \quad (9)$$

where E is the expectation operator, $\Delta_{t+1} = NE_{t+1} - NE_t$, and $Dummy_{\omega}$ denotes dummy variables for year and plot indexed by subscript ω . The ladybeetle species included in the quantification of natural enemy presence are *Harmonia axyridis* (multi-colored Asian ladybeetle) adult and larva, *Coccinella septempunctata* (seven-spotted

ladybeetle) adult and larva, *Coleomegilla maculata* (spotted ladybeetle) adult, *Cycloneda munda* (polished ladybeetle) adult and larva, and *Hippodamia convergens* (convergent ladybeetle) adult.

As Table 3 shows, the reproduction rate is found significant at the 90% confidence level only in stage R3, whereas the net decline rate is significant at the 95% and 99% confidence levels in R2 and R3, respectively. Estimates of the two parameters d_t and b_t conform to the theoretical expectation of negative decline rate and positive reproduction rate. Specifically, in the absence of SBA prey, the population density of natural enemies per soybean plant will decline from R2 to R3 and from R3 to R4 by 0.90 and 2.13 for each additional natural enemy in stage R2 and R3, respectively. For each SBA encountered by each additional natural enemy, the population density of natural enemies will grow from R3 to R4 by the amount of 0.002. The weak reproduction relationship between SBA and natural enemies is not uncommon because the population of generalist predators such as ladybeetles tends not to be perfectly coupled with one particular prey population (Brown, 1997). For example, the ladybeetle species included here prey upon a variety of other aphids in addition to SBA, as well as upon mites and insect eggs.

4.3. Yield response function

Data used to estimate the yield response function were collected from two field trials conducted at three Michigan sites in 2005.⁴ We fit the field trial data to the restricted form of the reformulated Cousens rectangular hyperbolic model as expressed in Eq. (4) using nonlinear least squares estimation. Maximum allowable yield loss (θ_t) is constrained to 100% in each stage.

Table 4 reports estimation results from the restricted Cousens model for each stage. SBA damage significantly affects soybean yield potential in stages R2, R3, and R4. Yield potential responds to pest damage the most in stage R3, with an estimated 0.03% of yield potential lost per SBA per plant. The proportion of yield lost per unit of pest density (η_t) in stage R2 is estimated to be negative, suggesting a “compensation” yield response relationship between pest injury and crop yield potential in R2 (Pedigo et al., 1986). Since field observations in Michigan do not support such a compensation relationship (C.D. DiFonzo, personal communication, 2007), we assume that yield potential in stage R2 is not responsive to pest injury (i.e., $\eta_2 = 0$) in the numerical exercise below.

4.4. Other parameters

Little is known about the predation rates of ladybeetle species on SBA. Here we propose an approximate range for the value of this important parameter. We suggest that scenario analysis be conducted to account for the uncertainty in the value of the parameter when applying the model to empirical studies. The biological literature suggests that mean daily aphid consumption by multi-colored Asian ladybeetle adults typically ranges from 15 to 65 aphids per day (Hukusima and Kamei, 1970; Lou, 1987; Hu et al., 1989; Lucas et al., 1997), whereas the average consumption rate for larval instars is 23 aphids per day (He et al., 1994) (see Koch, 2003 for details). Michigan field data show that in 2005, 69% of the ladybeetles are adult and larvae account for 31%. Assuming that each ladybeetle species is equally effective at consuming aphids as the multi-colored Asian ladybeetle, we obtain a range of weighted

³ Data were provided by A. Costamagna, graduate research assistant, Department of Entomology, Michigan State University at the time of the data collection.

⁴ Sites included the Bean and Beet farm in Saginaw County, the Kellogg Biological Station, and Sandusky in Sanilac County. Data were provided by C.D. DiFonzo, associate professor, Department of Entomology, Michigan State University.

Table 3
Natural enemy population growth parameters (Eq. (2)).

	Plant growth stage		
	R1	R2	R3
Net decline rate of NE (d_t)	-0.59 (0.38)	-0.90*** (0.28)	-2.13*** (0.86)
Reproduction rate of NE per prey encountered (b_t)	0.002 (0.003)	-0.0001 (0.0005)	0.002 (0.001)
Number of Observations	28	28	30
R^2	0.31	0.55	0.51

Robust standard errors in parentheses. Data: Kellogg Biological Station, Michigan, 2003 and 2005; provided by A. Costamagna, graduate research assistant, Department of Entomology, Michigan State University at the time of the data collection.

* Significant at 90%.

** Significant at 95%.

*** Significant at 99%.

Table 4
Nonlinear least squares estimation results from the dynamically reformulated Cousens rectangular hyperbolic model (Eq. (4)).

	Plant growth stage				
	R1	R2	R3	R4	R5
$E_t[y]$	37.22*** (1.95)				
η_t	0.0002 (0.001)	-0.001** (0.001)	0.0003* (0.0002)	0.0001* (0.00004)	0.0002 (0.001)
θ_t	1	1	1	1	1
Obs	43	43	43	43	43
Adj. R^2	0.92	0.93	0.93	0.94	0.94

Standard errors in parentheses. Data: multiple sites in Michigan, 2005; provided by C.D. DiFonzo, associate professor, Department of Entomology, Michigan State University.

* Significant at 90%.

** Significant at 95%.

*** Significant at 99%.

average number of aphids eaten per ladybeetle per day:

Lower bound : $15 \times 0.69 + 23 \times 0.31 = 17$ aphids/day/NE

Upper bound : $65 \times 0.69 + 23 \times 0.31 = 52$ aphids/day/NE

which gives a mean of 35 aphids/day per ladybeetle. The per stage predation rate pr_t is then computed by multiplying daily predation rate by the number of days in a given stage.

We assume that insecticide will kill 99% of the population of both SBA ($k_{S,t}$) and natural enemies ($k_{NE,t}$) upon each application during the season. This value is considered reasonable given the high efficacy of current foliar products treating SBA (C.D. DiFonzo, personal communication, 2005 and 2006). The mortality rate for natural enemies is difficult to monitor, but current products such as Lambda-cyhalothrin (Warrior with Zeon Technology®) are highly lethal to natural enemies (O'Neal, 2007).

For price and cost parameters, we use a long-term soybean trend price of $\$0.26 \text{ kg}^{-1}$ ($\$7/\text{bu}$) and a treatment cost of $\$29.63 \text{ ha}^{-1}$ ($\$12/\text{ac}$) for threshold-based integrated pest management using Warrior at 0.0947 l/ha (3.2 oz/ac). A break-down of the cost includes $\$17.28 \text{ ha}^{-1}$ ($\$7/\text{ac}$) insecticide cost, $\$4.94 \text{ ha}^{-1}$ ($\$2/\text{ac}$) for scouting, and approximately $\$7.41 \text{ ha}^{-1}$ ($\$3/\text{ac}$) for spraying (Song et al., 2006).⁵

4.5. Validation

To see how well the biological model describes the ladybeetle-SBA system, we plot model predictions of untreated SBA population densities during R1–R5 given selected natural enemy levels against field data. At Kellogg Biological Station in Hickory Corners, Michigan, the mean initial population densities were estimated at 50 aphids/plant and 1.5 NE/plant in R1 in 2003 and 70 aphids/plant and 2.5 NE/plant in R1 in 2005 (Fig. 3). At these natural enemy levels, the model's predicted SBA densities align fairly well with field observa-

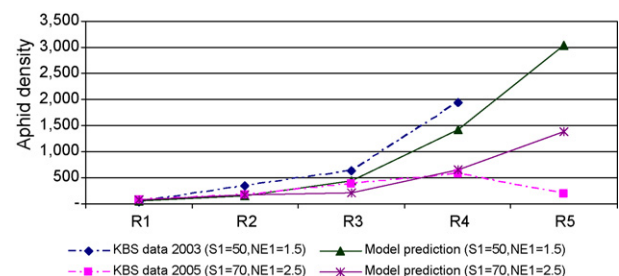


Fig. 3. Comparison of model prediction of untreated soybean aphid densities during soybean growth stages R1–R5 with field data for 2003 and 2005, Kellogg Biological Station, Michigan (field data were provided by A. Costamagna).

tions from R1 to R4 for both 2003 and 2005 data. Model predicted SBA density in stage R5, however, exceeds the field observation made in 2005 (data not available for stage R5 in 2003). Field population reduction around R5 is likely due to worsening plant condition (Costamagna et al., 2007b) and emigration of winged aphids (C.D. DiFonzo, personal communication, 2006). While the natural enemy model is estimated from field data so that the parameterization may be able to pick up some migration effect, the SBA model is developed from a simulation model parameterized from experimental data, which limits the model's ability to explicitly capture aphid migration. Fortunately, we do not expect the deviation in predicted R5-SBA density to significantly affect the treatment decision rules the model prescribes because soybean yield is not found responsive to SBA density in stage R5 (Table 4). The validity of the model results for the illustrative examples are discussed in the next section.

5. Illustrative examples

Numerical solutions to the SBA optimal management problem with respect to NEET can be achieved through an optimizing simulation approach as illustrated in Fig. 4. The approach solves the complete solution space for given initial values of S_1 , NE_1 , and $E_1[y]$ and key price and biological parameters. Since there are finite time

⁵ 1 US bushel = 60 lbs = 27.21 kg. 1 acre = 0.405 ha. 1 bu/ac soy = $27.21/0.405 = 67.2 \text{ kg/ha}$.

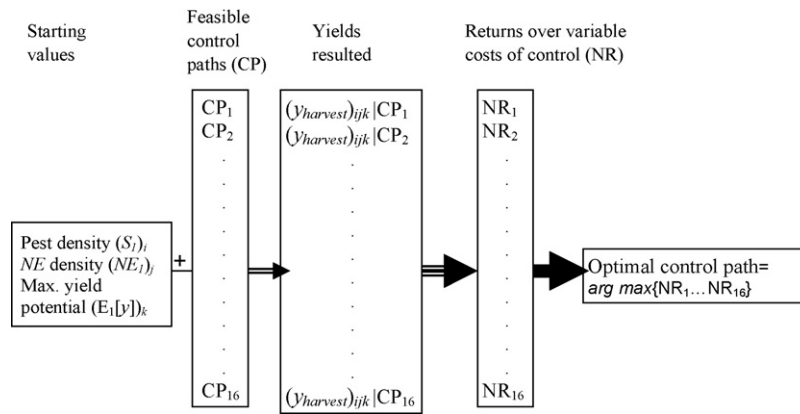


Fig. 4. Illustration of how optimal control path is reached for a given combination of initial values of pest density (S_1), natural enemy density (NE_1), and maximum yield potential ($E_1[y]$)_k.

steps, and since we know that it is optimal to perform no control in the last period R5, we can specify 16 distinct feasible control paths, each representing a unique sequence of four control choices made over the periods R1–R4 with stage R5 remaining “no control” for all 16 paths. We predict a representative soybean producer’s net return over variable costs of control for each control path and choose the one that yields the highest return as the optimal control path (optimal sequence of control decisions).

We consider a low (pest-free) yield potential level of 2690 kg/ha (40 bu/ac) and a high yield potential level of 4030 kg/ha (60 bu/ac). For each yield potential level, we present two examples of initial SBA population density in R1 along with various levels of initial natural enemy density to illustrate how the model works, assuming a daily predation rate of 35 aphids/NE (Table 5). In example 1, we consider a relatively low initial pest level of 40 aphids/plant in R1, whereas in example 2 the initial pest level is relatively high at 140 aphids/plant. Table 5 reports harvest yield, how population

densities of SBA and natural enemies advance from R1 to R5, and how the optimal control path changes when initial natural enemy density increases from 0 to 4 NE/plant in R1, a range that covers the estimated values from our Michigan field data. For instance, the population densities of ladybeetles are estimated at 1.3/plant and 2.3/plant in stage R1 at Kellogg Biological Station, Michigan in 2003 and 2005, respectively.

The optimal control paths call for decreasing frequency of spraying as the initial presence of natural enemies increases for given pest infestation level. The NEET and producer return over variable costs of control are sensitive to natural enemy numbers. For instance, regardless of initial yield potential levels, the pest density for spraying once in stage R1 is $S_1 = 40$ aphids/plant if $NE_1 \leq 1$ /plant. But if NE_1 is greater than 1 per plant, there is no need to spray for the same initial pest density. At the high initial yield potential level of 4030 kg/ha, the NEET for spraying twice in stage R1 and R2 is $S_1 = 140$ aphids/plant if natural enemies are not present. However, if

Table 5

Natural enemy-adjusted economic threshold (NEET) illustration for two initial soybean aphid densities ($S_1 = 40$ and 140 aphids/plant) at two initial maximum yield potential levels ($E_1[y] = 2688$ kg/ha and $E_1[y] = 4032$ kg/ha), given four initial values of NE_1 (0–4 NE/plant) and daily predation rate of 35 aphids/NE.

Natural enemy density at R1 (NE /plant)	Pest density (S_t) (aphids/plant)					Crop yield y_{harvest} (kg/ha)	Return over variable costs of control (\$/ha)	Optimal control path
	R1	R2	R3	R4	R5			
Initial maximum yield potential = 2688 kg/ha (low)								
Low initial pest density ($S_1 = 40$ aphids/plant)								
0	40	2.5	15.5	51.9	110.6	2662	646	Spray in R1
1	40	1.5	5.5	18.2	38.8	2679	650	Spray in R1
2	40	41.6	0	0	0	2688	683	No Spray
3	40	0	0	0	0	2688	683	No Spray
4	40	0	0	0	0	2688	683	No Spray
High initial pest density ($S_1 = 140$ aphids/plant)								
0	140	8.8	54.1	181.5	387.2	2598	630	Spray in R1
1	140	7.8	44.2	147.8	315.3	2614	634	Spray in R1
2	140	6.7	34.2	114.1	243.5	2631	638	Spray in R1
3	140	5.7	24.3	80.4	171.6	2647	642	Spray in R1
4	140	4.6	14.3	46.7	99.7	2664	646	Spray in R1
Initial maximum yield potential = 4032 kg/ha (high)								
Low initial pest density ($S_1 = 40$ aphids/plant)								
0	40	2.5	15.5	51.9	110.6	3992	983	Spray in R1
1	40	1.5	5.5	18.2	38.8	4019	990	Spray in R1
2	40	41.6	0	0	0	4032	1025	No Spray
3	40	0	0	0	0	4032	1025	No Spray
4	40	0	0	0	0	4032	1025	No Spray
High initial pest density ($S_1 = 140$ aphids/plant)								
0	140	8.8	0.5	1.8	3.9	4032	963	Spray in R1 and R2
1	140	7.8	44.2	147.8	315.3	3924	966	Spray in R1
2	140	6.7	34.2	114.1	243.5	3945	973	Spray in R1
3	140	5.7	24.3	80.4	171.6	3972	978	Spray in R1
4	140	4.6	14.3	46.7	99.7	3998	985	Spray in R1

Table 6

Summary of sensitivity analysis results (initial yield potential = 2688 kg/ha, daily predation rate = 35 aphids/NE).

Cases	$S_1 = 40$ aphids/plant		$S_1 = 140$ aphids/plant	
	Optimal control paths	Return over variable costs of control	Optimal control paths	Return over variable costs of control
ng_t up 5%	–	–	–	–
ng_t down 5%	–	–	–	–
$k_{S,t}$ down 5%	“Spray R1 + R2” replaces “Spray R1” if $NE_1 = 0$; “Spray R2” replaces “Spray R1” if $NE_1 = 1$	4% decrease if $NE_1 = 0$, 3% of decrease if $NE_1 = 1$	“Spray R1 + R2” replaces “Spray R1” for all levels of NE_1	3–5% decrease for all levels of NE_1
$k_{NE,t}$ down 5%	–	–	–	1–3% increase if $NE_1 > 0$
η_3 up 1 S.D.	–	–	–	–
η_3 down 1 S.D.	–	–	–	–
η_4 up 1 S.D.	–	–	–	–
η_4 down 1 S.D.	–	–	–	–
b_3 up 1 S.D.	–	–	–	–
b_3 down 1 S.D.	–	–	–	–
d_2 up 1 S.D.	–	–	–	–
d_2 down 1 S.D.	–	–	–	–
d_3 up 1 S.D.	–	–	–	–
d_3 down 1 S.D.	–	–	–	–
Price up 5%	–	5% increase	–	5% increase
Price down 5%	–	5% decrease	–	5% decrease
Cost up 5%	–	–	–	–
Cost down 5%	–	–	–	–

“–” represents change of less than 1%. See Tables 3 and 4 for standard deviations (S.D.).

$NE_1 \geq 1$ /plant and $S_1 = 140$ aphids/plant, the NEET calls for spraying only once in R1. Although the resultant harvest yield is smaller than in the two-spray case (i.e., $NE_1 = 0$ /plant and $S_1 = 140$ aphids/plant), producers gain from insecticide application savings due to natural enemies and realize higher economic returns, ranging from almost \$3/ha (if $NE_1 = 1$ /plant) to \$22/ha (if $NE_1 = 4$ /plant). At the specified soybean output price and costs of pest control, the initial yield potential affects the choice of treatment strategy, because the human manager balances the benefit of spraying against the costs. At the low initial yield potential level of 2690 kg/ha, the NEET calls for spraying only once as opposed to twice for $S_1 = 140$ aphids/plant if natural enemies are absent.

The illustrative examples demonstrate that at a high infestation rate of $S_1 = 140$ aphids/plant, the presence of a single natural enemy per plant in R1 results in increased return to the farmer of \$3/ha if treatment decisions take account of natural enemies, given a predation rate of 35 aphids/NE and initial yield potential of 4030 kg/ha. The economic gain increases to \$10 ha⁻¹ when there are two natural enemies per plant (instead of zero), at the same infestation level of 140 aphids/plant. When combined with social and environmental benefits of spray frequency reduction, the value of adopting the NEET insecticide management approach goes beyond private economic gains.

Informal assessment of the validity of the NEET bioeconomic model highlights one notable respect in which its recommendations diverge from farmer practice. The simulation model finds that spraying twice (once each in R1 and R2) is the optimal control path for the initial pest density of 140 aphids/plant when no natural enemies are present and the crop has a relatively high pest-free yield potential. By contrast, farmers and field entomologists tend to wait longer between sprays. One reason may be that additional low-level natural control is present in the field from species other than the ladybeetles modeled here, reducing the need for insecticide control. However, we should also emphasize that the two-spray recommendation results from an extraordinary confluence of initial conditions. The initial density of 140 aphids/plant represents an extremely severe infestation scenario as compared to the average aphid levels observed in Michigan R1-stage fields, which, together with the unusual absence of natural enemies and relatively high initial yield potential, triggers the NEET of “Spray in R1 and R2”.

Nevertheless, two limitations of the current NEET model should be taken into account when assessing the model results. First, the model does not capture the residual effect of insecticides, meaning that surviving insect population as modeled is not constrained from bouncing back immediately, potentially requiring another spray in the following stage to contain the infestation. Second, the model does not include the mobility of winged aphids or their natural enemies, an important but also rather difficult aspect of the aphid-ladybeetle system to model given the current monitoring capacity.

5.1. Sensitivity analysis

To assess the effect of uncertainty associated with the parameter values and assumptions, we perform a sensitivity analysis on selected, key parameters by changing parameters one at a time for a scenario in which daily predation rate is 35 aphids/NE and initial yield potential is 2690 kg/ha. A total of 18 cases are examined (Table 6). Parameters estimated from field data are varied by one standard deviation, whereas parameters that are assumed ($k_{S,t}$ and $k_{NE,t}$) or derived from other studies (output price and control costs) are varied by 5%, respectively.

We look at two aspects of changes due to varying parameters: choice of optimal control paths and values of return over variable costs of control. The choice of optimal control paths is not sensitive to parameter values and assumptions except for the mortality rate of SBA due to insecticides ($k_{S,t}$).⁶ The analysis shows that a lower efficacy rate of SBA treatment would prompt farmers to spray more frequently if natural enemies are not present or delay spraying if natural enemy level is low ($NE_1 = 1$ /plant) at relatively low initial aphid density ($S_1 = 40$ aphids/plant). When $NE_1 > 1$ /plant, however, reducing the mortality rate of SBA due to insecticides does not change the optimal control paths, i.e., “No Spray” is maintained. At relatively high aphid density ($S_1 = 140$ aphids/plant), and regardless of the levels of natural enemies, reducing the mortality rate of SBA by 5% from the assumed 99% level triggers spraying in both R1 and

⁶ Note that the sensitivity analysis excludes the cases for increasing the values of $k_{S,t}$ and $k_{NE,t}$ because the original assumption of 99% kill rate for each is already close to one.

R2 instead of just once in R1. The assumed SBA mortality rate also affects the return over variable costs of pest control, with a reduction of 5% in $k_{S,t}$ reducing returns by 3–4% if $S_1 = 40$ aphids/plant and $NE_1 \leq 1$ /plant and by 3–5% if $S_1 = 140$ aphids/plant. At the relatively high initial pest density of $S_1 = 140$, the model is moderately sensitive to assumptions on the collateral damage of insecticide on natural enemy population ($k_{NE,t}$) in predicting returns over variable costs of control (up to 3%). Modeled economic returns are proportionately sensitive to changes in crop price, but not to changes in pest control costs.

6. Discussion and conclusion

The control of pests by their natural enemies represents an important ecosystem service that has the potential to mitigate pest control costs both to private producers and to society. These services, however, are often ignored in pest management threshold decision rules. Profitability and efficiency of pest management can be improved by incorporating natural pest control services into pest management decision making.

Focusing on private economic incentives, this study develops an intra-seasonal, dynamic bioeconomic model, the first explicitly to take into account the effect of natural pest control services for a dynamic economic pest control threshold—the natural enemy-adjusted economic threshold (NEET). The model is applied to the case of soybean aphid management in Michigan. As illustrated by the numerical examples, such a natural enemy-adjusted threshold is likely to lead to fewer recommendations for insecticide use than naïve models that ignore natural enemies, resulting in less insecticide use, while maintaining profitability for farmers. While the current model focuses on pest management decision rules, this general modeling approach can be extended to the management of other regulating ecosystem services (e.g., pollination and soil fertility) that are essential to the functioning of agro-ecosystems but are also driven by human management.

For the specific case of soybean aphid, by incorporating the role of natural enemies in suppressing aphid population growth the model developed here improves upon the prior bioeconomic model of Olson and Badibanga (2005). Without accounting for natural enemies, they found that a threshold of three aphids per plant was the dominant strategy. They concluded that early and frequent treatments (as many as four) may be needed when aphids colonize early and enjoy good reproductive weather. By contrast, the NEET threshold was validated at moderate natural enemy population densities around 140 aphids per plant, much closer to the multi-state field research-based estimate of an economic threshold of 273 aphids per plant (Ragsdale et al., 2007), which does not account for the opportunity cost of insecticide use, nor does it specify the timing of application or field circumstances in terms of the presence of natural enemies.

The current model can benefit from improvement in three dimensions. First, because the species composition of natural enemy communities tends to vary from field to field, weighting factors could be developed to account for the different suppression levels associated with different natural enemy species. Second, refining and validation could yield better estimates of certain biological parameters such as predation rate, net decline rate and reproduction rate of natural enemies, and mortality rates of both pests and natural enemies by insecticides. Obtaining better parameter estimates will require new experimental designs that allow observation of biological effects by plant growth stage. In addition, the model can be strengthened by including the residual effect of insecticides and the migration behavior of insects, with the capacity of such expansion closely depending on improved data and ecological understanding of the system. Third, given that random effects such as weather play an important role in driving the underly-

ing biological processes (e.g., insect population dynamics and crop growth), introducing stochastic processes for Monte Carlo simulation would enhance the current deterministic model.

Several external conditions should be met for the NEET model to become a practical decision support tool. The pressing challenge is to develop cheap and easy ways to collect site-specific pest and natural enemy data. The prospect for implementation of the model may be particularly bright for pests whose natural enemies are few in species and easily identifiable. The current model could be used by agricultural advisors to generate easy-to-use charts or lookup tables for use as decision tools.

By describing biological processes and interactions and predicting their responses to management decisions, bioeconomic modeling can improve management of agro-ecosystems (King et al., 1993). The multi-stage dynamic optimization model presented here demonstrates how pest suppression by natural enemies can be incorporated into a natural enemy-adjusted economic threshold for insecticide use that can maintain or even increase profitability and reduce farmers' dependence on insecticides. The model can be used to conduct a wide variety of analyses including (i) identifying dynamically optimal spray strategies, (ii) estimating the implied economic value of natural control services, and (iii) developing alternative mechanisms such as habitat management to enhance natural pest control services and eventually to significantly reduce the use of chemical insecticides. Furthermore, with the incorporation of inter-year carry-over factors, such as overwintering of pests and natural enemies, the current model can contribute to building multi-year models for studying long-term pest management.

Acknowledgements

For constructive comments, the authors thank D.A. Landis, A. Costamagna, W. van der Werf, R. Horan, R. Myers, M.M. Gardiner, C.D. DiFonzo, M. Brewer, and two anonymous reviewers. The authors acknowledge financial support from the "KBS-LTER Project: Long-term Ecological Research in Row-crop Agriculture" of the National Science Foundation (NSF #0423647) and access to biological data collected under the project "Soybean Aphid in the North Central U.S.: Implementing IPM at the Landscape Scale" (USDA-CSREES 2004-04185). This research was conducted while the senior author was a Ph.D. candidate at Michigan State University.

References

- Bellman, R., 1957. Dynamic Programming. Princeton University Press, Princeton, NJ.
- Bianchi, F.J.J.A., van der Werf, W., 2004. Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes. *Ecol. Model.* 171, 177–193.
- Bommarco, R., Firlie, S.O., Ekbom, B., 2007. Outbreak suppression by predators depends on spatial distribution of prey. *Ecol. Model.* 201, 163–170.
- Bor, Y.J., 1995. Optimal pest management and economic threshold. *Agric. Syst.* 49, 113–133.
- Brown, G.C., 1997. Simple models of natural enemy action and economic thresholds. *Am. Entomol.* 43, 117–124.
- Calkins, C.O., 1983. Research on exotic pests. In: Wilson, C.L., Graham, C.L. (Eds.), *Exotic Plant Pests and North American Agriculture*. Academic Press, New York, NY, pp. 321–359.
- Costamagna, A.C., Landis, D.A., 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecol. Appl.* 16, 1619–1628.
- Costamagna, A.C., Landis, D.A., DiFonzo, C.D., 2007a. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecol. Appl.* 17, 441–451.
- Costamagna, A.C., van der Werf, W., Bianchi, F.J.J.A., Landis, D.A., 2007b. An exponential growth model with decreasing r captures bottom-up effects on the population growth of *Aphis glycines* Matsumura (Hemiptera: Aphididae). *Agric. Forest Entomol.* 9, 1–9.
- Costamagna, A.C., Landis, D.A., Brewer, M.J., 2008. The role of natural enemy guilds in *Aphis glycines* suppression. *Biol. Control.* 45, 368–379.
- Cousens, R., 1985. A simple model relating yield loss to weed density. *Ann. Appl. Biol.* 107, 239–252.

- DiFonzo, C.D., Hines, R., 2002. Soybean Aphid in Michigan: Update from the 2001 Season. Michigan State University Extension Bulletin E-2748, East Lansing, MI.
- Fehr, W.R., Caviness, C.E., 1977. Stages of Soybean Development. Iowa State University Special Report 80, 1–12, Ames, IA.
- Fox, T.B., Landis, D.A., 2002. Impact of habitat management on generalist predators of the soybean aphid, *Aphis glycines* Matsumura. Paper presented at the First International Symposium on Biological Control of Arthropods, Honolulu, HI, 13–18 January.
- Fox, T.B., Landis, D.A., Cardoso, F.F., DiFonzo, C.D., 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33, 608–618.
- Gould, W., Pitblado, J., Sribney, W., 2006. Theory and practice. In: Maximum Likelihood Estimation with Stata, 3rd ed. Stata Press, College Station, TX.
- Hall, D.C., Norgaard, R.B., 1973. On the timing and application of pesticides. *Am. J. Agric. Econ.* 55, 198–201.
- Harper, J.K., Mjelde, J.W., Rister, M.E., Way, M.O., Drees, B.M., 1994. Developing flexible economic thresholds for pest management using dynamic programming. *J. Agric. Appl. Econ.* 26, 134–147.
- He, J.L., Ma, E.P., Shen, Y.C., Chen, W.L., Sun, X.Q., 1994. Observations of the biological characteristics of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *J. Shanghai Agric. Coll.* 12, 119–124.
- Headley, J.C., 1972. Defining the economic threshold. In: Pest Control Strategies for the Future. National Academy of Sciences, Washington, D.C., pp. 100–108.
- Hu, Y.S., Wang, Z.M., Ning, C.L., Pi, Z.Q., Gao, G.Q., 1989. The functional response of *Harmonia* (Leis) axyridis to their prey of *Cinara* sp. *Natural Enemies Insects* 11, 164–168.
- Hukusima, S., Kamei, M., 1970. Effects of Various Species of Aphids as Food on Development, Fecundity and Longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), vol. 29. Research Bulletin of the Faculty of Agriculture, Gifu University, pp. 53–66.
- Jameson-Jones, S., 2005. Insect and Insect Management: Soybean Aphid. University of Minnesota Extension. <http://www.soybeans.umn.edu/crop/insects/aphid/aphid.htm> (accessed May 25, 2005).
- Kaiser, M.E., Noma, T., Brewer, M.J., Pike, K.S., Vockeroth, J.R., Gaimari, S.D., 2007. Hymenopteran parasitoids and dipteran predators found using soybean aphid after its midwestern United States invasion. *Ann. Entomol. Soc. Am.* 100, 196–205.
- Kamien, M.I., Schwartz, N.L., 1981. Dynamic Optimization: The Calculus of Variations Optimal Control in Economics and Management. North-Holland, New York, NY.
- Koch, R.L., 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and nontarget impacts. *J. Insect Sci.* 3, 32–47.
- King, R.P., Lybecker, D.W., Regmi, A., Swinton, S.M., 1993. Bioeconomic models of crop production systems: design, development, and use. *Rev. Agric. Econ.* 15, 389–401.
- Krishna, V.V., Byju, N.G., Tamizhenian, S., 2003. Integrated pest management in Indian agriculture: a developing economic perspective. In: Radcliff, E.B., Hutchison, W.D. (Eds.), IPM World Textbook. University of Minnesota, St. Paul, MN.
- Landis, D.A., Fox, T.B., Costamagna, A.C., 2004. Impact of multicolored Asian Lady Beetle as a biological control agent. *Bull. Entomol. Soc. Am.* 50, 153–154.
- Lotka, A.J., 1925. Elements of Physical Biology. Williams & Wilkins Co., Baltimore, MD.
- Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *Bioscience* 56, 311–331.
- Lou, H.H., 1987. Functional response of *Harmonia axyridis* to the density of *Rhopalosiphum prunifoliae*. *Natural Enemies Insects* 9, 84–87.
- Lucas, E., Coderre, D., Vincent, C., 1997. Voracity and feeding preferences of two aphidophagous coccinellids on *Aphis citricola* and *Tetranychus urticae*. *Entomol. Exp. Appl.* 85, 151–159.
- Mills, N.J., Getz, W.M., 1996. Modelling the biological control of insect pests: a review of host-parasitoid models. *Ecol. Model.* 92, 121–143.
- Musser, F.R., Nyrop, J.P., Shelton, A.M., 2006. Integrating biological and chemical controls in decision making: European corn borer (Lepidoptera: Crambidae) control in sweet corn as an example. *J. Econ. Entomol.* 99, 1538–1549.
- National Agricultural Statistics Service (NASS), 2007. Agricultural Chemical Usage Database. U.S. Department of Agriculture. <http://www.pestmanagement.info/nass/>.
- Naylor, R., Ehrlich, P., 1997. Natural pest control services and agriculture. In: Daily, G. (Ed.), Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, D.C., pp. 151–174.
- Nielsen, C., Hajek, A.E., 2005. Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), population by existing natural enemies in New York State, with emphasis on entomopathogenic fungi. *Environ. Entomol.* 34, 1036–1047.
- North Central Pest Management Center (NCPMC), 2005. National Pest Alert: Soybean Aphid. U.S. Department of Agriculture. http://www.ncpmc.org/alerts/soybean_aphid.cfm.
- Nyrop, J.P., Binns, M.R., van der Werf, W., Kovach, J., 1994. Cascading tripartite binomial classification plans to monitor European red mite (Acari Tetranychidae) through a season; development and evaluation of a new methodology for pest monitoring. *Exp. Appl. Acarol.* 18, 123–153.
- Olson, K., Badibanga, T., 2005. A bioeconomic model of the soybean aphid treatment decision in soybeans. Paper presented at American Agricultural Economics Association Annual Meeting, Providence RI, 24–27 July. <http://agecon.lib.umn.edu/cgi-bin/pdf.view.pl?paperid=16358&ftype=pdf>.
- O'Neal, M., 2007. Practices to Conserve and Use Natural Enemies in Soybean Aphid IPM. Distance education short course, Managing Soybean Aphids in 2007: How Will Biological Control Contribute? North Central Soybean Research Program, March 6, 2007.
- Pedersen, P., 2004. Soybean Growth and Development. Iowa State University Extension publication PM 1945, Ames, IA.
- Pedigo, L.P., Hutchins, S.H., Hingle, L.G., 1986. Economic injury levels in theory and practice. *Ann. Rev. Entomol.* 31, 341–368.
- Ragsdale, D.W., McCornack, B.P., Venette, R.C., Potter, B.D., MacRae, I.V., Hodgson, E.W., O'Neal, M.E., Johnson, K.D., O'Neil, R.J., DiFonzo, C.D., Hunt, T.E., Glogozia, P.A., Cullen, E.M., 2007. Economic threshold for soybean aphid (Hemiptera: Aphididae). *J. Econ. Entomol.* 100, 1258–1267.
- Risk Avoidance and Mitigation Program project on "Soybean Aphid in the North Central U.S.: Implementing IPM at the Landscape Scale" (RAMP), 2006. Project Update, vol. 2–2 (June). http://www.soybeans.umn.edu/crop/insects/aphid/aphid_ramp.htm.
- Rutledge, C.E., O'Neil, R.J., Fox, T.B., Landis, D.A., 2004. Soybean aphid predators and their use in IPM. *Ann. Entomol. Soc. Am.* 97, 240–248.
- Sharov, A.A., 1996, 1997, 1999. Quantitative Population Ecology On-line Lectures, vol. 2006, Virginia Tech University. <http://www.gypsymoth.ento.vt.edu/~sharov/PopEcol/popecol.html>.
- Smith, G.S., Pike, D., 2002. Soybean Pest Management Strategic Plan. U.S. Department of Agriculture North Central Region Pest Management Center and United Soybean Board.
- Song, F., Swinton, S.M., DiFonzo, C.D., O'Neal, M., Ragsdale, D.W., 2006. Profitability Analysis of Soybean Aphid Control Treatments in Three North-Central States. Department of Agricultural Economics Staff Paper No. 2006-24, Michigan State University, East Lansing, MI. <http://agecon.lib.umn.edu/cgi-bin/pdf.view.pl?paperid=23574&ftype=pdf>.
- Stern, V.M., Smith, R.F., van den Bosch, K., Ragen, K.S., 1959. The integrated control concept. *Hilgardia* 29, 81–101.
- Talpaz, H., Borosh, I., 1974. Strategy for pesticide use: frequency and applications. *Am. J. Agric. Econ.* 6, 769–775.
- Thomas, M.B., 1999. Ecological approaches and the development of 'truly integrated' pest management. *Proc. Natl. Acad. Sci. U.S.A.* 96 (May), 5944–5951.
- Thompson, A., German, T., 2003. Soybean aphid and virus incidence in snap beans. Paper presented at Wisconsin Fertilizer, Aglime, and Pest Management Conference, Madison, WI. <http://www.soils.wisc.edu/extension/wfapmc/>.
- van der Werf, W., Nyrop, J.P., Binns, M.R., Kovacs, J., 1997. Adaptive frequency classification: a new methodology for pest monitoring, and its application to European red mite (*Panonychus ulmi*, Acari Tetranychidae). *Exp. Appl. Acarol.* 21, 431–462.
- Volterra, V., 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Mem. R. Accad. Naz. dei Lincei. Ser. VI* 2, 31–113.
- Williams, I.S., van der Werf, W., Dewar, A.M., Dixon, A.F.G., 1999. Factors affecting the relative abundance of two coexisting aphid species on sugar beet. *Agric. Forest Entomol.* 1, 119–125.
- Zacharias, T.P., Grube, A.H., 1986. Integrated pest management strategies for approximately optimal control of corn rootworm and soybean cyst nematode. *Am. J. Agric. Econ.* 68, 704–715.