A Natural Enemies-Adjusted Economic Threshold for Pest Control

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Abstract

The control of pests by their natural enemies represents an important ecosystem service that maintains the stability of agroecosystems and has the potential to mitigate pest control costs both to private producers and to society. Extending the "economic threshold" concept, this paper proposes a "natural enemies-adjusted economic threshold" for pesticide use that takes into account the implicit cost of injury to natural enemies. By explicitly accounting for natural pest suppression, the natural enemies-adjusted economic threshold can potentially make pest management more cost-effective while reducing dependence on toxic insecticides. The threshold is illustrated via an intra-seasonal dynamic bioeconomic model of soybean aphid management in Michigan, USA. A dynamic optimization model quantifies the economic value of natural suppression to optimal pest control. The results highlight the importance of assessing both pest and natural enemy populations in making insecticide application decisions and accounting for the opportunity cost of insecticide use due to its collateral damage effect on natural enemies.We recommend that future research move beyond insecticide thresholds to develop guidelines for explicit management of habitat for the natural enemies of agricultural pests.

I. Introduction

The control of pests by their natural enemies represents an important ecosystem service that maintains the stability of agricultural systems and has the potential to mitigate pest control costs (Naylor and Ehrlich, 1997; Losey and Vaughan, 2006). In agro-ecosystems where natural enemies are relatively abundant, natural enemies play a key role in regulating pest population that may suppress it below the economic injury level. In addition to the well-documented limitations (e.g., pest resistance) and health and environmental risks (Naylor and Ehrlich, 1997; Thomas, 1999; Heimpel et al., 2004), untimely application of broad-spectrum insecticides can decimate natural enemy populations. Destruction of the predator-prey (or parasitoid-host) balance can exacerbate existing pest problems or even trigger the emergence of new pests (Calkins, 1983; Naylor and Ehrlich, 1997; Krishna et al., 2003). Focusing on the predator-pest complex of natural enemy communities and the soybean aphid (*Aphis glycines*, Matsumura), this study develops an intra-seasonal bioeconomic model to assess how pest suppression by natural enemies contributes to optimal insecticide strategies.

  Soybean aphid (SBA) is an invasive species that was first discovered in the United States in 2000 and has since spread to 21 U.S. states and south-central Canada (Landis, Fox and Costamagna, 2004). Not only is SBA capable of causing extensive damage to soybean yield (DiFonzo and Hines, 2002), but SBA outbreaks are also correlated with dramatic increases in virus incidence in vegetable crops (Alleman et al., 2002; Stevenson and Grau, 2003; Thompson and German, 2003; Fang et al., 1985; RAMP, 2006). Having been identified as one of the key drivers of insecticide use in the region (Smith and Pike, 2002), SBA was responsible for insecticide spray on 80% of

soybean acreage in Michigan and 50% Minnesota during the 2005 season (RAMP, 2006), compared with none before SBA was found in the U.S. in 1999 (NASS, 2000). The introduction of SBA into North America fundamentally changed insect management and insecticide use patterns in soybean in the Midwest (RAMP, 2006) and has challenged pest managers to rapidly develop insights to protect a major commodity in an environmentally responsible manner (Rutledge et al., 2004).

Existing natural enemies play a key role in suppressing SBA populations (Fox et al., 2004; Aponte and Calvin, 2004; Rutledge et al., 2004; Landis, Fox and Costamagna, 2004; Costamagna and Landis 2005; Berg 1997), including 22 predator species (Rutledge et al. 2004), 6 parasitoid species (Kaiser et al., 2005), and several species of fungi that cause disease in aphids (Nielsen and Hajek, 2005). Studies show that existing natural enemy communities contribute to SBA population regulation in Michigan soybeans (Fox and Landis, 2002; Rutledge et al., 2004) and under some conditions result in complete economic control (Fox, 2002). However, most insect natural enemies are susceptible to the major insecticides used to treat SBA[1]. While current recommendations generally lean towards using insecticides as the last resort after appropriate assessment of the situation in each field (Smith and Pike, 2002; NSRL, 2002; NCPMC, 2005), no applicable decision support has been offered to pest managers to capitalize upon the pest regulation ecosystem service supplied by ambient natural enemies.

To date, the economic benefit of biological pest control[2] has chiefly been assessed through *ex post* impact assessments (Hill and Greathead, 2000), with little economic

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[1] Christine DiFonzo, Associate Professor, Department of Entomology, Michigan State University, personal communications, October 4, 2005 and March 2, 2006.
[2] Most economic benefit estimates have been done for "classical biological control," which involves the artificial introduction or massive release of natural enemies (see Hill and Greathead, 2000 for example studies). This paper focuses instead on natural biological control, which involves the effect of ambient natural enemy populations.

research on the interaction between natural pest predation or parasitism and human pest management decisions. Insecticide application can affect the path along which the natural enemy-pest system approaches equilibrium over time, the likelihood of SBA population suppression below an economic injury level, and the resulting expected net returns and insecticide exposure of soybean producers. Olson and Badibanga (2005) used a bioeconomic model to conclude that "spraying 4 times using the 3 aphids/plant threshold" was the most profitable treatment among scenarios evaluated. One hypothesis for why their threshold for spraying was 98% below the prevailing North Central states extension recommendation of 250 SBA/plant (Ragsdale et al., 2006) is that the extension threshold implicitly accounts for natural pest control, whereas the Olson and Badibanga model did not.

The bioeconomic model presented here makes two contributions to estimating *ex ante* optimal strategies for pest management: i) it models an ambient natural enemy population in a dynamic natural enemy-pest interaction system, and ii) it explicitly accounts for mortality effects of major SBA insecticides on natural enemies. Extending the traditional concept of economic threshold for chemical treatment[3], this study offers a two-dimensional concept of "natural enemies-adjusted economic threshold". We develop the new threshold on a cumulative population day basis, which addresses both the intensity and duration of the presence and interactions of biological agents. Despite having been advocated in the entomological literature (e.g., Potter and Hansen, 2003), none of the existing recommendations of economic threshold are based on cumulative population days. Empirically solved with a dynamic optimizing simulation model, the

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[3] Economic threshold refers to the population density at which control measures should be initiated to prevent an increasing pest population from reaching the economic injury level (Pedigo et al., 1986).

natural enemies-adjusted economic threshold demonstrates that the optimal control

threshold depends not only on the pest population, but also on the population of ambient

natural enemies. In pest management, dynamic optimization has been used to solve for

optimal application rate or decision alternatives (e.g., Zacharias, Liebman and Noel,

1986; Pandey and Medd, 1991; Taylor and Burt, 1984; Zacharias and Grube, 1986) and

economic thresholds (e.g., Harper et al., 1994; Saphores, 2000). However, no studies that

we know of have explicitly included natural pest control services in optimizing

insecticide strategies. The model is developed using data from Michigan collected under

a multi-state soybean aphid USDA Risk Assessment and Mitigation Program (RAMP)

project on "Soybean Aphid in the North Central U.S.: Implementing IPM at the

Landscape Scale." Model results will compare optimal insecticide management strategies

with and without accounting for the presence of natural enemies of SBA and among

various levels of natural enemy population. The results will be used to make a

preliminary estimate of the value of natural predation as an ecosystem service in the

natural enemies-pest complex.

    Following this introduction section, we introduce the theoretical bioeconomic

model in section 2. In section 3, we construct an empirical dynamic optimizing

simulation model and derive numerical solutions to the single season optimization

problem. Section 4 reports findings from a sensitivity analysis of key parameters. Finally,

we identify applications for the effects of natural enemy populations on optimal SBA

control and suggest future research directions.

II. Bioeconomic model

Agricultural production processes are dynamic in nature, influenced by random effects, and based upon biological principles (Csáki, 1985). This study develops a deterministic plant growth stage-based bioeconomic model for SBA management. Soybeans are most susceptible to SBA damage in the five earlier reproductive stages of plant growth (Jameson-Jones, 2005; NCSRP, 2004). We therefore define management stages in relation to the first five reproductive stages of soybean growth, R1 through R5 (denoted by t and $t=1,2,3,4,5$). Because yield damage is influenced by both the intensity and duration of SBA infestation (Potter and Hansen, 2003), we measure pest pressure in a given stage in cumulative SBA population days. To be consistent, the natural enemy population is measured in cumulative units as well. Cumulative population variables approximate continuous processes in discrete time, thus providing a more accurate picture of the biological states than point-valued discrete variables[4].

  Farmers tend not to practice variable rate pesticide application due both to applicator time constraints and label rates being required for manufacturers to guarantee efficacy. Therefore, we define the control decision 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 during period t). We assume that no more than one spray may occur in each stage and that the projected yield potential in stage R5 is carried through to harvest so that SBA control is only meaningful during R1 to R4.

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[4] Note that since cumulative population days are observed at the end of as opposed to the beginning of each period, without loss of generality, we define the time index-subscripted variables somewhat unconventionally as states evaluated at the end of a given stage t or actions taken immediately after observing the states at the end of stage t. Similarly, parameters with subscript t denote effects or changes occurred between two consecutive observations, i.e., since the end of stage t to the end of stage $t+1$.

Soybean aphid population

The dynamics of SBA population in soybean is given by:

$$I_{t+1} = \max\{0, \ (I_t - k_{I,t} \cdot x_t \cdot I_t) + ng_t \cdot (I_t - k_{I,t} \cdot x_t \cdot I_t) - pr \cdot (NE_t - k_{NE,t} \cdot x_t \cdot NE_t)\} \quad (1)$$

($t=1,2,3,4$)

where I_{t+1} denotes cumulative population days of SBA at the end of stage $t+1$, NE_t denotes cumulative population days of natural enemies at the end of stage t, $k_{I,t}$ and $k_{NE,t}$ represent mortality rate of SBA and natural enemies due to insecticide application, respectively, ng_t denotes net growth rate of SBA population in the absence of "outside" regulation, and pr is the average predation rate per NE per stage.

Costamagna et al. (2006) have developed and validated a daily-based SBA growth model that describes population growth in the absence of natural suppression, based on Williams et al. (1999)'s discrete exponential population growth model. Parameterized using predator exclusion cage data collected in soybean fields at the Kellogg Biological Station (KBS) in Gull Lake, Michigan, the model is robust against variability within and between experiments (Costamagna et al., 2006). SBA *daily* population data for each of the five reproductive stages (R1 to R5) (plant phenology data collected in the same KBS site (Table 2)) are first simulated from the Costamagna et al. (2006) model, based on which we compute *cumulative* SBA population days for each stage, denoted by $\hat{I}_t$ ($t=1,2,3,4,5$). The net growth rates in the absence of natural suppression are then calculated from:

$$ng_t = (\hat{I}_{t+1} - \hat{I}_t)/\hat{I}_t \qquad (2)$$

Aggregate natural enemy population

Population modeling of natural enemies has been rare in the economic literature with a few exceptions that include population dynamics of some particular species introduced to regulate pests, for which effective natural regulation typically does not exist in the original system (e.g., Reichelderfer and Bender, 1979; Zavaleta and Ruesink, 1980; Boggess et al., 1985). Existing natural enemies that attack SBA are abundant in both quantity and number of species in the field, jointly contributing to population regulation in soybeans (Fox and Landis, 2002). Since viable biological control options are not available at present[5], this study focuses on insecticidal control, taking into account natural suppression and the non-target effect of insecticide on natural enemies[6].

   We treat natural enemies of SBA as an aggregate assemblage for two main considerations. First, the dominant regulating species vary both temporally and spatially. For instance, in Michigan, generalist predators *Coccinella septempunctata* (seven-spotted lady beetle) and *Harmonia axyridis* (multi-colored Asian lady beetle) provide sequential pest suppression mid season through harvest, with seven-spotted lady beetle dominating the mid season and multi-colored Asian lady beetle dominating the late season (McKeown, 2003). Data collected at the Kellogg Biological Station (KBS) Long-term Ecological Research (LTER) site show that the high populations of seven-spotted lady beetle may have aided in delaying SBA colonization of the KBS site as compared to other areas of the state (McKeown, 2003). The spread of SBA later in the season was subsequently hindered further by the high prevalence of multi-colored Asian lady beetle

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[5] Douglas Landis, Professor, Department of Entomology, Michigan State University, personal communication, September 27, 2005.
[6] Despite an ongoing trial of massive release of selected parasitoid species to treat SBA in Minnesota (Heimpel et al., 2004), entomologists are cautious about this option due to concern of intraguild and other possible non-target effects Landis, Fox and Costamagna, 2004).

(McKeown, 2003). Thus, the overall effect of natural suppression cannot be attributed to a single species but rather to the collective effect of the community of natural enemies. Including only one or a few major players may underestimate the overall impact and lead to biased prediction of the suppression effect. A second reason to model natural enemies as a community rather than as individual species is that detailed data are lacking on the biology and ecology of major predator species such as multi-colored Asian lady beetle, which compromises the feasibility of developing reliable population models for individual natural enemy species.

We adopt the dynamic Lotka-Volterra predator-prey system to model changes in the aggregate population of natural enemies as driven by prey availability. Denoted by NE_{t+1}, the cumulative population days for aggregate natural enemies in stage $t+1$ is given by:

$$NE_{t+1} = \max\{0,\ (NE_t - k_{NE,t} \cdot x_t \cdot NE_t) + d_t \cdot (NE_t - k_{NE,t} \cdot x_t \cdot NE_t) \\ + b_t \cdot (I_t - k_{I,t} \cdot x_t \cdot I_t) \cdot (NE_t - k_{NE,t} \cdot x_t \cdot NE_t)\} \tag{3}$$

$(t=1,2,3)$[7]

where d_t is the natural net decline rate that NE would suffer in the absence of prey and b_t is interpreted as the reproduction rate of NE per prey eaten (Sharov, 1996). We use robust OLS to estimate the following time-series regression equation, controlling for unobserved effect of observations within treatments:

$$E[\Delta_{t+1}] = d_t \cdot NE_t + b_t \cdot (I_t \cdot NE_t) \tag{4}$$

where E is the expectation operator and $\Delta_{t+1} = NE_{t+1} - NE_t$.

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[7] The natural enemy population model is estimated for stages R1 to R3 to predict natural enemy 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 yield damage in our model. Therefore, we do not need $t=4$ for the natural enemy population.

Soybean yield response

Farmers typically make sequential predictions on achievable yield over the course of the

growing season based on perception of initial yield potential, pest infestation and other

factors such as weather. We offer a conceptual model of yield-pest interaction that is

consistent with the process for updating yield potential described above. Mathematically,

projected yield potential at the beginning of stage $t+1$ (denoted by y_{t+1}) can be expressed

as:

$$y_{t+1} = f(y_t, I_t, \varepsilon_t) \tag{5}$$

$(t=1,2,3,4,5)$, and $y_1 = \bar{y}_h$

where ε_t denotes random factors such as weather, $\bar{y}_h$ is pest-free potential yield or average

historical yield upon which the season's first prediction is based, and the actual yield at

harvest (y_h) is assumed to be equal to yield potential evaluated at stage $t+1$ $(t=5)$. In a

linear prediction model, the proposed conceptual model can be implemented via

replacing the intercept term with fitted value of yield potential obtained in the previous

stage $(\hat{y}_t)$:

$$y_{t+1} = \alpha_t \cdot \hat{y}_t + \beta_t \cdot I_t + \varepsilon_t \tag{6}$$

where $\hat{y}_t = \hat{\alpha}_{t-1} \cdot \hat{y}_{t-1} + \hat{\beta}_{t-1} I_{t-1}$. Similarly in a non-linear yield-pest interaction model such

as the Cousens (1985) rectangular hyperbolic model, the conceptual model can be

implemented by replacing the parameter that represents maximum yield with the fitted

value of yield potential obtained in the previous stage $(\hat{y}_t)$:

$$y_{t+1} = \hat{y}_t \cdot (1 - \frac{\eta_t \cdot I_t}{1 + \eta_t \cdot I_t / \theta_t}) + \varepsilon_t \tag{7}$$

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

Non-linearity is particularly common in biological relations (Swinton et al., 1994). Three biologically-consistent non-linear models of yield-pest relationship are considered in this study: i) the Morgan-Mercer-Flodin or MMF sigmoidal model (Morgan et al.,

1975) $y_{t+1} = \dfrac{\widehat{y}_t \cdot \gamma_t + \mu_t \cdot (I_t)^{\delta_t}}{\gamma_t + (I_t)^{\delta_t}}$, where μ_t is the minimum yield asymptote as pest

population (I_t) approaches infinity, γ_t is a curvature measure that determines the rate at which yield reaches its lower asymptote, and δ_t is a curvature measure that determines the point at which yield begins to decline at a decreasing rate (Swinton and Lyford, 1996), ii) the modified MMF sigmoidal model which is reparameterized to reduce nonlinearity of

the parameter effects by substituting $\gamma_t^\delta = \tilde{\gamma}_t$ for γ_t to get $y_{t+1} = \dfrac{\widehat{y}_t + \mu_t \cdot (I_t/\tilde{\gamma}_t)^{\delta_t}}{1 + (I_t/\tilde{\gamma}_t)^{\delta_t}}$, where

$\tilde{\gamma}_t$ represents the pest population at which half of the yield is lost (see Swinton and Lyford, 1996 for details), and iii) Cousens' rectangular hyperbolic model (equation (7)) (Cousens, 1985). Biologically, crop yield damage per unit of pest density is greater at low density levels in a hyperbolic yield function than in a sigmoid function, so the hyperbolic form tends to generate a lower optimal pest control threshold (Swinton and Lyford, 1996).

We fit field trial data collected in Michigan to both restricted and unrestricted models using Nonlinear Least Squares estimation. The restrictions are imposed on parameter θ_t in the Cousens model ($\theta_t = 1$) and μ_t in the two MMF models ($\mu_t = 0$) to ensure non-negative minimum yield potential as pest population approaches to infinity. We then perform the Davidson-MacKinnon nested model specification test (Davidson

and MacKinnon, 1981) to test whether the simpler forms of the restricted MMF and hyperbolic functions differ in explanatory power from the full MMF form.

Intra-seasonal dynamic optimization problem

A persistent theme in economic research using dynamic optimization methods is that current actions affect future opportunities and so that optimal decision today depends on decisions which will be made in the future. The approach is necessary to study the decision problem of SBA management in which producers operate in an environment where time plays a fundamental role in the complex of human intervention and interactive biological agents of pests, natural enemies, and soybean plants. We define the producer's objective as maximizing the expected gross margin of pest management realized at harvest over a sequence of control actions at several decision points within a growing season, subject to a set of biological constraints on pest population, natural enemy population, and crop yield potential. The gross margin is derived by subtracting total SBA control cost from revenue. Mathematically, the objective function (denoted by *J*) can be written as:

$$J(I_1, NE_1, y_1) = \max_{\{x_t\}_{t=1}^{T}} \{p \cdot y_h - \sum_{t=1}^{T} c(x_t)\} \tag{8}$$

subject to equations (1), (3), and (5). I_1, NE_1, and y_1 are given. $\{x_t\}_{t=1}^{T}$ represents a sequence of control actions over the five stages. p denotes output price and $c(x_t)$ denotes control cost, including the cost of pest scouting to provide the basis for control decisions. No discount factor is included for this single-season optimization problem due to its relatively short duration.

III. Numerical results

The dynamic optimization problem is solved numerically via an optimizing simulation program in which we predict the values of gross margin for every possible control path and for every possible combination of initial values of SBA population, natural enemy population, and yield potential. Since we deal with a finite horizon discrete-state/action problem and control is only meaningful in four of the five stages considered (i.e., $x_5=0$ known), we can lay out a total of 16 distinct possible control paths with each path made up of four control decision stages, not counting the full maturing stage (R5) in which spraying would not affect yield (Table 1). The path that yields the highest gross margin is designated the optimal control path (OPC) for a given combination of possible initial values. Mathematically, the OCP for combination j of initial values (I_{1j}, NE_{1j}, y_{1j}) is expressed as:

$$OCP_{(I_{1j},NE_{1j},y_{1j})} = \arg Max \ \{(gross \ margin)_1, (gross \ margin)_2, ..., (gross \ margin)_{16}\} \quad (9)$$

where

$$(gross \ margin)_z = p \cdot y_h - \sum_{t=1}^{T} c(x_t) \quad (10)$$

z indexes possible control paths ($z=1,2,\ldots,16$), and state variables I, NE, and y evolve according to transition equations (1), (3), and (5).

The optimizing simulation technique has two major advantages over such dynamic programming computer program as "DDPSOLVE" that is developed by Fackler and Miranda (1997-2002): i) it allows the implementation of stage-specific parameters in the numerical optimization model, and ii) it significantly reduces computational expenses and thus enables us to use smaller and more accurate value intervals and wider ranges of possible initial values for the biological state variables.

Parameters

The empirical estimates of predation-free net growth rate of SBA population for each stage ng_t are computed using simulated SBA growth pseudo data generated by the Costamagna et al. (2006) model (Table 2). Free of predators, SBA population increases rapidly and peaks in stage R4, after which it declines. The net population growth rate is highest during R2 at 10.5692 and drops to a negative level after R4. These estimates have not been empirically validated because SBA population data collected in field trials are subject to natural suppression whereas the net growth rates computed from simulation output are not. However, the estimates conform to the theoretical expectation that the quality of the resources in a given system varies over time, and this change is directly translated into reduced reproduction of the species that relies on the resources (Costamagna et al., 2006)[8].

For natural enemy population dynamics, we estimate the net decline rate (d_t) and the reproduction rate (b_t) from visual count data collected at the KBS in 2005. As Table 2 shows, the net decline rate is found significant in stage R3 only, whereas the reproduction rate is significant at the 80% and 90% confidence levels in R1 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 of natural enemies will decline from stage R3 to R4 by -0.9396 for each additional natural enemy in stage R3. For each SBA eaten by each additional natural enemy, the population of natural enemies will grow from stage R1 to R2 and from R3 to R4 by the amounts ($0.0007*I_1$) and ($0.0002*I_3$), respectively.

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[8] Emigration of winged SBA in July and early August may also contribute to population reduction (Christine DiFonzo, Associate Professor, Department of Entomology, Michigan State University, personal communications, June 1, 2006).

Data used to estimate the yield response function were collected from two field trials conducted in three Michigan sites in 2005 (the Bean and Beet farm in the Thumb region of eastern Michigan [Saginaw County], the KBS in southwestern Michigan [Kalamazoo County], and a site located in Sanilac County). We report in Table 3 only estimation results from the restricted Cousens rectangular hyperbolic model (θ_t =1 or maximum allowable yield loss = 100%) using the pooled data, because the two MMF models did not fit the data well (Zhang, 2007). Pest damage significantly affects yield potential in stages R2, R3, and R4. The proportion of yield lost to per unit of pest population (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. While this is theoretically possible (Pedigo et al., 1986; Tammes, 1961; Fenemore, 1982), field observations in Michigan do not show evidence of it. Thus, we assume that yield potential in stage R2 is not responsive to pest injury (i.e., η_2=0) in the numerical optimization model. Yield potential responds to pest damage the most in stage R3, with an estimated 0.00004% of yield potential lost per SBA per plant. The Cousens rectangular hyperbolic model is preferred over the MMF alternatives as the simplest functional form that cannot be rejected under the Davidson-MacKinnon model specification test.

The natural enemy assemblage considered in this study consists of more than 19 species including seven-spotted lady beetle, multi-colored Asian lady beetle, *Orius*, spider, and unidentified small *Coccinellidae* larvae (Costamagna, 2006). While the relative contribution of each species is not fully understood yet, we use average consumption rate of multi-colored Asian lady beetle—a relatively abundant and effective

generalist predator of SBA—to approximate the range of daily predation rate (PR) used in the numerical optimization model and define five scenarios of predation rate ranging from 0 to 80 by interval of 20 SBA per day per natural enemy[9]. Stage-based predation per natural enemy is then computed by multiplying daily rate by number of days in each stage.

Other parameters used in the numerical optimization analysis include the efficacy rate of insecticides on SBA ($k_{I,t}$) and the mortality rate of natural enemies due to non-target effect of insecticides, both assumed to be 99% throughout the season. For price and cost parameters, we use a long-term soybean trend price of $6.91/bu and a treatment cost of $12.18/ac for the RAMP "best management practice" treatment using Warrior at 3.2 oz/ac with field scouting. A break-down of the cost includes $6.98/ac insecticide cost, $2.00/ac for scouting, and $3.20/ac for spraying (Song et al., 2006).

Because SBA was first detected in the United States so recently (2000), few years of data are available and sample sizes are small, making it difficult to estimate stage-specific population parameters. Nevertheless, the numerical analysis serves a valid exercise of using dynamic optimization model to solve for natural enemies-adjusted economic threshold, which provides an avenue to explore the effect of natural suppression on optimal insecticide strategies and a preliminary value of this ecosystem service.

Values of parameters used in the numerical optimization analysis are reported in the second column of Table 4. Specifically, estimated values of stage-specific parameters that are statistically significant (see Table 2) are used directly in the numerical

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[9] The conservative upper limit of predation rate of 80 SBA/day/*NE* is chosen because an adult multi-colored Asian lady beetle consumes 90 to 270 aphids per day whereas its larva consumes about 50 to 86 aphids per day (Weeden et al., 2006).

optimization analysis (with the sole exception of η_2—the proportion of yield lost to per unit of pest population in stage R2). For parameters that are found insignificant in their respective models, we use zeros instead in the numerical optimization analysis.

Numerical solution of the natural enemies-adjusted economic threshold

The natural enemies-adjusted economic threshold is the pest population density threshold at which pesticide control becomes optimal in spite of the opportunity cost of injury to natural enemies of the target pest. The natural enemies-adjusted economic threshold is calculated by solving the dynamic optimization problem for the threshold pest population density at which pesticide-based control would maximize the expected end-of-season gross margin over market-based pest control costs.

To illustrate how optimal control paths are determined by initial values of yield potential (y_1), SBA population per plant (I_1), and natural enemy population per plant (NE_1) and vary with predation rate, we present selected results from two extreme values of initial yield potential modeled ($y_1 = 30$ bu/ac and $y_1 = 70$ bu/ac) under three predation rate scenarios (PR=0, PR=20, and PR=80) in Figures 1 to 3. Each coordinate in the optimal control space corresponds to a natural enemies-adjusted economic threshold at which I_1 and NE_1 jointly determine the optimal control action throughout the season at given y_1. Our key results include:

1. *Early actions are preferred over late actions*.

A total of four distinct optimal control paths emerge in all non-zero predation rate scenarios: (i) no control in all stages ("No spray"), (ii) control in stage R1 only ("Spray R1"), iii) control in stage R2 only ("Spray R2"), and (iv) control in both R1 and R2

("Spray R1+R2"). The path "Spray R2" is not chosen for scenario PR=0 (Figure 1).

While it is obvious that no insecticide spray is necessary during the last stage (R5), stages

R3 and R4 are found to be too late to take control action either, regardless of initial yield

potential and populations of pest and natural enemies.

2. *Natural enemies reduce the need to spray insecticide at any non-zero predation rate.*

In the absence of natural enemies, chemical control is desired for the lowest positive

initial pest density modeled, i.e., 20 SBA/plant (Figure 1). This is consistent with the

empirical observation that producers do not hesitate to spray the fields, because of the

almost guaranteed positive return from spraying. As natural enemy population reaches

5/plant and with y_l= 70 bu/ac and PR= 20 SBA/day/*NE* (Figure 2(ii)), for instance,

chemical control in any stages becomes unnecessary for SBA population less than or

equal to 100/plant. Also shown in Figure 2(ii), when NE_l =5/plant, "Spray R1+R2"

would not be optimal unless SBA/plant exceeds 380. At I_l=380/plant, "Spray R2" would

be sufficient if the population of natural enemies is between 5 to 15/plant. For

NE_l>15/plant, however, the same initial pest population (380/plant) no longer justifies

any artificial control.

    In the non-zero predation rate scenarios (Figures 2 and 3), "Spray R1" is only

optimal when natural enemies are absent (the bottom line in the optimal control space).

This indicates that whenever there is effective regulation by natural enemies (i.e., PR>0

and NE_l>0), it becomes desirable to delay spraying until stage R2 in order to allow "co-

evolution" of the pest and natural enemies populations, which guarantees greater pest

suppression later into the season due to the non-target effect of insecticide on natural

enemies.

3. *Predation rate and initial yield potential both play significant roles in determining the choice of optimal control paths.*

When PR=0 (Figure 1), insecticide is the only tool producers have to battle with SBA, so the two preferred options are early control in R1 for relatively lower (but positive) initial pest population or spraying twice in both R1 and R2 for higher initial pest populations. For positive predation rates, the higher the initial yield potential, the higher the likelihood of "Spray R1+R2". These results conform to the general expectation that more productive fields justify more insecticide use than the less productive ones at given output price and control cost. Focusing on the case of y_I=70 bu/ac, a comparison of Figure 2(ii) and Figure 3(ii) shows that as predation rate increases from 20 to 80 SBA/day/*NE*, the percentage of time adopting "No spray" increases by 9% from 86% to 95%. While the chances of using "Spray R1" have remained the same over the same range of predation rate for y_I=70 bu/ac[10], "Spray R2" and "Spray R1+R2" are chosen 82% and 61% less frequently.

4. *Values of gross margins*

At PR=0, the gross margin of optimal SBA management accrued to producers is a monotonically decreasing function of initial pest population and is independent of natural enemies (Figure 4(i)), although fields with higher initial yield potential always maintain higher gross margins over the optimal control paths chosen. Specifically, at PR=0 and y_I=70 bu/ac, the gross margin peaks at $484/ac for pest-free fields, drops to $471/ac when initial pest population is 20/plant, and continues to decline steadily till the 300 SBA/plant level, from which the gross margin asymptotically approaches the lowest possible value of $459/ac occurred at the 800/plant SBA level. The more interesting cases

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[10] At positive predation rates, "Spray R1" is only preferred when NE_I =0 and is affected by initial yield potential, not predation rate.

are the ones with positive predation rates, as illustrated in Figure 4(ii) and (iii), in which

each curve depicts the values of gross margin associated with a particular natural enemy

population within the range of possible values of initial SBA population modeled. For

instance, the first curve (from the left) is associated with NE_I=0/plant, the second one is

associated with NE_I=10/plant, and so on. At PR=80 and y_I=70 bu/ac, the highest possible

value of gross margin ($484/ac) is maintained for all possible initial pest levels as long as

NE_I≥10/plant (Figure 4(iii)). At PR=20 and y_I=70 bu/ac, the highest possible value of

gross margin is guaranteed as long as the initial natural enemy population is no smaller

than 40/plant.

Economic value of natural pest control by natural enemies

These numerical results can be used to make a preliminary estimate of the value of the

ecosystem service from natural pest control. The value is calculated from increase in

gross margins as a result of higher population of natural enemies so it constitutes a lower

bound for the total economic value of this ecosystem service because it omits such

benefits as the avoidance of health and environmental risks from insecticide spraying.

The value is context-dependent, because the marginal value of an additional unit

of natural enemy population not only depends on the predation rate, initial yield potential

and pest population but also the baseline natural enemy population. To illustrate, we

report in Figure 5 the differences in predicted values of gross margin as natural enemy

population increases from the baseline of NE_I=0/plant to i) NE_I=5/plant, and ii)

NE_I=10/plant for a specific case in which predation rate is 40 SBA/day/NE and initial

yield potential is 50 bu/ac (both are medians of their respective possible values modeled).

An additional 5 natural enemies per plant (above the zero/plant baseline) in stage R1

given a predation rate of 40 SBA/day/*NE* and a yield potential of 50 bu/ac implies a

sequence of minimum values associated with given initial pest populations: for instance,

$12.80/ac when I_1= 20/plant, and peaks at $18.30/ac when I_1= 200/plant, from where the

value starts declining as I_1 increases.

IV. Sensitivity analysis

To assess the effect of uncertainty associated with the economic and biological

parameters used in the dynamic optimization analysis, we perform a sensitivity analysis

on parameters by changing parameters one at a time holding the rest constant and

comparing the results with the baseline model. A total of 32 scenarios are examined

(Table 4) for a specific case in which predation rate is 40 SBA/day/*NE* and initial yield

potential is 50 bu/ac. Parameters estimated from field data are increased and/or decreased

by one standard deviation, whereas parameters that are assumed or derived from other

studies are increased and/or decreased by 10% and 20%, respectively[11]. All variations are

made within constrained value ranges that are theoretically consistent.

Table 5 summarizes the major results from the sensitivity analysis. Specifically,

we look at three aspects of changes from baseline resulted from varying parameters:

1. Choice of optimal control paths:

Varying the values of most of the parameters does not alter the selection of optimal

control paths in most scenarios for the case of "PR=40 SBA/day/*NE* and y_1=50 bu/ac",

i.e., the same four paths, "No spray", "Spray R1", "Spray R2", and "Spray R1+R2", are

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[11] Although not explicitly included in the sensitivity analysis, the effects of biological parameters "predation rate" and "initial yield potential" are exhibited through scenario analysis within the numerical optimization model.

adopted as in the baseline. The exceptions are: i) reducing the mortality rate of SBA to insecticide by 10% results in the inclusion of one additional optimal control path of "Spray R1+R2+R3", ii) reducing the mortality rate of SBA to insecticide by 20% results in the inclusion of two additional optimal control paths of "Spray R2+R3" and "Spray R1+R2+R3", whereas the strategy "Spray R1+R2" is dropped, and iii) reducing the mortality rate of natural enemies to insecticide by 10% and 20% leads to the dropping of one optimal control path of "Spray R2", and iii) increasing the proportion of yield lost to per unit of SBA population in stage R2 by one standard deviation also causes the dropping of "Spray R2".

2. *Percentage of time that spray is not needed:*

Varying the values of most of the parameters does not change the chances of solely relying on natural regulation and spraying no insecticide for the case of "PR=40 SBA/day/*NE* and y_1=50 bu/ac" with some exceptions that are found to differ little from the baseline model. The exceptions include: i) the maximum daily intrinsic growth rate of SBA (r_{max}, see detailed definition below Table 4), which directly affects the magnitude of net growth rates of SBA population, ii) the reciprocal of the time to peak population (C, see detailed definition below Table 4), which affects the turning point of SBA intrinsic growth rate from increasing to decreasing, iii) mortality rate of SBA to insecticide (down by 10% and 20%), iv) the proportion of yield lost to per unit of SBA population in R3, v) the reproduction rate of natural enemies in R1, and vi) the natural net decline rate of natural enemies in R1. Varying the maximum intrinsic growth rate of SBA r_{max} has the greatest impact on the percentage of time that no artificial control is necessary by

reducing the chances by 1.02% when deflated by one standard deviation and decreasing the chances by 0.94% when inflated.

3.   Values of gross margins

While individually varying the economic parameters (output price and control cost) does not affect the choice of optimal control paths or the percentage of time that "No spray" is adopted, their variations have the greatest impact on gross margin (tied with scenario "reducing the mortality rate of SBA to insecticide by 20%"). Specifically, increasing (or decreasing) output price by 20% leads to up to 22% of increase (or decrease) in gross most with relatively low initial natural enemy populations (between 0 and 15 per plant) corresponding to slightly greater changes. Reducing the mortality rate of SBA to insecticide by 10% and 20% results in losses in gross margin by up to 10% and 22%, respectively, for positive initial pest population and relatively low initial natural enemy populations (i.e., $0 \leq NE_I \leq 15$). The other three scenarios that have an impact of over 10% on gross margin are increasing the proportion of yield lost to per unit of pest population in R1 and changing output price (up and down) by 10%. In all three scenarios, impact grows as initial pest population rises (after certain threshold) but relatively low natural enemy populations are always responsible for greater effects. The rest parameter-varying scenarios have either no impact on gross margin (in particular, variations in the reproduction rate and the natural net decline rate of natural enemies) or impact of magnitude no greater than 4%.

V. Conclusion

The natural control of pests by their natural enemies represents an important ecosystem service that maintains pest population below economic injury level in agroecosystems. Extending the "economic threshold" concept, this paper proposes a "natural enemies-adjusted economic threshold" for pesticide use that takes into account the implicit cost of injury to natural enemies. By explicitly accounting for natural pest suppression, the natural enemies-adjusted economic threshold can potentially make pest management more cost-effective while reducing dependence on toxic insecticides. The threshold is illustrated via an intra-seasonal dynamic bioeconomic model of soybean aphid management in Michigan, USA. A dynamic optimization model quantifies the contribution of natural suppression to optimal pest control. The results highlight the importance of assessing both pest and natural enemy populations in making insecticide application decisions and accounting for the opportunity cost of insecticide collateral damage to natural enemies.

This research into improved human management of ecosystem services points to four important research directions for refinement and application of this dynamic bioeconomic model. First, because the species composition of natural enemy communities varies from field to field, weighting factors should be developed to account for the different suppression levels associated with different natural enemy species. Second, certain biological parameter estimates needs refining and validation. Sensitivity analysis indicates that results are especially sensitive to changes in mortality rates from insecticide, natural population growth rates, and soybean growth stage-specific yield loss per soybean aphid. Obtaining these improved parameter estimates will require new

experimental designs that allow observation of effects by plant growth stage. Third, once refined and validated, this bioeconomic model can be applied to estimate the regional value of pest regulation services contributed by natural enemies. Finally, given that random effects such as weather play an important role in determining the underlying biological processes (notably insect population dynamics and crop growth), introducing stochastic processes for Monte Carlo simulation would enhance the current deterministic model.

By describing biological processes and interactions and predicting their response to management decisions, bioeconomic modeling can improve human management of agroecosystems (King et al. 1993). The model presented here demonstrates how pest suppression by natural enemies can significantly reduce farmers' dependence on insecticide. In the long run, however, effective agroecosystem management will demand more of managers than simply to reduce the non-target effect of pesticides on natural enemies. Habitat management that improves landscapes complexity can potentially benefit natural enemies and in most cases result in enhanced biological control of pests (Thies and Tscharntke, 1999; Wilby and Thomas, 2002; Cardinale et al., 2003; Ostman, Ekbom and Bengtsson, 2003; Thies, Steffan-Dewenter and Tscharntke, 2003). Future research should move beyond insecticide use thresholds to develop landscape-scale guidelines for explicit management of habitat for the natural enemies of agricultural pests.

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Table 1. Summary of all 16 possible control paths over the course of R1 to R5

Path	R1	R2	R3	R4	R5
1	No spray	No spray	No spray	No spray	No spray
2	No spray	Spray	No spray	No spray	No spray
3	No spray	No spray	Spray	No spray	No spray
4	No spray	Spray	Spray	No spray	No spray
5	No spray	No spray	No spray	Spray	No spray
6	No spray	Spray	No spray	Spray	No spray
7	No spray	No spray	Spray	Spray	No spray
8	No spray	Spray	Spray	Spray	No spray
9	Spray	No spray	No spray	No spray	No spray
10	Spray	Spray	No spray	No spray	No spray
11	Spray	No spray	Spray	No spray	No spray
12	Spray	Spray	Spray	No spray	No spray
13	Spray	No spray	No spray	Spray	No spray
14	Spray	Spray	No spray	Spray	No spray
15	Spray	No spray	Spray	Spray	No spray
16	Spray	Spray	Spray	Spray	No spray

Table 2. Key biological parameter estimates

Stage transition	Days in prior stage	Net growth rate of cumul. SBA population (ng_t)[1]	Net decline rate of NE (d_t)	Reproduction rate of NE per prey eaten (b_t)
R1→R2	4	7.9740	-0.4321	0.0007*
R2→R3	8	10.5692	-0.2459	-0.0001
R3→R4	13	3.6423	-0.9396****	0.0002**
R4→R5	15	-0.3483		

* Significant at 20%; ** significant at 10%; *** significant at 5%; **** significant at 1%.
[1] Net growth rates of cumulative SBA population are computed from simulated data from Costamagna et al. (2006)'s model and number of days in plant growth stages. Net decline and reproduction rates are estimated from field data collected in Michigan, USA, during 2005, and provided by Alejandro Costamagna, Department of Entomology, Michigan State University.

Table 3. Estimation results from the restricted Cousens rectangular hyperbolic model (Data: multiple sites in Michigan, 2005; provided by Christine DiFonzo, Department of Entomology, Michigan State University)

	R1 Restricted	*R2* Restricted	*R3* Restricted	*R4* Restricted	*R5* Restricted
$\hat{y}_t$	36.92345***				
	(2.00588)				
η_t	0.00000	-0.00010**	0.00004*	0.00001*	0.00001
	(0.00017)	(0.00004)	(0.00002)	(0.000003)	(0.00011)
θ_t	**1**	**1**	**1**	**1**	**1**
	(imposed)	(imposed)	(imposed)	(imposed)	(imposed)
Obs	43	43	43	43	43
Adj R-sq	0.92	0.93	0.94	0.94	0.94

Standard errors in parentheses.
* Significant at 10%; ** significant at 5%; *** significant at 1%.

Table 4. Parameter values used in the sensitivity analysis

Parameters	Baseline	Standard deviation	Up 1 s.d.	Down 1 s.d.	Up 10%	Up 20%	Down 10%	Down 20%
r_{max}*	0.3978	0.0306	0.4284[1]	0.3672[2]				
C*	0.024	0.001	0.025	0.023				
$k_{I,t}$	0.99						0.891	0.792
$k_{NE,t}$	0.99						0.891	0.792
η_1	0	0.00017	0.00017					
η_2	0	0.00004	0.00004					
η_3	0.00004	0.00002	0.00006	0.00002				
η_4	0.00001	0.000003	0.000013	0.000007				
η_5	0	0.00011	0.00011					
d_1	0	0.36294		-0.36294				
d_2	0	0.47765		-0.47765				
d_3	-0.93961	0.25383	-0.68578	-1.19344				
b_1	0.00072	0.00051	0.00123	0.00021				
b_2	0	0.00028	0.00028					
b_3	0.00017	0.00009	0.00026	0.00008				
COST	12.18				13.398	14.616	10.962	9.744
PRICE	6.91				7.601	8.292	6.219	5.528

* In the Costamagna et al. (2006) model, SBA population on day $d+1$ (a_{d+1}) is described by:

$$a_{d+1} = a_d \cdot e^{r_d}$$

where $r_d = r_{max}(1 - C \cdot d)$ (Williams et al., 1999). r_d is SBA's intrinsic growth rate that decreases in time (d), and C is the reciprocal of the time to peak population. Starting at r_{max} (the maximum intrinsic rate of increase) when $d = 0$ (and the population is at its peak), r_d decreases linearly until $r_d = 0$ when $d = 1/C$ (Costamagna et al., 2006). Varying r_{max} and C would have an impact on the net growth rates of SBA population computed from the simulated data.

[1] Net growth rates associated with r_{max}= 0.4284 are: 9.1345 (R1), 12.4830 (R2), 4.1228 (R3), and -0.3333 (R4)

[2] Net growth rates associated with r_{max}= 0.3672 are: 6.9527 (R1), 8.9292 (R2), 3.2024 (R3), and -0.3632 (R4)

Table 5. Summary of sensitivity analysis results

| Sensitivity analysis scenarios	Changes from baseline		
	Optimal control path (OCP)	Chances of no control	Gross margin (GM)
r_{max} up 1 s.d.	Same OCPs	-0.94%	$\leq$4% of losses where $I_1 \geq 140$ and $0 \leq NE_1 \leq 20$
r_{max} down 1 s.d.	Same OCPs	1.02%	$\leq$4% of gains where $I_1 \geq 200$ and $0 \leq NE_1 \leq 15$
C up 1 s.d.	Same OCPs	0.34%	$\leq$4% of gains where $I_1 \geq 220$ and $0 \leq NE_1 \leq 15$
C down 1 s.d.	Same OCPs	-0.26%	$\leq$4% of Losses where $I_1 \geq 200$ and $0 \leq NE_1 \leq 15$
Mortality rate of SBA to insecticide down 10% ($k_{I,t}$)	Add "Spray "R1+R2+R3"	0.17%	$\leq$10% of losses where $I_1 \geq 20$ and $0 \leq NE_1 \leq 15$
Mortality rate of SBA to insecticide down 20% ($k_{I,t}$)	Add "Spray R2+R3" & "Spray R1+R2+R3", drop "Spray R1+R2"	0.34%	$\leq$22% of losses where $I_1 \geq 20$ and $0 \leq NE_1 \leq 15$
Mortality rate of NE to insecticide down 10% ($k_{NE,t}$)	Drop one OCP: "Spray R2"	0%	$\leq$4% of gains where $I_1 \geq 280$ and $0 \leq NE_1 \leq 15$
Mortality rate of NE to insecticide down 20% ($k_{NE,t}$)	Drop one OCP: "Spray R2"	0%	
% of yield lost to per unit of pest population in R1 up 1 s.d. (η_1)	Same OCPs	0%	SBA<40 no change; $I_1 \geq 40$, losses ($\leq$13%) rise as I_1 increases but are particularly higher when $0 \leq NE_1 \leq 15$
% of yield lost to per unit of pest population in R2 up 1 s.d. (η_2)	Drop one OCP: "Spray R2"	0%	$\leq$3% of losses for $I_1 \geq 380$ and $10 \leq NE_1 \leq 20$
% of yield lost to per unit of pest population in R3 up 1 s.d. (η_3)	Same OCPs	0%	$\leq$1% of losses for $I_1 \geq 240$ and $0 \leq NE_1 \leq 10$
% of yield lost to per unit of pest population in R3 down 1 s.d. (η_3)	Same OCPs	0.09%	$\leq$1% of gains for $I_1 \geq 240$ and $0 \leq NE_1 \leq 10$
% of yield lost to per unit of pest population in R4 up 1 s.d. (η_4)	Same OCPs	0%	*No change*
% of yield lost to per unit of pest population in R4 down 1 s.d. (η_4)	Same OCPs	0%	$\leq$1% of gains for $I_1 \geq 340$ and $0 \leq NE_1 \leq 10$
% of yield lost to per unit of pest population in R5 up 1 s.d. (η_5)	Same OCPs	0%	$\leq$3% of losses for $I_1 \geq 20$ and $0 \leq NE_1 \leq 15$
Reproduction rate of NE per prey eaten in R1 up 1 s.d. (b_1)	Same OCPs	0.26%	*No change*
Reproduction rate of NE per prey eaten in R1 down 1 s.d. (b_1)	Same OCPs	-0.17%	*No change*
Reproduction rate of NE per prey eaten in R2 up 1 s.d. (b_2)	*No change*	0%	*No change*
Reproduction rate of NE per prey eaten in R3 up 1 s.d. (b_3)	*No change*	0%	*No change*
Reproduction rate of NE per prey eaten in R3 down 1 s.d. (b_3)	*No change*	0%	*No change*
Natural net decline rate of NE in the absence of prey in R1 down 1 s.d. (d_1)	Same OCPs	-0.17%	*No change*
Natural net decline rate of NE in the absence of prey in R2 down 1 s.d. (d_2)	Same OCPs	0%	*No change*
Natural net decline rate of NE in the absence of prey in R3 up 1 s.d. (d_3)	*No change*	0%	*No change*
Natural net decline rate of NE in the absence of prey in R3 down 1 s.d. (d_3)	*No change*	0%	*No change*
price up 10%	Same OCPs	0%	10% of gains in most cases; 11% of gains where $I_1 \geq 400$ and $0 \leq NE_1 \leq 5$
price up 20%	Same OCPs	0%	$\leq$22% of gains for all cases, higher gains where $0 \leq NE_1 \leq 15$
price down 10%	Same OCPs	0%	reverse of "price up 10%
price down 20%	Same OCPs	0%	reverse of "price up 20%
cost up 10%	Same OCPs	0%	$\leq$1% of losses where $I_1 \geq 440$ and $0 \leq NE_1 \leq 5$
cost up 20%	Same OCPs	0%	$\leq$2% of losses where $I_1 \geq 20$ and $0 \leq NE_1 \leq 15$
cost down 10%	Same OCPs	0%	$\leq$1% of gains where $I_1 \geq 380$ and $0 \leq NE_1 \leq 5$
cost down 20%	Same OCPs	0%	reverse of "cost up 20%"
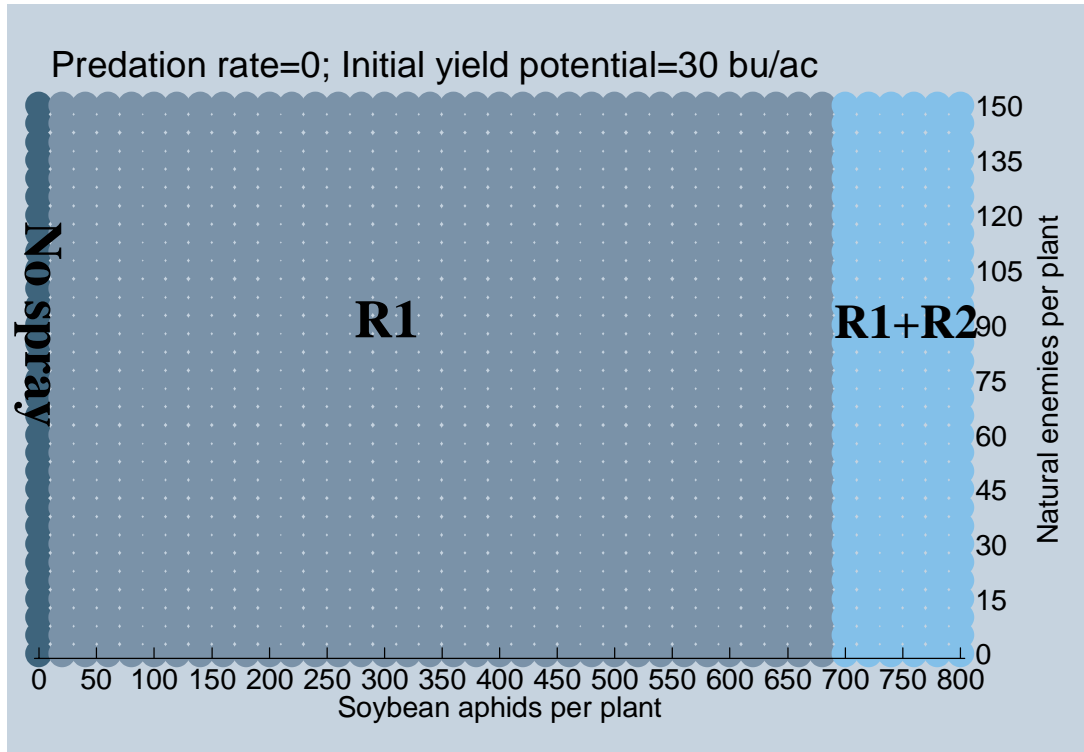
(i)
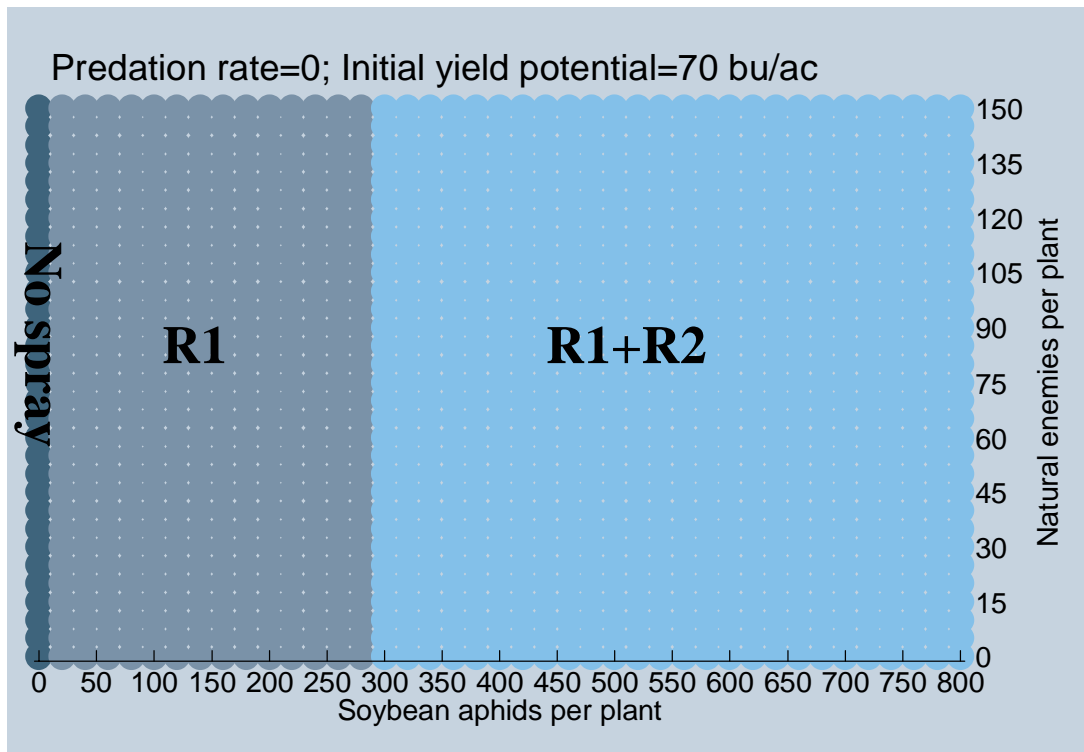
(ii)

Figure 1. Predation rate = 0: Optimal control paths for initial yield potential of 30 bu/ac (i) and 70 bu/ac (ii).
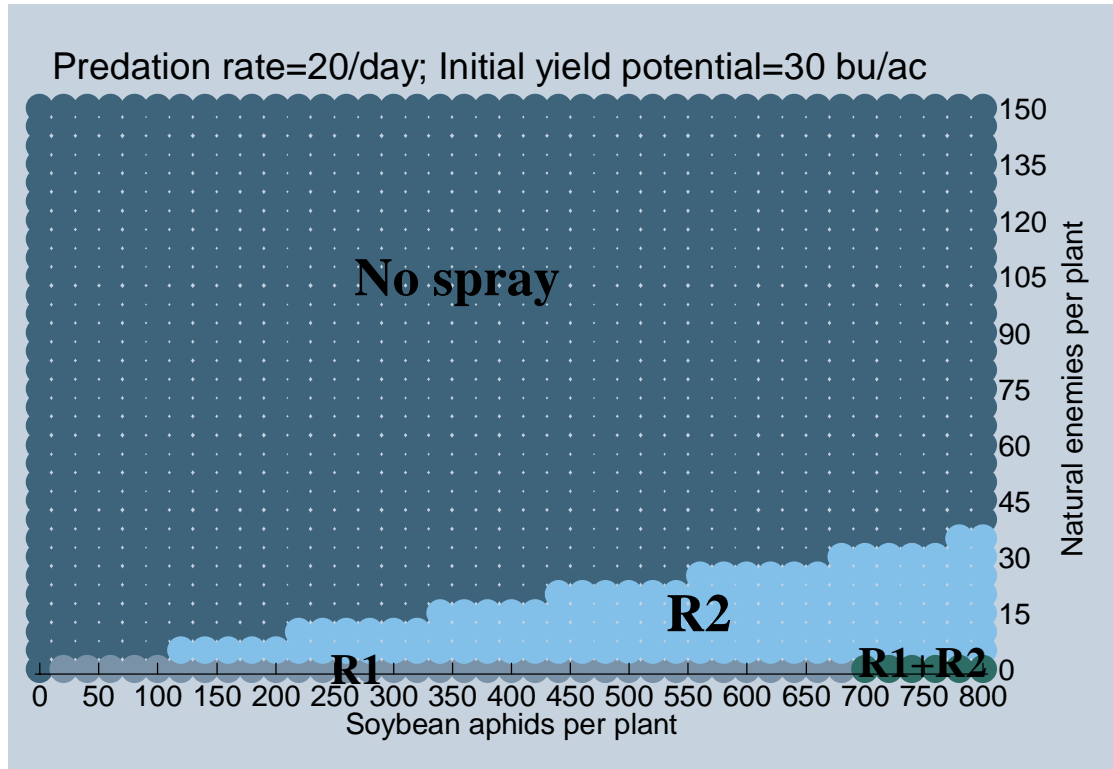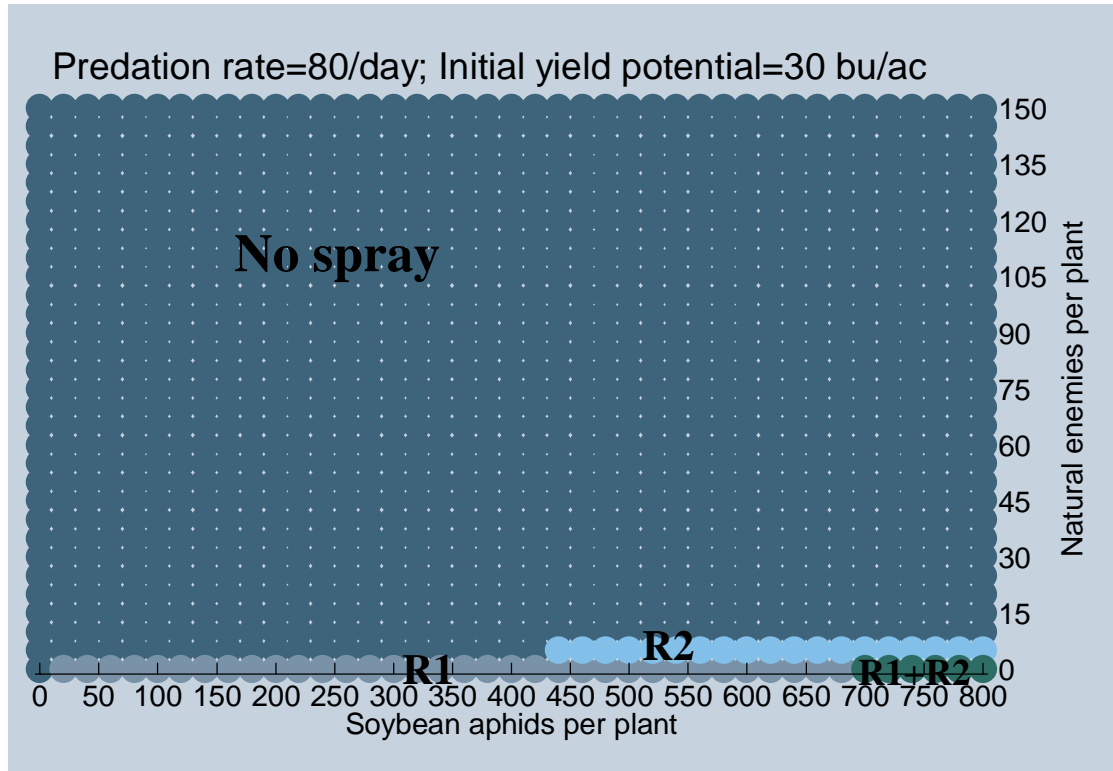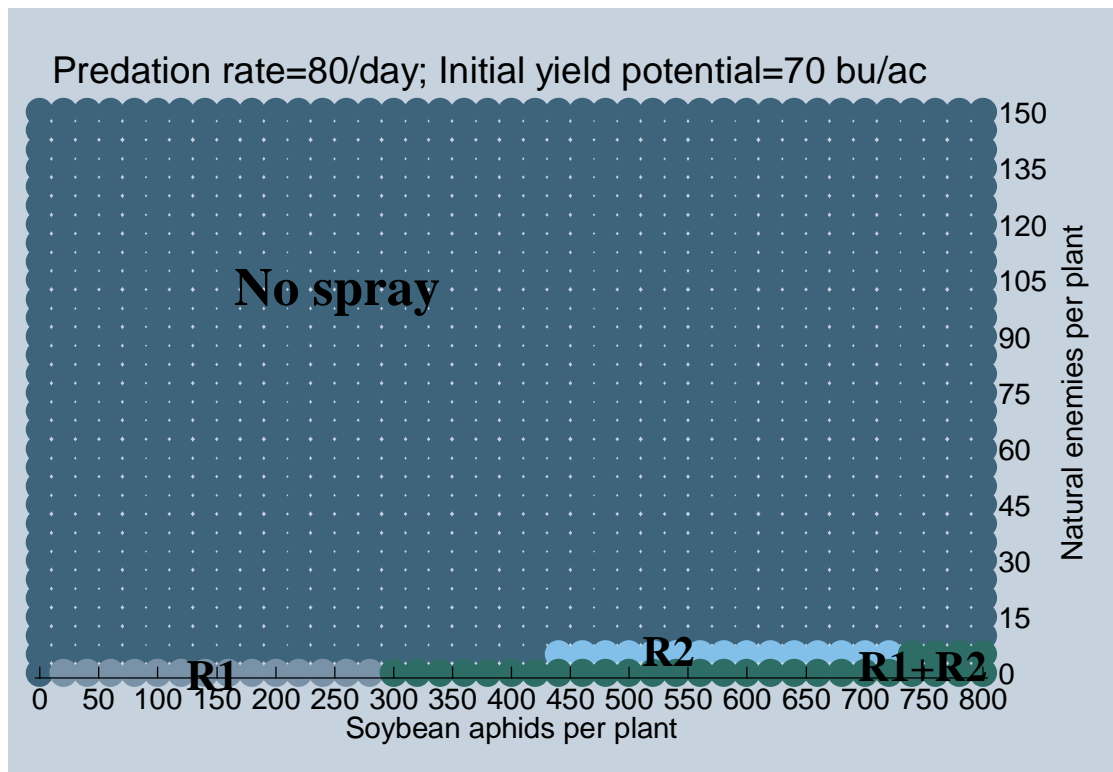
(i)
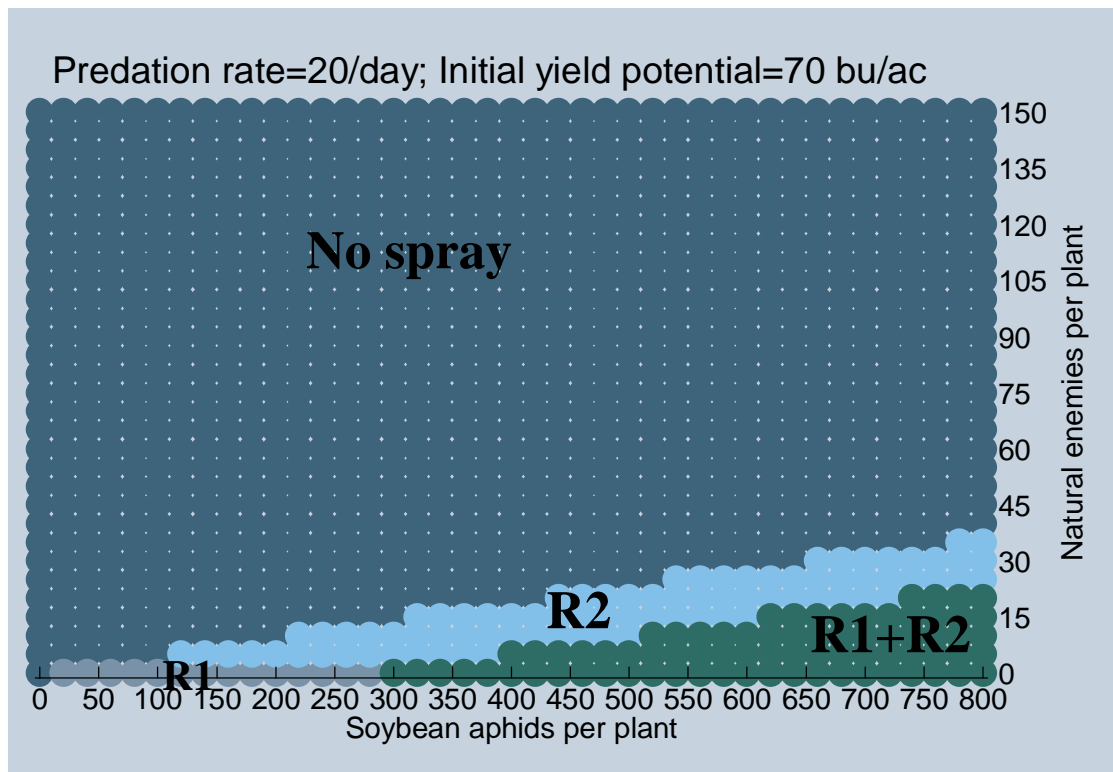
(ii)

Figure 2. Predation rate = 20: Optimal control paths for initial yield potential of 30 bu/ac (i) and 70 bu/ac (ii).
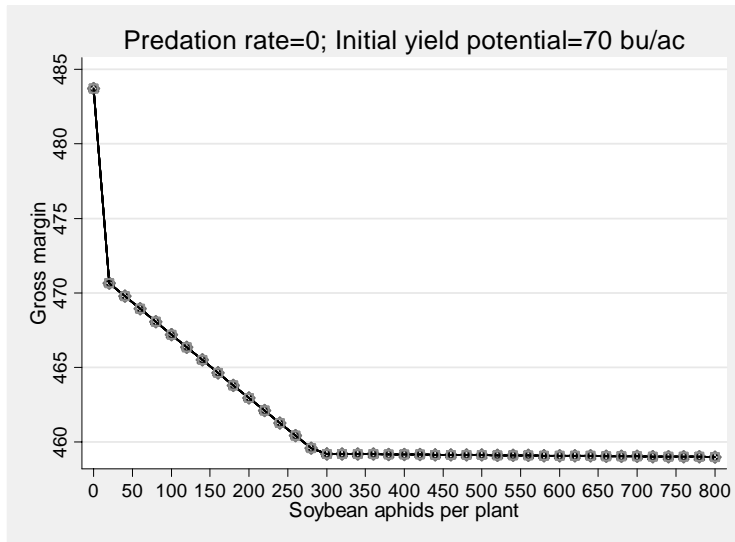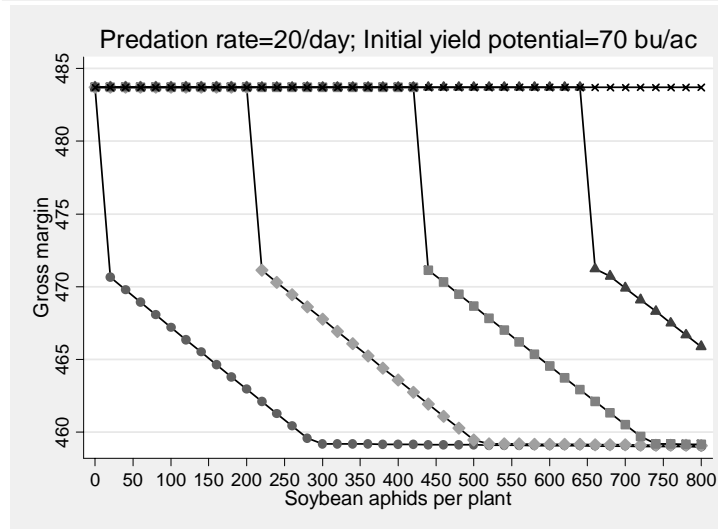
(i)

(ii)

Figure 3. Predation rate = 80: Optimal control paths for initial yield potential of 30 bu/ac (i) and 70 bu/ac (ii).
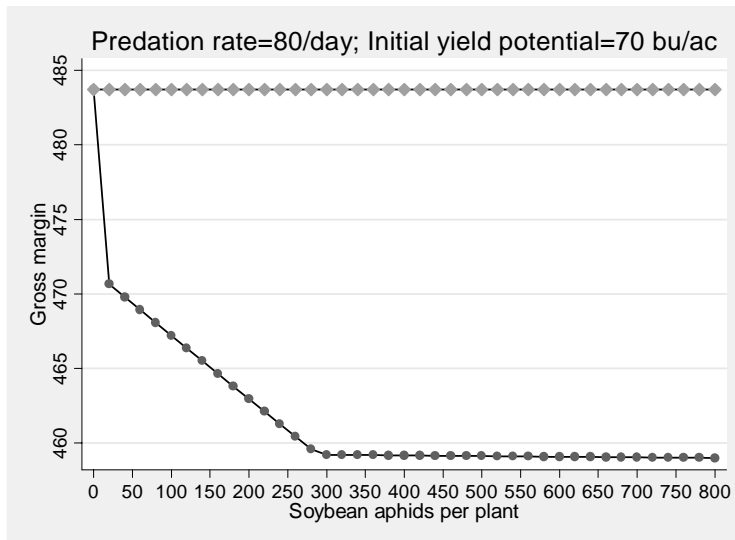
Figure 4. Initial yield potential=70 bu/ac: Gross margins for (i) PR=0, (ii) PR=20, and (iii) PR=80 SBA/day/*NE.*
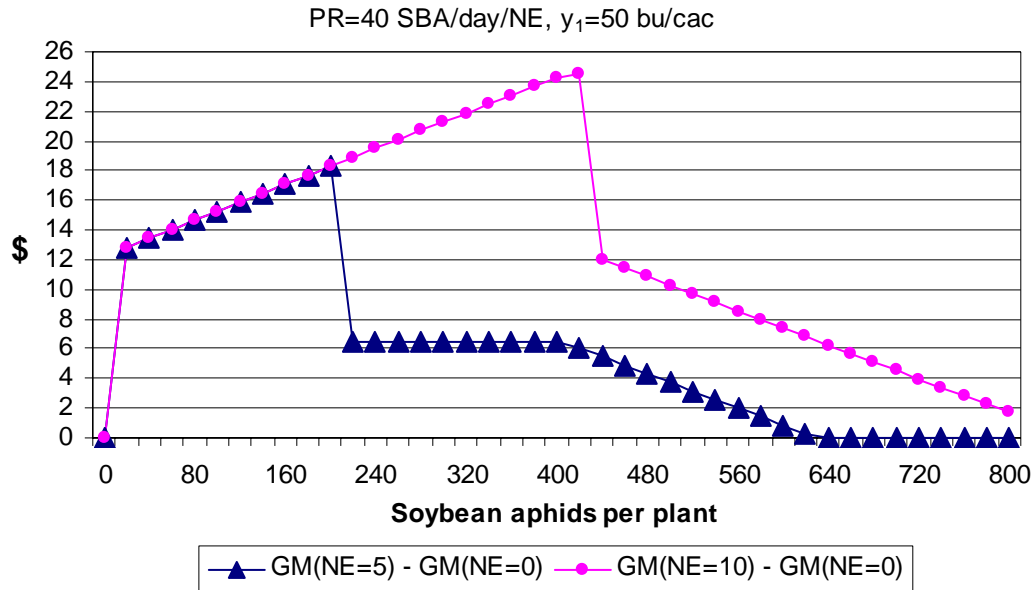
Figure 5. PR=40 and initial yield potential=50 bu/ac: Differences in the values of gross margin between (i) NE_1=5 and NE_1=0, and (ii) NE_1=10 and NE_1=0.