

# Research and Extension Supporting Ecologically Based IPM Systems

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**SUMMARY.** Integrated Pest Management (IPM) has a long history of developing pest management strategies based on ecological principles.

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While IPM systems differ in their reliance on chemical controls, an ecological approach to IPM offers opportunities both to test ecological theory and to develop novel pest management techniques. We review ecological concepts relevant to habitat management as a tool for managing pest and natural enemy populations in annual cropping systems, and we describe a case study of the impacts of habitat management on predatory ground beetles (Coleoptera: Carabidae) in annual cropping systems. Experimental manipulation of carabid population density revealed a positive relationship between the abundance of carabids in cropland and prey removal. Provision of stable refuge habitats in annual crops increased carabid species richness and abundance. Further studies demonstrated that the presence of refuge habitats mitigated the impacts of insecticide disturbance on carabid abundance and community structure in adjacent cropland. These results were used as part of a program to educate extension agents and producers in the principles of agroecology and ecologically based pest management. We encourage extension agents and producers to test novel practices using adaptive management. In this approach, predictions are formulated regarding specific management practices and evaluated against the results. Based on these observations, management is then adapted to yield the desired outcome. Such an approach recognizes the inherent uncertainty of multifactor ecological manipulation while providing producers with methods to manage this uncertainty. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-HAWORTH. E-mail address: <docdelivery@haworthpress.com> Website: <<http://www.HaworthPress.com>> © 2004 by The Haworth Press, Inc. All rights reserved.]

**KEYWORDS.** Agroecology, ecologically based pest management, biological control, adaptive management

### INTRODUCTION

In a review of the history of Integrated Pest Management (IPM), Kogan (1998), states that IPM has emerged as one of the most recognizable and robust concepts in modern agriculture. In spite of, or perhaps due to its wide acceptance, there are many definitions of IPM. Most modern definitions of IPM include an emphasis on; (1) use of appropriate pest control measures either singly or in concert, (2) economic benefits to producers and society, (3) environmental benefits, and (4) the need to consider multiple pests (Kogan, 1998).

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Prior to the advent of synthetic organic pesticides, pest control was achieved primarily through knowledge of pest biology integrated with multiple control practices such as variety selection, crop rotation, cultural and biological controls (National Research Council, 1996). A sound understanding of the interactions between a pest and its crop environment was fundamental for the success of such systems. However, with the advent of highly effective chemical pest controls in the late 1940s, emphasis began to shift towards their use in a single tactic approach (Newsom, 1980). The concepts of integrated control and eventually IPM grew out of the recognition that chemical controls needed to be integrated into a broader concept of pest management (Stern et al., 1959).

In spite of this recognition, it has been argued that most IPM systems are still dominated by an over-reliance on chemical pest controls (National Research Council, 1996). In addition, because it is possible to implement such approaches with little consideration of the characteristics, processes, and dynamics of agroecosystems (Levins and Wilson, 1980), producers have lost some of their former appreciation for the ecology of their production systems. This situation poses a challenge to agroecologists. How do we conduct IPM research in a way that enhances our fundamental understanding of agroecosystems and, at the same time, allows us to effectively educate growers regarding their management options?

In this contribution we specifically examine the potential for incorporating an ecological approach to aid in the development and application of IPM systems for sustainable annual crop agriculture. We utilize a case study from our work on carabid beetles (Coleoptera: Carabidae) dynamics as an example of the potential importance of incorporating an ecological perspective in the design of IPM programs. We do so by first, introducing the ecological concepts and research background related to this particular case study. We then describe a series of experiments aimed at understanding the ecology of carabid beetles as generalist predators of weeds and insects in annual row crop agriculture. Finally, we discuss how adaptive management, a concept developed by ecosystem managers, may be useful in the implementation of such ecologically based IPM systems.

We acknowledge that due to the case-specific nature of many ecological processes, there are undoubtedly exceptions to any ecological principles presented here (Letourneau, 1998). However, despite this limitation, ecological properties emerging from natural systems have been successfully used to model perennial grain cropping systems (Jackson and

Piper, 1989) and tropical agricultural systems (Ewel, 1986). We also acknowledge an entomological bias on our part and an emphasis on annual row-crop agriculture that we hope will not distract from the main points of the manuscript. Our goal is that the concepts presented here might stimulate critical thinking on how ecological principles may be further used to define and implement ecologically-based IPM systems for a variety of pests and cropping systems.

### **ECOLOGICAL CONCEPTS AND INTEGRATED PEST MANAGEMENT**

Modern industrial agriculture can be described as a human-dominated enterprise in which the pressure towards increasing crop yield generates ecosystems characterized by biological simplification, output specialization, subsidized off-farm chemical and energetic inputs, and decreasing environmental heterogeneity (Altieri and Nicholls, 1999; Letourneau and Altieri, 1999; Swift and Anderson, 1993; Tscharntke and Kruess, 1999). There is an increasing body of ecological principles and empirical studies showing that such farming systems may pose long-term risks to sustainability and environmental health (Matson et al., 1997). In this section, we analyze three ecological concepts we believe are relevant to the successful implementation of IPM strategies in annual crop production systems: (1) resource predictability, (2) habitat simplification and fragmentation, and (3) disturbance regimes. A brief summary of the ecological concepts discussed in the next sections is presented in Table 1.

#### ***Resource Predictability and Arthropod Abundance***

Crop populations in large-scale annual monocultures represent a stable and predictable resource for herbivores. However, because of density-independent oscillations in their populations, herbivores in annual crops represent a less predictable resource for their predators and parasites. This differential predictability in resources for herbivores versus natural enemies contributes to the increased extinction rates of organisms occupying higher trophic levels of annual crops (Tscharntke and Kruess, 1999). From an applied point of view, this low resource predictability may partially explain the lower rates of success of imported biological control agents in annual crop agriculture (Hall and Ehler, 1979; Hall, Ehler, and Bisabri-Ershadi, 1980).

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TABLE 1. Summary description of several ecological concepts related to the development and implementation of ecologically based IPM.

Ecological Concept	Reference	Applicability to IPM
Resource predictability	Tscharntke and Kruess, 1999	While crops represent a stable and predictable resource for herbivores, herbivores present lower predictability for higher trophic levels resulting in increased local extinction of predators and parasitoids.
Enemy impact hypothesis	Pimentel, 1961	Increased plant community diversity correlates with higher food and host resources for natural enemies resulting in higher probability of maintaining pest populations at reduced levels.
Resource concentration hypothesis	Root, 1973	Pest outbreaks are commonly observed in large monocultures because herbivores can easily find food in systems with low plant species diversity.
Cyclic colonization	Wissinger, 1997	Stable habitats such as woodlots provide resources that promote natural enemy survivorship. Early in the growing season, natural enemies colonize crop fields from these stable habitats.
Island biogeography	MacArthur and Wilson, 1967	Maintaining large stable habitats in agricultural landscapes increases natural enemy species immigration rates and decreases extinction favoring natural enemy conservation.
Metapopulations	Levins, 1969	A network of stable habitats scattered across agricultural landscapes maintains a series of genetically interconnected local populations of natural enemies.
Disturbance	Pickett and White, 1985	Agricultural management practices such as tillage, pesticide application, nutrient management, cultivation, and harvest represent ecological disturbances that kill natural enemies.
Habitat management	Landis, Wratten, and Gurr, 2000 Lee, Menalled, and Landis, 2001	Stable habitats in agroecosystems can increase natural enemy survivorship and community recovery following disturbance.

Two complementary hypotheses have been proposed to explain the relationship between resource accessibility and pest outbreak in low diversity systems: the enemy impact hypothesis (Pimentel, 1961), and the resource concentration hypothesis (Root, 1973). The enemy impact hypothesis postulates three mechanisms responsible for the relationship

between pest regulation and system diversity. First, an increase in plant community diversity is correlated with higher diversity of herbivore species as well as pollen and nectar that provide alternative food or host supplies to predators or parasitoids. Second, an associated increase in the stability of parasitoid or predator resources secures higher diversity at the primary carnivore trophic level and a greater probability that herbivore species will be maintained below threshold levels. Finally, diverse arthropod communities typically contain many generalist predators with potential to suppress a variety of pest species. The resource concentration hypothesis also proposes three mechanisms to explain the observed high rate of pest outbreaks occurring in large monocultures. First, herbivores can easily find food resources in these conspicuous and low diversity systems. Second, due to the existence of large amount of resources, herbivores often remain in such habitats. Finally, the resource availability in low diverse systems translates into increased herbivore reproduction and greater potential for population (i.e., pest) outbreaks.

### *Habitat Simplification and Fragmentation*

As noted in the previous section, simplified annual cropping systems provide stable and predictable resources for herbivores. For predators and parasitoids, however, the simplification of the agricultural landscape can be viewed as habitat fragmentation because the crop habitat does not by itself provide sufficient resources for their survival. In an agricultural landscape, non-crop habitats can serve as refuges for natural enemies that colonize agricultural fields, kill pests, and return to refuges following a 'cyclic colonization pattern' (Wissinger, 1997). In this context, fencerows, woodlots, and herbaceous strips can be regarded as isolated islands where beneficial organisms can thrive within otherwise inhospitable environments. In a similar way, the theory of island biogeography (MacArthur and Wilson 1967) has been applied to help understand the occurrence of organisms in agricultural landscapes (Kruess and Tscharntke, 1994; Price and Waldbauer, 1994; Simberloff, 1986; Thies and Tscharntke, 1999; Zabel and Tscharntke, 1998). However, in highly simplified agroecosystems, a large species donor area [i.e., the continent as defined by MacArthur and Wilson (1967)] may not exist and the metapopulation model proposed by Levins (1969) can be used as an appropriate theoretical framework for pest control.

In agroecosystems, a metapopulation can be regarded as a series of genetically interconnected local populations living in hedgerows, fence-

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rows, woodlots, and riparian strips. It has been shown that in a metapopulation, dispersal between patches allows local nonequilibrium populations to persist at the regional scale (Murdoch, Chesson, and Chesson, 1985; Murdoch and Briggs, 1996). Although the metapopulation approach has been widely adopted by conservation biologists (McCullough, 1996), agroecologists have yet to incorporate these ideas strongly in the development of IPM systems (Landis and Menalled, 1998; Letourneau, 1998). However, several empirical studies have demonstrated that habitat fragmentation can disrupt ecosystem functions such as host-parasitoid interactions (Kruess and Tscharntke, 1994; Roland, 1993; Tscharntke, 2000), and alter overall natural enemy abundance (Marino and Landis, 1996; Menalled et al., 1999; Nicholls, Parrella, and Altieri, 2001; Thies and Tscharntke, 1999), community richness and diversity (Gut et al., 1982; Colunga-Garcia, Gage, and Landis, 1997), and fecundity (Bommarco, 1998).

### *Disturbance in Annual Crop Systems and Generalist Predators*

In the ecological literature, disturbance is defined as a "relatively discrete event in time that disrupts ecosystems, community or population structure, and changes resources, substrate availability, or the physical environment" (Pickett and White, 1985). In this context, common agricultural practices such as primary and secondary tillage, herbicide and pesticide applications, nutrient management, cultivation, and harvest can each be characterized as disturbance events. Ecologists have long recognized the importance of magnitude, frequency, and predictability of disturbances in determining the species composition and other characteristics of biological communities (Sousa, 1984). At a larger scale, the area and distribution of disturbances influence the spatial arrangement of plant communities in landscapes. Due to bottom-up influences of vegetation on insect communities, plant species composition has been hypothesized to determine the structural and chemical environment for beneficial insects (Askew, 1980; Hawkins and Lawton, 1987; Price, 1991). Therefore, the disturbance regime associated with a given agricultural management system is of vital importance in determining the possibility of implementing an IPM program that incorporates natural enemies as a primary mechanism of pest control.

Landis and Menalled (1998) discuss the importance that agricultural disturbances can have on the abundance, diversity, and effectiveness of beneficial organisms. They argue that management practices can have both direct and indirect effects, and can act at various spatial scales:

within crop fields, at the farm-level, and/or at the landscape-level. The impact that a disturbance regime has on the organisms living in a certain area and on the physical environment can be observed at different time intervals. The short-term impact of agricultural disturbances is to disrupt some portion of the microbial, plant, and animal communities present in the crop field (Booij and Noorlander, 1988; Croft, 1990; Los and Allen, 1983). This is followed by a gradual recolonization of the disturbed area by individuals remaining in the systems or from surrounding areas. Several studies have shown that agricultural practices such as insecticide applications can also have long-term impacts on natural enemy community structure and function (Basedow, 1990; Burn, 1989).

### **HABITAT MANAGEMENT IN ANNUAL CROP IPM SYSTEMS**

From the previous discussion it is clear that a common outcome of modern annual crop agriculture is a reduction in natural enemy effectiveness in association with high abundance of resources that favor herbivore colonization and population growth. This situation ultimately leads to poor pest control and the need for additional disturbances (e.g., pesticide applications) to restrict pest damage (Brust, Stinner, and McCartney, 1985; 1986; Edwards, Sunderland, and George, 1979). To use predators and parasitoids successfully for pest management, it is necessary to modify agroecosystems to conserve natural enemies and enhance their impacts. While use of "soft pesticides" and practices such as application of food sprays can mitigate the immediate impact of disturbance, a comprehensive solution should address the ultimate cause, i.e., the disturbance regime and resulting habitat simplification that reduces habitat suitability for beneficial organisms (Landis and Menalled, 1998). Habitat management, defined as a series of practices meant to "alter habitats to improve availability of resources required by natural enemies for optimal performance," represents a comprehensive approach to reduce the negative impact of agricultural management practices and favor natural enemies in annual crop agriculture (Landis, Wratten, and Gurr, 2000).

Habitat management practices can be implemented at the within-field level, farm level, or landscape level and include practices such as conservation tillage, cover crops, intercropping, and creation of sown plant strips (Altieri and Letourneau, 1982; Landis, Wratten, and Gurr, 2000; Pickett and Bugg, 1998). A common feature of these practices is



at the landscape-level. The organisms living in a certain area are observed at different time intervals. Disturbances to natural animal communities present, 1988; Croft, 1990; Los and al recolonization of the disturbed systems or from surrounding agricultural practices such as long-term impacts on natural enemies (Basedow, 1990; Burn, 1989).

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that a common outcome of reduction in natural enemy effectiveness of resources that favor herbivores. This situation ultimately leads to additional disturbances (e.g., damage (Brust, Stinner, and al., 1979). To address the ultimate cause, habitat simplification that reduces natural enemies (Landis and Menalled, 1999). A series of practices meant to conserve natural enemies and pesticides and practices such as conservation of natural enemies and pesticides. The immediate impact of disturbance is to address the ultimate cause, habitat simplification that reduces natural enemies (Landis and Menalled, 1999). A series of practices meant to conserve natural enemies and pesticides and practices such as conservation of natural enemies and pesticides.

implemented at the within-field level include practices such as strip cropping, and creation of sown cover crops (Landis, Wratten, and Gurr, 1999). A feature of these practices is

an increase in the planned biodiversity (organisms purposely included in the agroecosystem) and the associated biodiversity (soil flora and fauna, herbivores, carnivores, etc.) that colonize the crop fields (Vandermeer and Perfecto, 1995). However, increasing diversity *per se* is not the final objective of habitat management. A key component is to identify the elements of diversity that enhance ecological services and then determine the management practices that will allow establishment, survivorship, and reproduction of these organisms (Altieri and Nicholls, 1999; Nentwig, Frank, and Lethmayer, 1998).

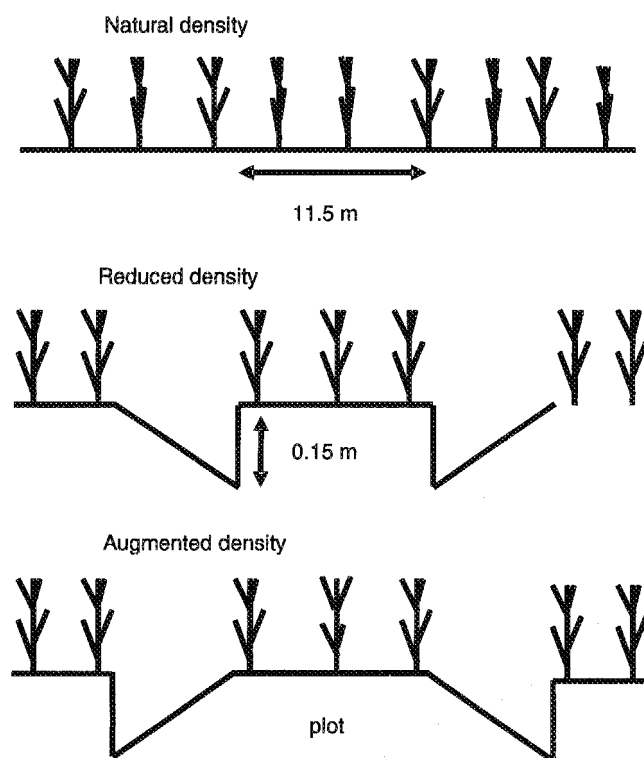
## Can Habitat Management Enhance Carabid Communities? A Case Study

Carabid beetles (Coleoptera: Carabidae) are polyphagous predators commonly found in agricultural systems that have the potential of consuming many pest species (Sopp et al., 1992; Sunderland, 1975; Sunderland et al., 1987; Vickerman and Sunderland, 1975). Several studies have demonstrated that common agricultural practices such as tillage, cultivation and pesticide application frequently reduce carabid abundance (Basedow, 1990; Brust, 1994; House and Parmelee, 1985; Stinner and House, 1990; Terry, Potter, and Spicer, 1993), and alter community characteristics (Cárcamo, Niemelä, and Spence, 1995; Clark, Gage, and Spence, 1997; Kromp, 1989).

We utilized ground beetles as a model system to evaluate the response of beneficial organisms to different types of agricultural management practices. We first evaluated if altering carabid beetle abundance *per se* would influence rates of prey removal in the field. To do so, we manipulated carabid numbers with minimal habitat alteration by creating plots surrounded by different boundaries that selectively affected carabid dispersal (Menalled, Lee, and Landis, 1999). Three treatments were established: (1) naturally occurring communities, (2) augmented communities using ingress boundaries, and (3) reduced communities using egress boundaries (Figure 1). In comparison to the no boundary treatment, carabids increased 54% and decreased 83% in plots surrounded by ingress and egress boundaries respectively. Predation of sentinel onion fly pupae (*Delia antiqua* (Meigen)) was positively correlated with carabid abundance ( $r^2 = 0.70$ ,  $P < 0.0001$ ) confirming the importance of developing a habitat management strategy aimed at increasing the abundance of carabid beetles in crop fields.

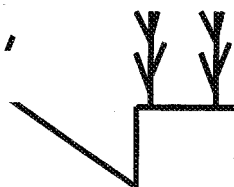
Next, we tested the concept that providing less disturbed habitats in close spatial association with crop fields represents a viable approach to

FIGURE 1. Experimental manipulation of ground-dwelling arthropod density. Top: natural occurring density with no boundary. Center: reduced density, where the number of invertebrates is decreased using egress boundaries. Bottom: augmented density by means of ingress boundaries, i.e., devices that allow invertebrates to move into but not out of a plot.



conserving carabid communities. Undisturbed vegetative refuge habitats such as grasslands, hedgerows, field margins, or grassy strips within a field can enhance carabid abundance, fecundity, and species diversity by supplying overwintering sites, food, and shelter (Lys and Nentwig, 1992; Zangger, Lys, and Nentwig, 1994). We evaluated the importance of herbaceous refuge strips in carabid beetle conservation in a 1.4 ha site arranged in a split-plot design with four 32 m  $\times$  66 m blocks. Each block contained two main plots, one with a 3 m wide refuge strip in the center and the other with a control strip planted with corn (*Zea mays* L.). The refuge strips were established in 1995 using orchard

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grass (*Dactylis glomerata* L.), white clover (*Trifolium repens* L.), and sweet clover (*Melilotus officinalis* L.) surrounding a central strip of perennial flowering plants to provide supplementary food for predators and parasitoids (Carmona and Landis, 1999). Soybean (*Glycine max* L. Merr.) was planted in the crop areas in 1995 followed by oats (*Avena sativa* L.) in 1996 and then three successive years of corn. Between 1996 and 1999, we used a grid of pitfall traps to sample activity-density of adult carabid beetles. Over this period, we detected a steady increase in the number of carabid species (Figure 2) with consistently more individuals trapped in refuge strips than in control strips comprised of corn only (Figure 3) (Carmona and Landis, 1999; Lee, Menalled, and Landis, 2001).

The next step was to assess if refuge habitats could act as sources of natural enemies colonizing adjacent fields, thereby mitigating the consequences of insecticide disturbance. We hypothesized that insecticide application would reduce carabid activity-density, species richness and alter community composition, but that the presence of refuges would allow carabid assemblages to recover in treated crop areas. We utilized the field plots described above to test these hypotheses (Lee, Menalled, and Landis, 2001). Between 1998 and 1999, main plots were divided into two subplots, one of which was treated with terbufos (S-[[[(1,1-dimethylethyl) thio] methyl]; Counter™ 20 CR American Cyanamid), a soil insecticide commonly used in non-rotated corn to control corn

FIGURE 2. Species richness (number of species) of carabid beetles captured in pitfall traps over time in refuge habitat study, E. Lansing, Michigan. Number per year represents total species capture in refuges and crop areas combined. Crop areas planted to oats in 1996 and corn 1997-1999.

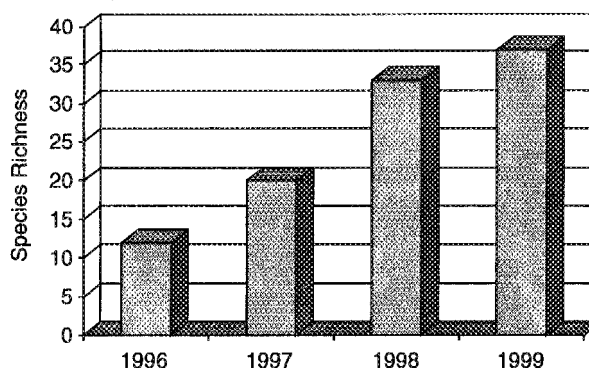
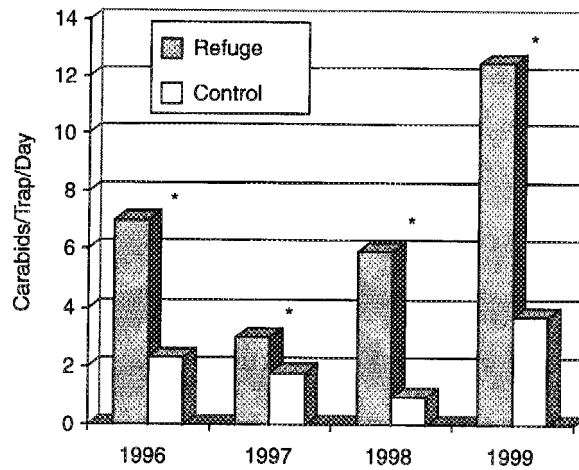


FIGURE 3. Activity density of carabids in refuge strips and corresponding control (crop) strips in refuge habitat study, E. Lansing, Michigan, May-October 1995-1999. Crop areas planted to oats in 1996 and corn 1997-1999. An \* indicates a significant difference ( $p > 0.05$ ) in season long abundance between refuge and control plots within a year as indicated by a t-test.



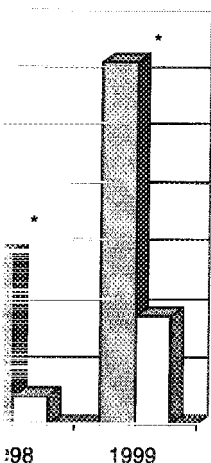
rootworm larvae (*Diabrotica* spp.). Four treatments were established and are referred to as: (1) refuge-untreated crop, (2) refuge-treated crop, (3) control-untreated crop, and (4) control-treated crop.

Before planting and insecticide application in 1998 and 1999, carabid activity-density in the crop area was similar across all treatments. In both years, insecticide application significantly reduced carabid activity-density, species richness and altered community composition in the crop area. Contrary to our predictions, refuge strips did not consistently augment carabid numbers in areas where insecticide was applied. As insecticide toxicity declined, carabid captures in insecticide treated crop areas adjacent to refuges surpassed those where insecticide was not applied, suggesting an interaction between refuges and disturbances that determine the net movement of beneficial organisms in agricultural landscapes (Lee, Menalled, and Landis, 2001).

### *A Refined View*

Results of our studies support the concept of habitat management maintaining higher species diversity and abundance of generalist preda-

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tors in annual crops. Specifically, our work reveals that refuges can in-  
crease carabid movement into disturbed crop habitats, moderating the  
impact of disturbance on communities of these natural enemies. How-  
ever, contrary to our predictions, the interactions between refuges and  
adjacent crop areas were not straightforward. Two different mecha-  
nisms may be responsible for the observed results. If insecticide distur-  
bance reduced the long-term availability of prey, high rates of carabid  
captures in the crop areas could be due to an increase in activity of hun-  
gry carabids (Chiverton, 1984; Frampton et al., 1995; Mauremooto et  
al., 1995; Wheeler, 1991). Alternatively, insecticide disturbance may  
have actually increased prey availability in crop areas in the long term.  
When insecticide inputs eliminate early-season predators, certain prey  
species may thrive and become abundant once toxicity levels have de-  
clined. Under this scenario, the abundance of prey and chemical cues  
emanating from prey may attract or arrest more beetles into the crop  
area (Kielty et al., 1996; Wheeler, 1991). Despite the ultimate cause,  
while refuges harbor many carabids, more carabids might eventually be  
drawn into treated crop areas than untreated crop areas. The mecha-  
nisms responsible for the observed results represent both testable hy-  
potheses for future studies on habitat management and challenges to  
refinement of our ecological understanding of these systems. Although  
lack of correspondence between ecological concepts and practical ap-  
plication can lead to underutilization of ecological knowledge as a  
source of useful IPM guidelines (Dyer and Gentry, 1999), we believe  
that collaboration among ecologists, agronomists, and pest manage-  
ment specialists can address these challenges in a productive fashion.

### EXTENSION OF ECOLOGICALLY BASED IPM SYSTEMS

In our extension programs, we have attempted to provide producers  
and extension agents with an understanding of ecological processes oc-  
curring in annual cropping systems. Two publications have been partic-  
ularly directed towards this effort; "Michigan Field Crop Ecology"  
(Cavigelli et al., 1998) and "Michigan Field Crop Pest Ecology and  
Management" (Cavigelli et al., 2000). Both provide a general frame-  
work of ecological principles as a basis for crop production and pest  
management. Participants in our extension programs have appreciated  
this conceptual framework, but they have also asked for specific man-  
agement practices. However, the recommendations we can provide of-  
ten do not resemble the "recipes" producers have come to expect in the

conventional IPM approach. The ecological management tools we suggest are expected to affect many species and influence processes at different levels of organization. Although implementation of these tools is based on generally applicable ecological principles, the outcomes will be influenced by site and case specific variables. How can we as researchers and educators help producers to manage this complexity? Developments in the concept of ecosystem management over the last decade (Christensen et al., 1996) may provide a guide.

Ecosystem management has emerged as a process for managing public lands with multiple stakeholders, such as rangelands, forested areas and watersheds. It has been adopted as a land management policy by several federal agencies including U.S. Fisheries and Wildlife (Beattie, 1996), Bureau of Land Management (Dombeck, 1996) and U.S. Forest Service (Thomas, 1996). It is also becoming policy for many state government agencies and non-governmental organizations (Yaffee et al., 1996). Although there is no single definition or process for ecosystem management, some basic characteristics are emerging (Christensen et al., 1996). The system must be managed to achieve measurable economic, environmental and social goals while maintaining ecosystem integrity. Sustainability of ecosystem structure and function is a central tenet of ecosystem management, so practices that deplete the system are unacceptable. Ecosystems are dynamic and our knowledge of them is incomplete and constantly changing. Managers must make decisions and take action in this environment of uncertainty. Adaptive management is the key element that transforms ecosystem management from a philosophical or policy framework into a management process.

An adaptive management process acknowledges uncertainty, makes decisions based on the best available knowledge, formulates testable hypotheses about management outcomes with specific, measurable predictions, and proceeds with monitoring to test those management hypotheses (Christensen et al., 1996; Walters and Holling, 1990). Walters and Holling (1990) describe three approaches to adaptive management. First, in an evolutionary approach management is gradually improved as better management options emerge through trial and error. Second, a passive adaptive approach strives for one best model of ecosystem function, and modifies the model as experiments and observation of management outcomes indicate inadequacies. Third, an active adaptive approach acknowledges uncertainty, admits several alternative models and generates hypotheses that would distinguish between those models. They argue that learning will be most rapid with an active adaptive approach.

management tools we suggest influence processes at different scales. Implementation of these tools is not simple. In principle, the outcomes will be variable. How can we as resource managers manage this complexity? Developing a process for managing public lands over the last decade provides a guide.

A process for managing public lands, rangelands, forested areas, and land management policy by the U.S. Forest Service and Wildlife (Beattie, Beck, 1996) and U.S. Forest Service policy for many state government organizations (Yaffee et al., 1998) is a process for ecosystem management (Christensen et al., 1999). The process for achieving measurable ecosystem maintenance and function is a central theme. Factors that deplete the system are identified, and our knowledge of them is increased. Managers must make decisions in the face of uncertainty. Adaptive management is a process for ecosystem management from a management process.

Adaptive management acknowledges uncertainty, makes hypotheses, formulates testable hypotheses, and tests those management hypotheses (Walters and Holling, 1990). Walters (1990) describes adaptive management. Management is gradually improved through trial and error. Second, a model of ecosystem function and observation of management.

Third, an active adaptive management process involves several alternative models and a process to distinguish between those models. Finally, an active adaptive ap-

The need for an ecosystem management approach to management of agricultural pests has been widely recognized (Lewis et al., 1997; Speight, 1983; Sustainable Agriculture Network, 2000). As with other land managers, farmers must make decisions and act in the face of uncertainty when incorporating ecological tools for pest management into their farming operations. Adapting a process developed largely for public lands to agroecosystems under private ownership presents challenges, especially for those changes that are more meaningful if made over significant portions of landscapes (Roberts and Parker, 1998; Jackson and Jackson 2002). Nevertheless, adaptive management may provide a useful process for making management decisions and evaluating outcomes.

Staver (2001) proposed a model for farmer, extensionist and scientist collaboration to implement adaptive management of agricultural weeds. In this approach a group meets at critical points in the crop cycle to identify problems and make management plans, do experiments and monitoring, evaluate the observed results of management, and revise management plans. A great strength of this approach is combining the knowledge and ways of learning of scientists and farmers. Periodic interactions enables the group to revise their understanding of ecosystem functioning, critically examine hypotheses for management, and propose outcomes from diverse perspectives. Farmers, extensionists, and scientists together decide what experiments and observations would best test those hypotheses.

An adaptive management approach thus represents a suitable framework by which ecological knowledge can be applied to IPM decisions. Farmers' intuitive understanding of pest ecology has formed part of crop production technology from the beginning of agriculture (Staver, 2001). Through a process of on-farm observation, logic, experimentation, extrapolation, risk calculation, and communication farmers have accumulated a vast understanding of how an agricultural system works. This "evolutionary" adaptation can be enhanced by an "active" adaptive management approach (Walters and Holling, 1990). The adaptive management hypothesis-testing approach is a decision-making process that may accelerate the application of ecological knowledge to farming practices. This process requires effective interaction between scientists, extension educators, and farmers with all participants agreeing on research priorities, temporal and spatial scales of trials, and decision-making processes (Staver, 2001).

### CONCLUSIONS

The development of IPM reveals a long history of using ecological principles as the basis for understanding agricultural systems and the manipulations necessary to manage pests. However, even within an IPM context, the level of necessary ecological knowledge varies from system to system. In IPM programs where scouting, thresholds and use of chemical pesticides dominate, the need to understand all of the ecological interactions of the system may be reduced. However, advocates of sustainable agriculture generally favor a more ecologically based approach to pest management.

Research on ecologically based IPM opens opportunities to test current ecological concepts in managed systems. In our work, this has yielded confirmation of hypotheses in some cases and lack of correspondence in others. This is to be expected given the complexity of interactions at work in these systems. By formulating applied studies that test ecological predictions we hope to contribute to both refinement of ecological knowledge and to generate specific management recommendations for producers to test.

One of the greatest continuing challenges for sustainable agriculture lies in how to educate producers and extension educators in the principles of agroecology. Teaching ecological concepts in extension education represents a major paradigm shift and requires new approaches. Many involved in extension education (ourselves included) have been used to "having all the answers" regarding a particular pest situation. Unfortunately, ecologically based IPM approaches seldom lend themselves to such easy recipes. Recognizing this, we have adopted the approach of educating clientele in the principles of agroecology and sharing the results of our ongoing studies, even if they have not yet resulted in a series of clearly stated management recommendations. Often this approach is effective at stimulating producers to evaluate similar practices on their own farms. We encourage and support these efforts by teaching producers how to interpret their findings using an adaptive management paradigm.

### REFERENCES

- Altieri, M. A. and D. Letourneau. (1982). Vegetation management and biological control in agroecosystems. *Crop Protection* 1:405-430.
- Altieri, M. A. and C. I. Nicholls. (1999). Biodiversity, ecosystem function, and insect pest management in agricultural systems. In *Biodiversity in Agroecosystems*, eds., W. W. Collins and C. O. Qualset, Boca Raton, FL: CRC Press, pp. 69-84.



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 y, ecosystem function, and insect diversity in Agroecosystems, eds., : CRC Press, pp. 69-84.

- Askew, R. R. (1980). The diversity of insect communities in leaf-mines and plant galls. *Journal of Animal Ecology* 49:817-829.
- Basedow, Th. (1990). Effects of insecticides on Carabidae and the significance of these effects for agriculture and species number. In *The Role of Ground Beetles in Ecological and Environmental Studies*, ed. N. E. Stork, Andover, UK: Intercept, pp. 115-125.
- Beattie, M. (1996). An ecosystem approach to fish and wildlife conservation. *Ecological Applications* 6: 696-699.
- Bommarco, R. (1998). Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity. *Ecological Applications* 8: 846-853.
- Booij, C. J. H. and J. Noorlander. (1988). Effects of pesticide use and farm management on carabids in arable crops: Environmental effects of pesticides. *Agriculture, Ecosystems and Environment* 40:199-125.
- Brust, G. E. (1994). Natural enemies in straw mulch reduce Colorado potato beetle populations and damage in potato. *Biological Control* 4:163-169.
- Brust, G. E., B. R. Stinner, and D. A. McCartney. (1985). Tillage and soil insecticides effects on predator-black cutworm (Lepidoptera: Noctuidae) interactions in corn agroecosystems. *Journal of Economic Entomology* 78:1389-1392.
- Brust, G. E., B. R. Stinner, and D. A. McCartney. (1986). Predator activity and predation in corn agroecosystems. *Environmental Entomology* 15:1017-1021.
- Burn, A. J. (1989). Long-term effects of pesticides on natural enemies of cereal crop pests. In *Pesticides and Non-Target Invertebrates*, ed., P. C. Jepson, Andover, UK: Intercept, pp. 177-193.
- Cárcamo, H. A., J. K. Niemelä, and J. R. Spence. (1995). Farming and ground beetles: Effects of agronomic practice on populations and community structure. *The Canadian Entomologist* 127:123-140.
- Carmona, D. A. and D. A. Landis. (1999). Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. *Environmental Entomology* 28:1145-1153.
- Cavigelli, M. A., S. R. Deming, L. K. Probyn, and D. R. Mutch (eds.). (2000). *Michigan Field Crop Pest Ecology and Management*. East Lansing, MI: Michigan State University Extension Bulletin E-2704, 108 pp.
- Cavigelli, M. A., S. R. Deming, L. K. Probyn, and R. R. Harwood (eds.). (1998). *Michigan Field Crop Ecology: Managing Biological Processes for Productivity and Environmental Quality*. East Lansing, MI: Michigan State University Extension Bulletin E-2646, 92 pp.
- Colunga-Garcia, M., S. H. Gage, and D. A. Landis. (1997). Response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. *Environmental Entomology* 26:797-804.
- Chiverton, P. A. (1984). Pitfall-trap catches of the carabid beetle *Pterostichus melanarius*, in relation to gut contents and prey densities, in insecticide treated and untreated spring barley. *Entomologia Experimentalis et Applicata* 36:23-30.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. G. Woodmansee. (1996). The report of the Ecological Society of

- America Committee on the scientific basis for ecosystem management. *Ecological Applications* 6:665-691.
- Clark, M. S., S. H. Gage, and J. R. Spence. (1997). Habitat and management associated with common ground beetles (Coleoptera: Carabidae) in a Michigan agricultural landscape. *Environmental Entomology* 26:519-527.
- Croft, B. A. (1990). *Arthropod Biological Control Agents and Pesticides*. New York, NY: Wiley Interscience.
- Dombeck, M. P. (1996). Thinking like a mountain: BLM's approach to ecosystem management. *Ecological Applications* 6:699-702.
- Dyer, L. A. and G. Gentry. (1999). Predicting natural-enemy responses to herbivores in natural and managed systems. *Ecological Applications* 9:402-408.
- Edwards, C. A., K. D. Sunderland, and K. S. George. (1979). Studies on polyphagous predators of cereal aphids. *Journal of Applied Ecology* 16: 811-823.
- Ewel, J. J. (1986). Designing agricultural ecosystems for the humid tropics. *Annual Review of Ecology and Systematics* 17:245-271.
- Frampton, G. K., T. Çilgi, G. L. A. Fry, and S. D. Wratten. (1995). Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. *Biological Conservation* 71:347-355.
- Gut, L. J., C. E. Jochums, P. H. Westigard, and W. J. Liss. (1982). Variations in pear psylla (*Psylla pyricola* Foerster) densities in southern Oregon orchards and its implications. *Acta Horticulturea* 124:101-111.
- Hall, R. W. and L. E. Ehler. (1979). Rate of establishment of natural enemies in classical biological control. *Bulletin of the Entomological Society of America* 25:280-82.
- Hall, R. W., L. E. Ehler, and B. Bisabri-Ershadi. (1980). Rate of success in classical biological control of arthropods. *Bulletin of the Entomological Society of America* 26:111-114.
- Hawkins, B. A., and J. H. Lawton. (1987). Species richness for parasitoids of British phytophagous insects. *Nature* 326:788-790.
- House, G. J. and R. W. Parmelee. (1985). Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. *Soil Tillage Research* 5:351-360.
- Jackson, D. L. and L. L. Jackson. (2002). *The Farm as Natural Habitat*. Washington, DC: Island Press.
- Jackson, W. and J. Piper (1989). The necessary marriage between ecology and agriculture. *Ecology* 70:1591-1593.
- Kielty, J. P., L. J. Allen-Williams, N. Underwood, and E. A. Eastwood. (1996). Behavioral responses of three species of ground beetle (Coleoptera: Carabidae) to olfactory cues associated with prey and habitat. *Journal of Insect Behavior* 9:237-250.
- Kogan, M. (1998). Integrated pest management: Historical perspectives and contemporary developments. *Annual Review of Entomology* 43:243-270.
- Kromp, B. (1989). Carabid beetle communities (Carabidae: Coleoptera) in biologically and conventionally farmed ecosystems. *Agriculture, Ecosystems and Environment* 27:241-251.
- Kruess, A. and T. Tscharntke. (1994). Habitat fragmentation, species loss, and biological control. *Science* 264:1581-1584.

- ecosystem management. *Ecological Applications* 9:402-408.
- Habitat and management associated with Carabidae in a Michigan agricultural landscape. *Ecology* 80:527.
- Agents and Pesticides*. New York, NY: Academic Press.
- in: BLM's approach to ecosystem management. *Ecological Applications* 12:1068-1072.
- al-enemy responses to herbivores in agroecosystems. *Ecological Applications* 9:402-408.
- re. (1979). Studies on polyphagous predators. *Ecology* 60:811-823.
- is for the humid tropics. *Annual Review of Entomology* 15:237-240.
- Wratten. (1995). Effects of grassy habitats on Carabidae on farm-land. *Ecological Applications* 5:287-308.
- J. Liss. (1982). Variations in pear orchards and its impact on Carabidae. *Entomological Society of America* 25:280-82.
- (1980). Rate of success in classical biological control. *Entomological Society of America* 25:280-82.
- richness for parasitoids of British Columbia. *Ecological Applications* 6:276-284.
- ison of soil arthropods and earthworms in agroecosystems. *Soil Tillage Research* 37:1-14.
- as Natural Habitat. Washington, DC: Island Press.
- age between ecology and agriculture. *Ecological Applications* 6:276-284.
- and E. A. Eastwood. (1996). Behavior of Carabidae to olfactory cues. *Journal of Insect Behavior* 9:237-250.
- historical perspectives and contemporary perspectives. *Ecological Applications* 43:243-270.
- Carabidae: Coleoptera) in biological control. *Ecosystems and Environment* 125:344-366.
- Landis, D. A. and F. D. Menalled. (1998). Ecological considerations in conservation of parasitoids in agricultural landscapes. In *Conservation Biological Control*, ed., P. Barbosa, San Diego, CA: Academic Press. pp. 101-121.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45:175-201.
- Lee, J. C., F. Menalled, and D. Landis. (2001). Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *Journal of Applied Ecology* 38:472-483.
- Letourneau, D. K. (1998). Conservation biology: Lessons for conserving natural enemies. In *Conservation Biological Control*, ed., P. Barbosa, San Diego, CA: Academic Press. pp. 9-38.
- Letourneau, D. K. and M. A. Altieri. (1999). Environmental management to enhance biological control in agroecosystem. In *Handbook of Biological Control*, eds., S. Bellows and T. W. Fisher, San Diego, CA: Academic Press. pp. 319-354.
- Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomology Society of America* 15:237-240.
- Levins, R. and M. Wilson. (1980). Ecological theory and pest management. *Annual Review of Entomology* 25:287-308.
- Lewis, W. J., J. C. van Lenteren, S. C. Phatak, and J. H. Tumlinson. (1997). A total system approach to sustainable pest management. *Proceedings of the National Academy of Science USA* 94:12243-12248.
- Los, L. M. and W. A. Allen. (1983). Abundance and diversity of adult Carabidae in insecticide-treated and untreated alfalfa fields. *Environmental Entomology* 12:1068-1072.
- Lys, J. A. and W. Nentwig. (1992). Augmentation of beneficial arthropods by strip-management. 4. Surface activity, movements and activity density of abundant carabid beetles in cereal fields. *Oecologia* 92:373-382.
- Marino, P. C. and D. A. Landis. (1996). Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications* 6:276-284.
- Matson, P. A., W. J. Parton, A. G. Power, and M. J. Swift. (1997). Agricultural intensification and ecosystem properties. *Science* 277:504-509.
- Mauremootoo, J. R., S. D. Wratten, S. P. Worner, and G. L. A. Fry. (1995). Permeability of hedgerows to predatory carabid beetles. *Agriculture, Ecosystems and Environment* 52:141-148.
- MacArthur, R. H. and E. O. Wilson. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- McCullough, D. R. (1996). *Metapopulations and Wildlife Conservation*. Washington, DC: Island Press.
- Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. (1999). Does agricultural landscape structure affect parasitism and parasitoid diversity? *Ecological Applications* 9:634-641.
- Menalled, F., J. Lee, and D. Landis. (1999). Manipulating carabid beetle abundance alters prey removal rates in corn fields. *Biocontrol* 43:441-456.
- Murdoch, W. W., J. Chesson, and P. L. Chesson. (1985). Biological control in theory and practice. *American Naturalist* 125:344-366.

- Murdoch, W. W. and C. J. Briggs. (1996). Theory for biological control: Recent developments. *Ecology* 77:2001-2013.
- National Research Council. (1996). *Ecologically Based Pest Management: New Solutions for a New Century*. Washington, DC: National Academy Press.
- Nentwig, W., T. Frank, and C. Lethmayer. (1998). Sown weed strips: artificial ecological compensation areas as an important tool in conservation biological control. In *Conservation Biological Control*, ed. P. Barbosa, San Diego, CA: Academic Press. pp. 133-153.
- Newsom, L. D. (1980). The next rung up the integrated pest management ladder. *Bulletin of the Entomological Society of America* 26:369-374.
- Nicholls, C. I., M. Parrella, and M. A. Altieri. (2001). The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. *Landscape Ecology* 16: 133-146.
- Pickett, C. H. and R. L. Bugg. (1998). *Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pest*. Berkeley, CA: University of California Press.
- Pickett, S. T. A. and P. S. White. (1985). *The Ecology of Natural Disturbance and Patch Dynamic*. San Diego, CA: Academic Press.
- Pimentel, D. (1961). Species diversity and insect population outbreaks. *Annals of the Entomological Society of America* 54: 76-86.
- Price, P. W. (1991). Evolutionary theory of host and parasitoid interactions. *Biological Control* 1:83-93.
- Price, P. W. and G. P. Waldbauer. (1994). Ecological aspects of pest management. In *Introduction to Pest Management*, eds., R. L. Metcalf and W. H. Luckmann, New York, NY: Wiley-Interscience, pp. 33-65.
- Roberts, S. D. and G. R. Parker. (1998). Ecosystem management: Opportunities for private landowners in the central hardwood region. *Northern Journal of Applied Forestry* 15:43-48.
- Roland, J. (1993). Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 93:25-30.
- Root, R. B. (1973). Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassicae oleraceae*). *Ecological Monographs* 43:95-124.
- Simberloff, D. (1986). Island biogeography and integrated pest management. In *Ecological Theory and Integrated Pest Management Practices*, ed., M. Kogan, New York, NY: John Wiley and Sons, pp. 19-35.
- Sopp, P. I., K. D. Sunderland, J. S. Fenlon, and S. D. Wratten. (1992). An improved quantitative method for estimating invertebrate predation in the field using an enzyme-linked immunosorbent assay (ELISA). *Journal of Applied Ecology* 29: 295-302.
- Sousa, W. O. (1984). The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Speight, M. R. (1983). The potential of ecosystem management for pest control. *Agriculture, Ecosystems and Environment* 10:183-199.

- for biological control: Recent developments. *Integrated Pest Management: New Solutions*. Academic Press.
- Sown weed strips: artificial ecological conservation biological control. In *Conservation Biological Control*, ed. J. A. Drake, San Diego, CA: Academic Press.
- Integrated pest management ladder. *Bulletin of the Entomological Society of America* 369-374.
- (1). The effects of a vegetational corridor on biodiversity within a northern California landscape. *Conservation Biology* 133-146.
- Biological Control: Habitat Management for Agricultural Pests*. Berkeley, CA: University of California Press.
- Ecology of Natural Disturbance and Ecosystems*. Academic Press.
- Population outbreaks. *Annals of the Entomological Society of America* 100-110.
- 1 parasitoid interactions. *Biological Control* 10:1-10.
- Ecological aspects of pest management. In *Ecological Aspects of Pest Management*, ed. J. H. Lawton, New York: Academic Press.
- Integrated pest management: Opportunities for the future. *Northern Journal of Applied Entomology* 10:1-10.
- Integrated pest management increases the duration of tent caterpillar outbreaks. *Ecological Monographs* 69:1-10.
- Integrated pest management. In *Ecological Aspects of Pest Management*, ed. J. H. Lawton, New York: Academic Press.
- D. Wratten. (1992). An improved method for biological control in the field using and enhancing natural enemies. *Journal of Applied Ecology* 29:1-10.
- Ecological communities. *Annual Review of Ecology and Systematics* 20:1-20.
- Management for pest control. *Agricultural Entomology* 10:1-10.
- Staver, C. P. (2001). Knowledge, science, and practice in ecological weed management: farmer-extensionist-scientist interactions. In *Ecological Management of Agricultural Weeds*, eds., M. Liebman, C. Mohler, and C. Staver, Cambridge, UK: Cambridge University Press. pp. 99-138.
- Stern, V. M., R. F. Smith, R. van den Bosch, and K. S. Hagen. (1959). The integrated control concept. *Hilgardia* 29:81-101.
- Stinner, B. R. and G. J. House. (1990). Arthropods and other invertebrates in conservation-tillage agriculture. *Annual Review of Entomology* 35:299-318.
- Sunderland, K. D. (1975). The diet of some predatory arthropods in cereal crops. *Journal of Applied Ecology* 12:507-515.
- Sunderland, K. D., N. E. Crook, D. L. Stacey, and B. J. Fuller. (1987). A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *Journal of Applied Ecology* 24:907-933.
- Sustainable Agriculture Network. (2000). *Naturalize Your Farming System: A Whole-farm Approach to Managing Pests*. Burlington, VT: University of Vermont, Sustainable Agriculture Network. 20 pp.
- Swift, M. J. and J. M. Anderson. (1993). Biodiversity and ecosystem function in agroecosystems. In *Biodiversity and Ecosystem Function*, eds., E. Schultz and H. A. Mooney, New York, NY: Springer-Verlag. pp. 57-83.
- Terry, L. A., D. A. Potter, and P. C. Spicer. (1993). Insecticides affect predatory arthropods and predation on Japanese beetle (Coleoptera: Scarabaeidae) eggs and fall armyworm (Lepidoptera: Noctuidae) pupae in turfgrass. *Horticultural Entomology* 86:871-878.
- Thies, C. and T. Tscharntke. (1999). Landscape structure and biological control in agroecosystems. *Science* 285:893-895.
- Thomas, J. W. (1996). Forest Service perspective on ecosystem management. *Ecological Applications* 6:703-705.
- Tscharntke, T. (2000). Parasitoid populations in the agricultural landscape. In *Parasitoid Population Biology*, eds., M. E. Hochberg and A. R. Ives, Princeton, NJ: Princeton University Press. pp. 235-253.
- Tscharntke, T. and A. Kruess. (1999). Habitat fragmentation and biological control. In *Theoretical Approaches to Biological Control*, eds., B. A. Hawkins and H. W. Cornell, Cambridge, UK: University Press. pp. 190-205.
- Vandermeer, J. and I. Perfecto. (1995). *Breakfast of Biodiversity: The Truth About Rainforest Destruction*. Oakland, CA: Food First Book.
- Vickerman G. P. and K. D. Sunderland. (1975). Arthropods in cereal crops: Nocturnal activity, vertical distribution and aphid predation. *Journal of Applied Ecology* 12:755-766.
- Walters, C. J. and C. S. Holling. (1990). Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068.
- Wheater, C. P. (1991). Effects of starvation on locomotor activity in some predaceous Coleoptera (Carabidae, Staphylinidae). *Coleopterists Bulletin* 45:371-378.
- Wissinger, S. A. (1997). Cyclic colonization in predictably ephemeral habitats: A template for biological control in annual crop systems. *Biological Control* 10:4-15.

- Yaffee, S. L., A. F. Phillips, I. C. Frentz, P. W. Hardy, S. M. Maleki, and B. E. Thorpe. (1996). *Ecosystem Management in The United States: An Assessment of Current Experience*, Washington, DC: Island Press.
- Zabel, J. and T. Tscharntke. (1998). Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* 116:419-425.
- Zangger, A., J. A. Lys, and W. Nentwig. (1994). Increasing the availability of food and the reproduction of *Poecilus cupreus* in a cereal field by strip-management. *Entomologia Experimentalis et Applicata* 71:11-120.