



AgEcon SEARCH
RESEARCH IN AGRICULTURAL & APPLIED ECONOMICS

The World's Largest Open Access Agricultural & Applied Economics Digital Library

This document is discoverable and free to researchers across the globe due to the work of AgEcon Search.

Help ensure our sustainability.

Give to AgEcon Search

AgEcon Search
<http://ageconsearch.umn.edu>
aesearch@umn.edu

*Papers downloaded from **AgEcon Search** may be used for non-commercial purposes and personal study only. No other use, including posting to another Internet site, is permitted without permission from the copyright owner (not AgEcon Search), or as allowed under the provisions of Fair Use, U.S. Copyright Act, Title 17 U.S.C.*

Pest Control in the Presence of Pest Suppression by Natural Enemies

Wei Zhang and Scott M. Swinton*

**Department of Agricultural Economics
Michigan State University
East Lansing, MI, USA 48824-1039**

Selected Paper prepared for presentation at the American Agricultural Economics Association Annual Meeting, Long Beach, California, 23-26 July 2006.

Copyright 2006 by Wei Zhang and Scott M. Swinton. All rights reserved. Readers may make verbatim copies of this document for non-commercial purposes by any means, provided that this copyright notice appears on all such copies.

* Wei Zhang (zhangwe9@msu.edu) is a Ph.D. candidate and Scott M. Swinton (swintons@msu.edu) is a professor, Department of Agricultural Economics, Michigan State University, East Lansing, MI 48824-1039, USA.

The authors are grateful for support from the “KBS-LTER Project: Long-term Ecological Research in Row-crop Agriculture” (NSF #0423647). They thank Richard Horan and Robert Myers for comments, Douglas Landis, Christine DiFonzo, Michael Brewer, Alejandro Costamagna, and Mary M. Gardiner for data and other members of the USDA Risk Avoidance and Mitigation Program project on “Soybean Aphid in the North Central U.S.: Implementing IPM at the Landscape Scale” for informative discussions.

Pest Control in the Presence of Pest Suppression by Natural Enemies

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 an “ecological 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 ecological 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 programming 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. The paper offers a preliminary, lower bound estimate of the value of natural pest predation as inferred from the insecticide input replacement cost per acre for the area where the natural enemy complex can suppress pest population below the level at which it causes damage. A sensitivity analysis shows that numerical solutions for the ecological economic threshold are sensitive to biological parameters such as predation rate and net growth rate of pest population. 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) 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 in 1999 (RAMP, 2004 and 2006). The SBA 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 SBA¹. 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 control² has chiefly been assessed through *ex post* impact assessments (Hill and Greathead, 2000), with little economic 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

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.

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 aphids/plant (Ragsdale et al., 2006) is that the extension threshold 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 treatment³, this study offers a two-dimensional concept of “ecological economic threshold”. Empirically solved with the dynamic programming (DP) technique, the ecological 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, DP 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

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).

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 DP model and derive a numerical solution 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 by cumulative population (cumulative aphid days). To be consistent, the natural enemy population is measured in cumulative units as well. Cumulative population (or “population” for short hereafter) variables approximate continuous processes in discrete time, thus providing a more accurate picture of the biological states than point-valued discrete variables.

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 predicted yield at stage R5 is carried through to the final reproductive stage (R8), when harvest occurs so that SBA control is only meaningful during R1-R4.

Soybean aphid population

The dynamics of field SBA population 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 SBA population at the beginning of stage $t+1$, NE_t denotes population of natural enemies in 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 trial (Table 1)) are first simulated from the Costamagna et al. (2006) model, based on which we derive *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:

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

Note that \hat{I}_t differs from I_t in equation (1) in that \hat{I}_t , computed from simulation output, is subsequently used to estimate model parameters ng_t , whereas I_t represents field population that is subject to both natural suppression and human control.

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 the field, jointly contributing to population regulation in soybeans (Fox and Landis, 2002). Since

viable biological control options are not available at present⁴, this study focuses on insecticidal control, taking into account natural suppression and the non-target effect of insecticide on natural enemies⁵.

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 (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,

⁴ Douglas Landis, Professor, Department of Entomology, Michigan State University, personal communication, September 27, 2005.

⁵ 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).

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 aggregate natural enemy population in stage $t+1$ is given by:

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

$(t=1,2,3)^6$

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 (Table 1):

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

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

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:

⁶ Note we do not need $t=4$ for the natural enemy population because SBA population in the last stage I_5 is affected by $NE_{t+1=4}$ ($t=3$).

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

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

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

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):

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

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.

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

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 $y_{t+1} = \frac{\hat{y}_t + \mu_t \cdot (I_t / \tilde{\gamma}_t)^\delta}{1 + (I_t / \tilde{\gamma}_t)^\delta}$, 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

We define the producer's objective as maximizing the expected gross margin of pest management, derived by subtracting total control cost from revenue, subject to a set of biological constraints on pest population, natural enemy population, and yield potential. Mathematically, the objective function can be written as:

$$J(I_1, N_1, y_1) = \underset{x_t=0 \text{ or } 1}{\text{Max}} \left\{ p \cdot y_h - \sum_{t=1}^T c(x_t) \right\} \quad (8)$$

subject to equations (1), (3), and (5). I_t , NE_t , and y_t are given. 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 Bellman equation for the dynamic problem (Bellman, 1957) is given by:

$$V_t(I_t, NE_t, y_t) = \underset{x_t=1 \text{ or } 0}{\text{Max}} \{f_t(x_t) + E_t[V_{t+1}(I_{t+1}, NE_{t+1}, y_{t+1})]\}^7 \quad (9)$$

subject to equations (1), (3), and (5), and I_t , NE_t , and y_t given, where the reward function $f_t(x_t)$ equals the control cost if $x_t=1$ and equals zero if $x_t=0$. The Bellman equation is solved via backward recursion with a terminal reward of sale revenue in period $T+1$ ($t=T=5$). The empirical model was solved using the discrete-state/action dynamic program “DDPSOLVE”, a MatLab code developed by Fackler and Miranda (1997-2002).

III. Empirical results

Parameters used in the DP model

The empirical estimates of predation-free net growth rate of SBA population for each stage ng_t are computed using simulated SBA growth pseudodata from the Costamagna et al. (2006) model, starting with an average infestation population of 1.8175 SBA per plant observed on the initial colonization day in 2005 (June 6) at the KBS (Table 1). Free of predators, the simulated SBA population increases rapidly after colonization and peaks in stage R4, after which it starts to crash. The net population growth rate peaks during stage R3 at a level 23.73 times the population in R2. Empirical validation of our estimates is not feasible, because SBA population data collected in field trials are subject to natural suppression whereas the net growth rates computed from simulation output are not.

⁷ No discount factor is included for this single-season optimization problem due to its relatively short duration.

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).

For natural enemy population dynamics, the net decline rate (d_t) and the reproduction rate (b_t) were statistically estimated from field trial data collected at KBS in 2005 (Table 1). Unfortunately, estimates for only one stage (R3) both attain significance at the 90% confidence level and conform to the theoretical expectation of negative decline rate and positive reproduction rate.⁸ Specifically, if SBA prey are absent, for each additional natural enemy in stage R3, the population of natural enemies will decline from stage R3 to R4 by -0.9396. For each SBA eaten by each additional natural enemy in stage R3, the population of natural enemies will grow from stage R3 to R4 by $0.0002 \cdot I_3$.

Data used to estimate the yield response function were collected from two sites (the Bean and Beet farm in the Thumb region of eastern Michigan [Saginaw County] and KBS in southwestern Michigan [Kalamazoo County]) in 2004 and 2005. Table 2 reports only estimation results from the Cousens rectangular hyperbolic model using the pooled data from both sites and years because the two MMF models did not fit the data well. Pest damage significantly affects yield potential in stages R1, R3, and R4 in models where the maximum yield loss parameter θ_i is restricted to be one (maximum allowable yield loss = 100%). In stage R1, the estimate of \hat{y}_i indicates that pest-free potential yield or average historical yield is 45.57 bu/ac, of which 0.00056% would be lost to each SBA per plant in that stage. Yield potential responds to pest damage most in stage R3, with an

⁸ In addition to data limitations, the lack of desired estimation outcomes may also be due to the degree to which basic assumptions for the simple predatory-prey model are violated in field-level data, such as closed system and no alternative prey. Indeed, it is reasonable to expect different parameter signs in more complicated systems (for example, in open systems, generalist predators are highly mobile, actively migrate, and prey on multiple prey species).

estimated 0.00011% of previous yield potential forgone due to per SBA per plant. The Cousens rectangular hyperbolic model is preferred as the simplest functional form that cannot be rejected under the Davidson-MacKinnon model specification test.

For the DP analysis, constant parameters are employed in the transition equations. 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 growth parameters. We therefore apply to all growth stages the estimated coefficients that are both statistically significant and with theoretically consistent signs. Specifically, we assume the proportion of yield potential lost per unit of pest population to be 0.00011, the most significant estimated value in the restricted Cousens model for stage R3. For SBA population, we use the constant net growth rate per stage of 12, the mean value of ng_t in Table 1⁹. An adult multi-colored Asian lady beetle consumes 90 to 270 aphids per day with its larvae consuming about 50 to 86 aphids per day (Weeden et al., 2006). A conservative predation rate of 80 SBA/day/NE is chosen for the DP model. The efficacy rate of insecticides on SBA ($k_{I,t}$) and the mortality rate of natural enemies due to non-target effect of insecticides are both assumed to be 99% throughout the season. We use the constant per stage parameter estimates of -0.9396 for the net decline rate of natural enemies (d_t) and 0.0002 for the reproduction rate of natural enemies per prey eaten (b_t). While losing some prediction accuracy in doing so, the exercise serves a valid illustration of using DP to solve for an ecological economic threshold, which provides an

⁹ Obviously, the use of mean net growth rate would affect the predicted dynamics of SBA population, and in turn, the numerical solution of the DP model. The current choice is made in order to accommodate the DDPSOLVE program that was not originally designed to solve for problems with stage-specific parameters. Future research will address this problem.

avenue to explore the effect of natural suppression on optimal insecticide strategies and a preliminary value of this ecosystem service.

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).

Numerical solution of the ecological economic threshold

The ecological 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 ecological economic threshold is calculated by solving the dynamic programming 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.

Not surprisingly, the DP model found that no insecticide spray is necessary during the last stage, regardless of the yield potential and the population of SBA and natural enemies. For yield potential of 25 to 60 bu/ac during stages R1-R4 and for yield potential of 10 to 20 bu/ac during stages R2-R4, the optimal control actions are depicted in Figure 1 (where dots represent “spray” and diamonds represent “no spray” for respective combinations of possible values of pest population and natural enemy population). Figure 1 illustrates that natural enemies reduce the need to spray insecticide. Specifically, in the absence of natural enemies, insecticides are optimal for the lowest positive pest density

modeled, 100 SBA/plant¹⁰. When the natural enemy population reaches 15/plant, chemical control becomes unnecessary until the SBA population reaches 1000/plant. At $I=4,000$ /plant for example, the optimal control is to spray only if the population of natural enemies is less than or equal to 60/plant. At $NE \geq 75$, the same pest level of $I=4,000$ /plant no longer warrants control.

Another key parameter is the expected yield at each soybean growth stage. When the expected initial pest-free yield at R1 is low, insecticide application is not justified for high pest populations, as Figure 2 shows. For instance, with a yield potential of 20 bu/ac during stage 1, a farmer is better off not spraying once SBA population exceeds 15,000/plant, regardless of the population of ambient natural enemies (Figure 2). Too little yield would be saved at the assumed soybean price of \$6.91/bu to justify the cost of SBA control. For lower yield potentials, the range of SBA populations within which spraying is optimal shrinks further. An extreme case is illustrated by Figure 3a for stage R1 yield potential of only 5 bu/ac. Note, however, that if yield potential remains at 5 bu/ac by stages R2-R4, it is optimal to spray at a wider range of higher pest populations when natural enemy populations are low (Figure 3b).

These DP 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 cost savings on insecticide application, 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 also context-dependent,

¹⁰ Note that intervals for possible values of the state variables in our DP model have to be set large enough to ensure that the model does not exceed the MatLab memory limit. For instance, possible values of SBA population only include 0, 100, 200, ..., 500, 1000, 1500, 2000, 3000, 4000, ..., 16000. Hence, we cannot compare our results with Olson and Badibanga (2005)'s conclusion of "spraying 4 times using the 3 aphids/plant threshold". The same precision problem arises when computing the effect of natural enemies, for which possible values rise by intervals of 15.

because the marginal value of an additional unit of natural enemy population depends on the yield potential and the existing pest population. For example, an additional 15 natural enemies per plant (above a 60/plant baseline) in stage 1 given a yield potential of 60 bu/ac implies at a minimum value of \$12.18/ac when the pest population is 4,000/plant.

IV. Sensitivity analysis

To assess the effect of uncertainty associated with some of the economic and biological parameters used in the DP analysis, we perform a sensitivity analysis on selected parameters. Results from six scenarios are compared with the baseline model based on the parameters described above. We report here the results for yield potential of 60 bu/ac in stage R1.

Predation rate increase by 20%. Increasing predation rate by 20% (from 80 to 96 SBA per natural enemy per day) reduces the spray need significantly. For instance, insecticide spray is required regardless of natural enemy population once pest population exceeds 9000 per plant under the new predation rate (Figure 4a), reduced by 2000 SBA per plant as compared to the baseline (Figure 1). The effect is more obvious if a maximum predation rate of 170 (i.e., the mean of the maximum adult consumption rate of 270 SBA/day and the maximum larvae consumption rate of 86 SBA/day by multi-colored Asian lady beetles (Weeden et al., 2006)) is assumed, in which case no spray is necessary at $NE=150$ per plant regardless of pest population (not reported in Figure 4), whereas the same natural enemy population can only sustain a “no spray” decision for pest population lower than 9000 per plant (Figure 1)—a 8000 SBA per plant difference.

Net growth rate increase of 20%. Inflating net growth rate of SBA population by 20% (to 14.4 from 12) only slightly increases the probability of spraying. For instance, at $NE=150$ per plant, spray is not needed if pest population is 8000 per plant when net growth rate of SBA is 12 (Figure 1), whereas it is optimal to spray if pest population is only 7000 per plant when net growth rate is 14.4 (Figure 4b).

100% mortality rate of natural enemies due to insecticide use. Using a 100% mortality rate (instead of 99%) results in only one detectable change to the optimal spray decisions (not reported in Figure 4): At $NE=120$ per plant, spray is necessary if pest population is 7000 per plant and 99% of natural enemies would die from spraying, whereas no spray is required for the same levels of natural enemies and pest if we assume the insecticide completely eliminates the natural enemies.

Optimal control decisions were found to differ little from the baseline model for the following three scenarios: i) control cost of \$18.27/ac (50% inflated from the baseline), ii) output price of \$8.29/bu (20% inflated from the baseline), or iii) output price of \$5.53/bu (20% deflated from the baseline). Overall, the optimal insecticide spray decision was found to be most sensitive to changes in the natural enemy predation rate and the pest population growth rate.

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 an “ecological 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 ecological 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 programming 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. Results from sensitivity analysis show that optimal control decisions are most responsive to changes in predation rate and SBA net growth rate, whereas varying economic parameters (control cost by 50% and output price by 20%) do not change the optimal solution at least within the range of value intervals assumed in our DP model. The finding highlights the importance of getting the biological parameters right.

Based on the DP results, we make a preliminary, lower bound estimate of the value of natural pest predation ecosystem service as inferred from insecticide input replacement cost per acre for the area where the natural enemy complex can suppress SBA population below the level at which it causes damage. Extrapolation of this estimate to the broad region is difficult because we cannot observe the correct area where insecticide treatment could have been (or was) averted because natural enemies suppressed SBA numbers adequately to attribute to effective natural suppression. The problem is that in the real world we do not observe the counterfactual cases of (a) acres that never reached threshold because of natural enemies, and (b) acres that were treated but did not need it because natural enemies would have contained SBA damage.

This research into improved human management of ecosystem services points to important research directions both for the adaptation of the current dynamic bioeconomic model and for tackling fresh modeling challenges. The ongoing research is subject to improvement in five respects. First, the prediction accuracy of the numerical solution obtained from the dynamic programming analysis could be improved by using stage-specific parameters and smaller intervals for possible values of the state variables. This can be done either by modifying the original DDPSOLVE program (Fackler and Miranda, 1997-2002) or by writing new DP code. Second, random effects such as weather play an important role in determining the underlying biological processes (notably insect population dynamics and crop growth) and should be addressed by making the dynamic programming model stochastic. Third, 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 species mixes. Fourth, the uneven quality of the biological parameter estimates needs improvement, which should be possible as more field trial data become available in the future. Finally, improving parameter estimates from the stage-specific yield response to pest damage function will require new data under an experimental design that explicitly records pest exposure within each stage, so that plant response to pest injury in a given stage can be singled out.

Bioeconomic modeling of ecological communities has the advantages of systematically describing biological processes and interactions and predicting their response to management decisions (King et al. 1993). As such, it is an important approach to improving our management of agroecosystems. This study has demonstrated that the ecosystem service of pest suppression by natural enemies can significantly reduce

farmers' dependence on insecticide spraying to control agricultural pests. 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.

References cited

- Alleman, R. J., C. R. Grau and D. B. Hogg (2002). Soybean aphid host range and virus transmission efficiency." Wisconsin Fertilizer, Aglime, and Pest Management Conference, Madison, WI. <http://www.soils.wisc.edu/nextension/FAPM/fertaglime02.htm>
- Aponte, W. and D. Calvin (July 2004). "Entomological notes: soybean aphid", Department of Entomology, Pennsylvania State University, <http://www.ento.psu.edu/extension/factsheets/soybeanAphid.htm>
- Bellman, R. (1957). *Dynamic Programming*. Princeton, NJ: Princeton University Press.
- Berg, H. van den, D. Ankasah, A. Muhammad, R. Rusli, H. A. Widayanto, H. B. Wirasto and I. Yully (1997). "Evaluating the role of predation in population fluctuations of the soybean aphid *Aphis glycines* in farmers' field in Indonesia." Journal of Applied Ecology 34(4): 971-984.
- Bogges, W. G., D. J. GCardelli and C. S. Barfield (1985). "A bioeconomic simulation approach to multi-species insect management." Southern Journal of Agricultural Economics December 1985: 43-55.
- Calkins, C.O. (1983). "Research on exotic pests", In: C. L. Wilson and C. L. Graham (Editors), *Exotic Plant Pests and North American Agriculture*. New York, Academic Press, pp. 321-359.

- Cardinale, B.J., C.T., Harvey, K. Gross, A.R., Ives (2003). "Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem." Ecology Letters, 6: 857-65.
- Costamagna, A. C. and D. A. Landis (2005). "Predators exert top-down control of soybean aphid across a gradient of agricultural management systems." Unpublished manuscript, Department of Entomology, Michigan State University, East Lansing, MI.
- Costamagna, A. C., W. van der Werf, F. J. J. A. Bianchi, and D. A. Landis (2006). "Predictive model for the growth of field populations of *Aphis glycines* (Hemiptera: Aphididae) in soybean." Unpublished manuscript, Department of Entomology, Michigan State University, East Lansing, MI
- Cousens, R. "A simple model relating yield loss to weed density." Annals of Applied Biology 107(1985): 239-252.
- Csáki, C. (1985). *Simulation and Systems Analysis in Agriculture*, Amsterdam: Elsevier.
- Davidson, R., and J. G. MacKinnon (1981). "Several Tests for Model Specification in the Presence of Alternative Hypotheses." Econometrica Vol. 49, no. No. 3. (May, 1981): pp. 781-793.
- DiFonzo, C. D. and R. Hines (2002). "Soybean aphid in Michigan: update from the 2001 season." MSU Extension Bulletin E-2748. Michigan State University. East Lansing, MI
- Fackler, P. L., and M. J. Miranda (1997-2002). "CompEcon Toolbox", developed to accompany: *Applied Computational Economics and Finance*, MIT Press, <http://www4.ncsu.edu/~pfackler/compecon/toolbox.html>
- Fang, H. S., H. H. Nee and T. G. Chou (1985). "Comparative ability of seventeen aphid species to transmit tobacco vein-banding mosaic virus." Bull. Taiwan Tobacco Res. Inst. 22: 41-46.
- Fox, T. B. (2002). "Biological control of the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae)." M.S. Thesis. Department of Entomology. East Lansing, Michigan State University.
- Fox, T. B. and D. A. Landis (2002). "Impact of habitat management on generalist predators of the soybean aphid, *Aphis glycines* Matsumura." First International Symposium on Biological Control of Arthropods, Honolulu, HI, Jan 13-18, 2002.
- Fox, T. B., D. A. Landis, F. F. Cardoso and C. D. Difonzo (2004). "Predators Suppress *Aphis glycines* Matsumura Population Growth in Soybean." Environmental Entomology 33(3): 608-618.

- Harper, J. K., J. W. Mjelde, M. E. Rister, M. O. Way and B. M. Drees (1994). "Developing flexible economic thresholds for pest management using dynamic programming." Journal of Agricultural and Applied Economics 26(1): 134-147.
- Heimpel, G. E., D. W. Ragsdale, R. Venette, K. R. Hopper, R. J. O'Neil, C. E. Rutledge and Z. Wu (2004). "Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits." Ann. Entomol. Soc. Am. 97(2): 249-258.
- Hill, G. and D. Greathead (2000). "Economic evaluation in classical biological control." In: *The Economics of Biological Invasions*, C. Perrings, M. Williamson and S. Dalmazzone. Cheltenham (Editors), UK, Northampton, MA, USA, Edward Elgar: 208-226.
- Jameson-Jones, S. (2005). "Insect and Insect Management: Soybean Aphid", University of Minnesota. <http://www.soybeans.umn.edu/crop/insects/aphid/aphid.htm>. Last updated March 22, 2005, accessed May 25, 2005.
- Kaiser, M. E., T. Noma and M. Brewer (2005). "Hymenopteran parasitoids and dipteran predators of soybean aphid in Michigan." Unpublished manuscript, Department of Entomology, Michigan State University, East Lansing, MI.
- King, R. P., D. W. Lybecker, A. Regmi and S. Swinton (1993). "Bioeconomic models of crop production systems: design, development, and use." Review of Agricultural Economics 15(2): 389-401.
- Krishna, V.V., N.G., Byju and S., Tamizheniyan (2003). "Integrated pest management in Indian agriculture: a developing economic perspective." In: E.B. Radcliff, W.D. Hutchison (Editors), *IPM World Textbook*, St. Paul, MN.
- Landis, D. A., T. B. Fox and A. C. Costamagna (Fall 2004). "Impact of multicolored Asian Lady Beetle as a biological control agent." American Entomologist 50(3): 153-154.
- Losey, J. E. and M. Vaughan (2006). "The economic value of ecological services provided by insects." Bioscience, 56(4): 331-323.
- McKeown, C. H. (2003). "Quantifying the Roles of Competition and Niche Separation in Native and Exotic Coccinellids, and the Changes in the Community in Response to an Exotic Prey Species." M.S. Thesis, Michigan State University.
- Morgan, P. H., L. P. Mercer and N. W. Flodin (1975). "General model for nutritional responses of higher organisms." Proceedings of the National Academy of Sciences of the USA 72: 4327-4331.

- National Soybean Research Laboratory (NSRL) (2002). "Illinois soybean pathology and entomology research: soybean aphid", NSRL Factsheet #4, University of Illinois, Urbana-Champaign. <http://www.nsrl.uiuc.edu/>.
- Naylor, R. and P. Ehrlich (1997). "Natural pest control services and agriculture." In: *Nature's Services: Societal Dependence on Natural Ecosystems*, G. Daily (Editor), Washington DC, Island Press. pp. 151-74.
- Nielsen, C. and A. E., Hajek (2005). "Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), population by existing natural enemies in New York State, with emphasis on entomopathogenic fungi." *Environmental Entomology*, 34(5): 1036-1047.
- North Central Pest Management Center (NCPMC) (2005). "National pest alert: soybean aphid", USDA North Central Pest Management Center. <http://www.ncpmc.org/alerts/soybeanaphid.cfm>.
- North Central Soybean Research Program (NCSRP) (2004). "Soybean aphid research update", North Central Soybean Research Program. www.planthealth.info
- Olson, K. and T. Badibanga (2005). "A bioeconomic model of the soybean aphid treatment decision in soybeans." Selected paper, American Agricultural Economics Association Annual Meeting, Providence, RI, July 24-27, 2005.
- Ostman, O., B., Ekbom and J. Bengtsson (2003). "Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden." *Ecological Economics*, 45: 149-58.
- Pandey, S., and R. W. Medd (1991). "A Stochastic Dynamic Programming Framework for Weed Control Decision Making: An Application to *Avena fatua* L." *Agricultural Economics* 6, no. 2: 115-128.
- Pedigo, L. P., S. H. Hutchins and L. G. Higley (1986). "Economic injury levels in theory and practice." *Ann. Rev. Entomol.* 31: 341-68.
- Potter, B. and W. Hansen (2005). "Seed applied insecticide efficacy against the soybean aphid (*Aphis glycines*) and bean leaf beetle (*Certonma trifurcata*)", University of Minnesota. <http://www.soybeans.umn.edu/crop/insects/aphid/aphid.htm>. Accessed May 25, 2005.
- Ragsdale, D. W., E. W. Hodgson, B. P. McCornack, K. A. Koch, R. C. Venette and B. D. Potter (2006). "Soybean Aphid and the Challenge of Integrating Recommendations within an IPM System." *Illinois Crop Protection Technology Conference: 2006 Proceedings*. University of Illinois Extension. Champaign-Urbana, January 4-6, 2006. <http://www.ipm.uiuc.edu/conferences/cptc/proceedings.pdf>. Pages 103-110. Accessed May 30, 2006.

- Reichelderfer, K. H., and F. E. Bender (1979). "Application of a simulative approach to evaluating alternative methods for the control of agricultural pests." American Journal of Agricultural Economics 61: 258-267.
- 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 2006). http://www.soybeans.umn.edu/crop/insects/aphid/aphid_ramp.htm
- Risk Avoidance and Mitigation Program project on "Soybean Aphid in the North Central U.S.: Implementing IPM at the Landscape Scale" (RAMP) (2004). Project update, Vol. 0-1 (Dec 2004). http://www.soybeans.umn.edu/crop/insects/aphid/aphid_ramp.htm
- Rutledge, C. E., R. J. O'Neil, T. B. Fox and D. A. Landis (2004). "Soybean aphid predators and their use in IPM." Annals of the Entomological Society of America 97: 240-248.
- Saphores, J.-D. M. (2000). "The Economic Threshold with a Stochastic Pest Population: A Real Options Approach." American Journal of Agricultural Economics 82, no. 3: 541-555.
- Sharov, A. A. (1996, 1997, 1999). "Quantitative Population Ecology On-line Lectures," vol. 2006, Department of Entomology, Virginia Tech University, Blacksburg, VA. <http://www.gypsy moth.ento.vt.edu/~sharov/PopEcol/popecol.html>
- Smith, G. S. and D. Pike (2002). "Soybean Pest Management Strategic Plan". St. Louis, Missouri, USDA North Central Region Pest Management Center and United Soybean Board.
- Song, F., S. M. Swinton, C. DiFonzo, M. O'Neal, and D. W. Ragsdale (2006). "Profitability Analysis of Soybean Aphid Control Treatments in Three North-central States." Staff Paper No. 2006-24. Department of Agricultural Economics, Michigan State University, East Lansing, MI.
- Stevenson, W. R. and C. R. Grau (2003). "Virus resistance: a possible solution to snap bean loss." Wisconsin Fertilizer, Aglime, and Pest Management Conference, Madison, WI. <http://www.soils.wisc.edu/nextension/FAPM/fertaglime02.htm>
- Swinton, S. M. and C. P. Lyford (1996). "A test for choice between hyperbolic and sigmoidal models of crop yield response to weed density." Journal of Agricultural, Biological, and Environmental Statistics 1(1): 97-106.
- Swinton, S., J. Sterns, K. Renner and J. Kells (1994). "Estimating weed-crop interference parameters for weed management models." Research Report 538. Michigan Agricultural Experiment Station, Michigan State University, East Lansing, MI.

- Taylor, C. R., and O. R. Burt (1984). "Near-Optimal Management Strategies for Controlling Wild Oats in Spring Wheat." American Journal of Agricultural Economics 66: 50-60.
- Thies, C. and T. Tscharntke (1999). "Landscape structure and biological control in agroecosystems." Science, **285**(5429): 893-895.
- Thies, C., I. Steffan-Dewenter and T. Tscharntke (2003). "Effects of landscape context on herbivory and parasitism at different spatial scales." Oikos, 101: 18-25.
- Thomas, M. B. (1999). "Ecological approaches and the development of "truly integrated" pest management." Proceedings of the National Academy of Sciences of the USA, 96(May 1999): 5944-5951.
- Thompson, A. and T. German (2003). "Soybean aphid and virus incidence in snap beans." Wisconsin Fertilizer, Aglime, and Pest Management Conference, Madison, WI. <http://www.soils.wisc.edu/nextension/FAPM/fertaglime02.htm>
- Weeden, C., T. Shelton, Y. Li and M. Hoffmann (2006). "Biological Control: A Guide to Natural Enemies in North America", Cornell University. <http://www.nysaes.cornell.edu/ent/biocontrol/predators/harmonia.html>
- Wilby, A. and M.B. Thomas (2002). "Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification." Ecology Letters, 5: 353-60.
- Williams, I. S., W. van der Werf, A. M. Dewar, and A. F. G. Dixon (1999). "Factors affecting the relative abundance of two coexisting aphid species on sugar beet." Agricultural and Forest Entomology 1: 119-125.
- Zacharias, T. P., and A. H. Grube (1986). "Integrated Pest Management Strategies for Approximately Optimal Control of Corn Rootworm and Soybean Cyst Nematode." American Journal of Agricultural Economics 68, no. 3: 704-715.
- Zacharias, T. P., J. S. Liebman, and G. R. Noel (1986). "Management Strategies for Controlling Soybean Cyst Nematode: An Application of Stochastic Dynamic Programming." North Central Journal of Agricultural Economics 8, no. 2: 175.
- Zavaleta, L., and W. Ruesink (1980). "Expected benefits from nonchemical methods of alfalfa weevil control." American Journal of Agricultural Economics 62: 801-805.

Table 1. Key biological parameters estimated from 2005 field trial data at Kellogg Biological Station (Kalamazoo County, Michigan)

	Number of days in plant growth stages	Net growth rate of cumulative SBA population (ng_t) ¹	Net decline rate of NE (d_t)	Reproduction rate of NE per prey eaten (b_t)
R1	4			
R2	8	19.94	-0.4321	0.0007
R3	13	23.73	-0.2459	-0.0001
R4	15	4.36	-0.9396***	0.0002*
R5	7	0.34	3.0597***	-0.0006***

* significant at 10%; ** significant at 5%; *** significant at 1%

¹ Computed from simulated data from Costamagna et al. (2006)'s model and number of days in plant growth stages.

Table 2. Estimation results from the Cousens rectangular hyperbolic model

	<i>R1</i>		<i>R2</i>		<i>R3</i>		<i>R4</i>		<i>R5</i>	
	Unrestricted	Restricted	Unrestricted	Restricted	Unrestricted	Restricted	Unrestricted	Restricted	Unrestricted	Restricted
\hat{y}_t	50.50273*** (1.38206)	45.57249*** (1.16535)								
η_t	0.88833 (1.68182)	0.00056** (0.00025)	0.00002 (0.00005)	-0.00001 (0.00005)	0.00428 (0.00942)	0.00011*** (0.00003)	0.00001 (0.00000)	0.00001* (0.00000)	0.00000 (0.00000)	-0.00021** (0.00010)
θ_t	0.24226*** (0.03809)	1	-0.02383 (0.03814)	1	0.09050** (0.03920)	1	2.13365 (6.53003)	1	-0.00250 (0.02241)	1
Obs	115	115	115	115	115	115	95	95	43	43
Adj R-sq	0.95	0.94	0.95	0.94	0.96	0.95	0.96	0.95	0.94	0.94

Standard errors in parentheses

* significant at 10%; ** significant at 5%; *** significant at 1%

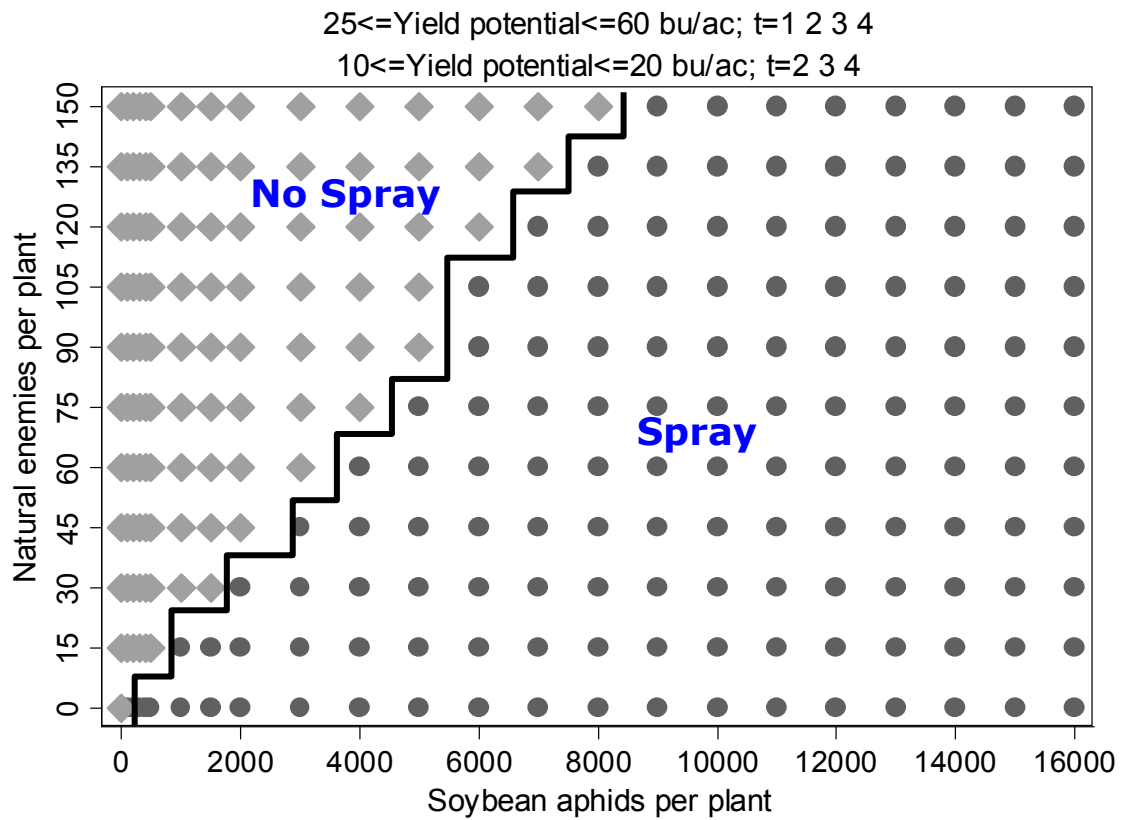


Figure 1. Optimal control actions for yield potential of 25 to 60 bu/ac during stages R1 to R4 and for yield potential of 10 to 20 bu/ac during stages R2 to R4

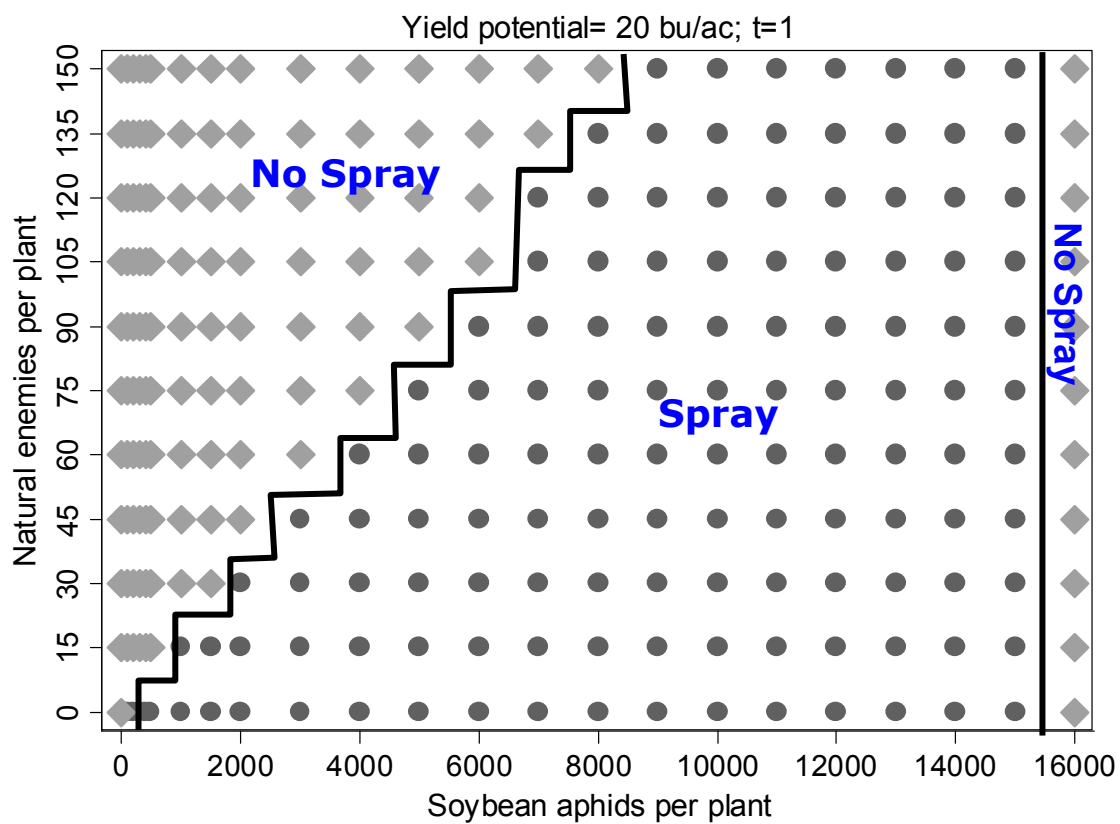
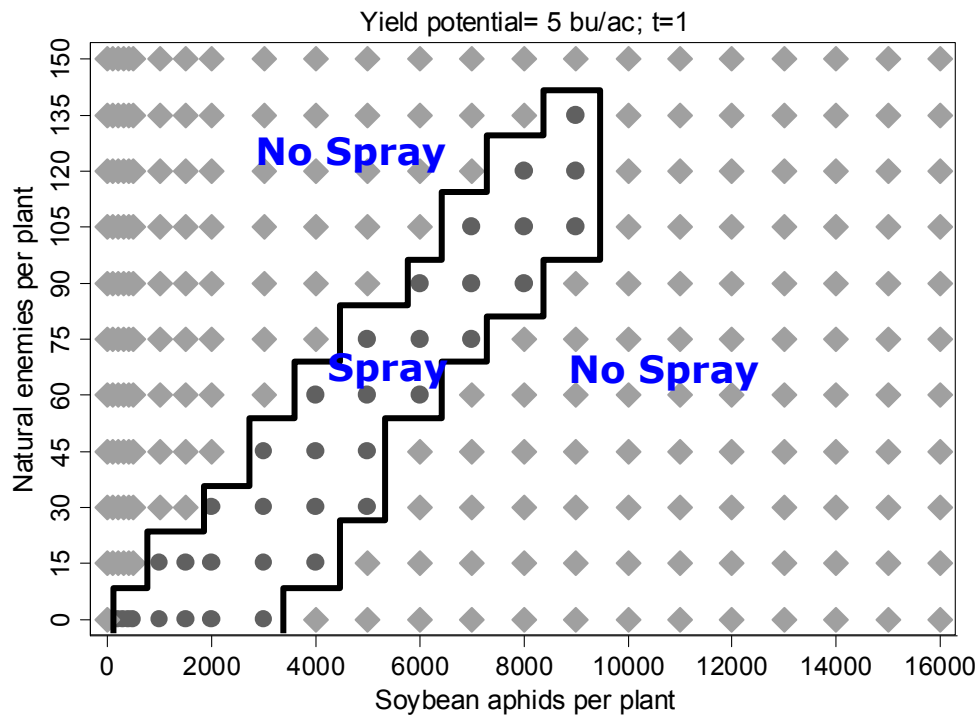
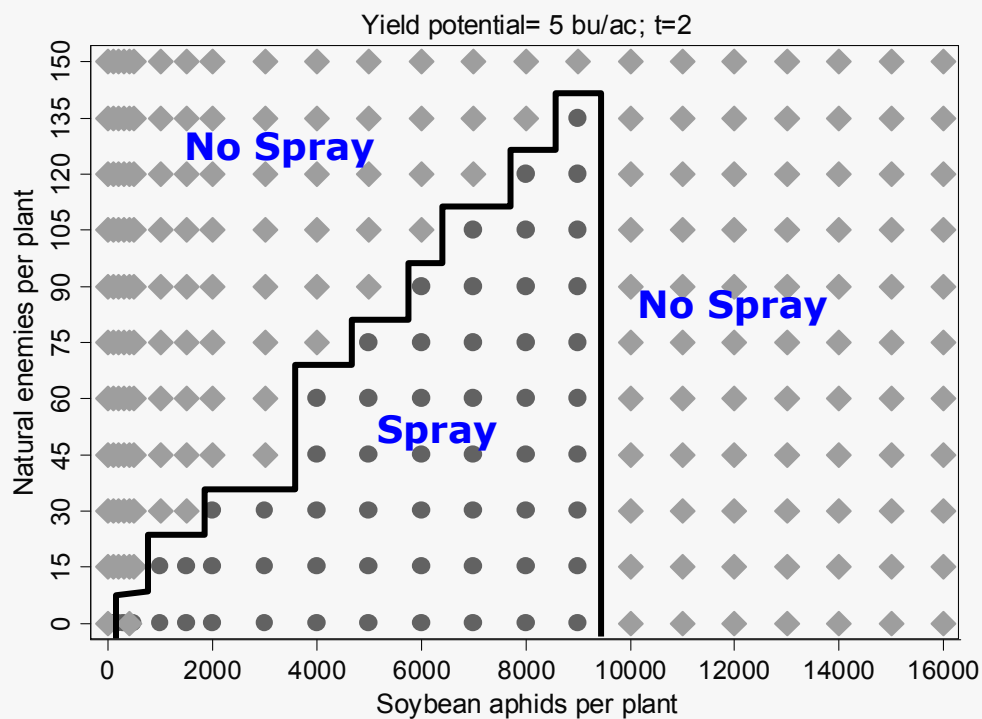


Figure 2. Optimal control actions for yield potential of 20 bu/ac in stage R1

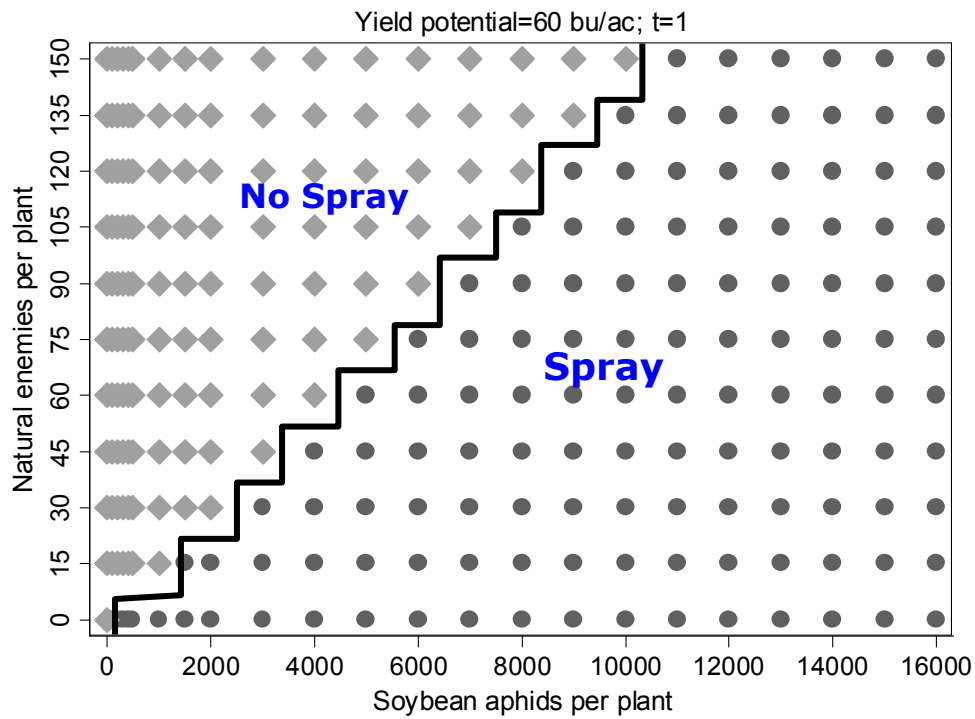


(a)

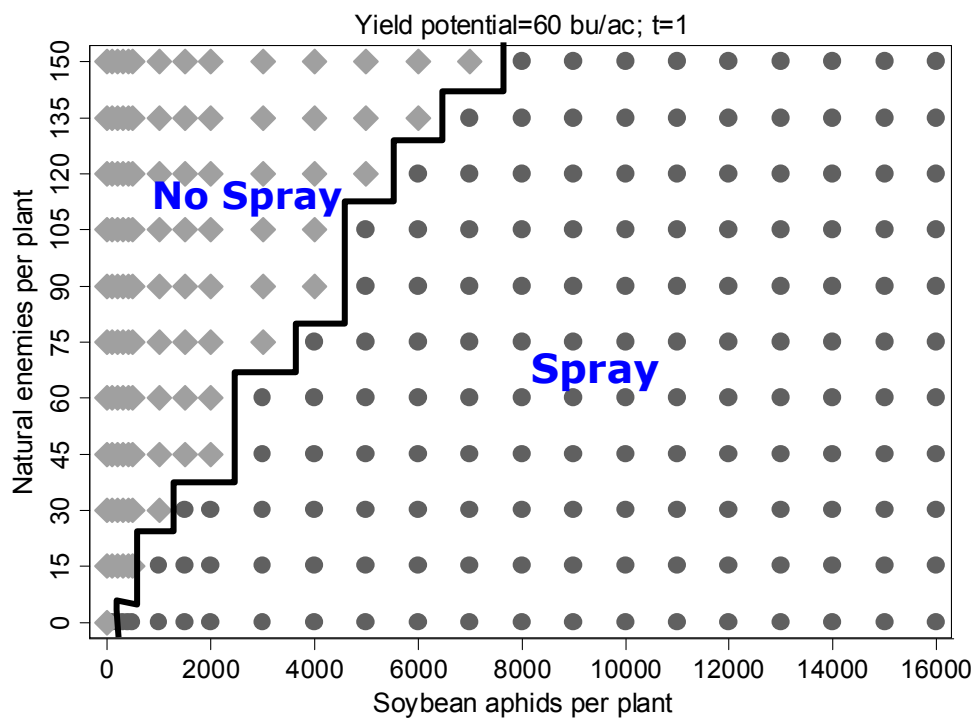


(b)

Figure 3. Optimal control actions for yield potential of 5 bu/ac during stages R1 to R2 (Optimal control actions during stages R3 and R4 are similar to those in stage R2 with only minor differences (not reported).)



(a)



(b)

Figure 4. Optimal control actions for yield potential of 60 bu/ac in R1 for two sensitivity analysis scenarios: a) predation rate increases by 20%, and b) net growth rate of SBA increases by 20%