

Symposium

Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes

Douglas A. Landis

Corresponding author. Department of Entomology, 204 CIPS, Michigan State University, East Lansing, MI 48824; landisd@msu.edu

Fabián D. Menalled

Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717-3120

Alejandro C. Costamagna

Tammy K. Wilkinson

Department of Entomology, 204 CIPS, Michigan State University, East Lansing, MI 48824

Annual crop fields typically are simple habitats dominated by a few plant species where pesticides play a major role in managing weed and insect infestations. Recently, there has been significant interest in the potential to reduce reliance on pesticides by manipulating plant species and communities to benefit natural enemies of insects and weeds. Such efforts aim to enhance natural enemy impact by providing appropriate food, shelter, and hosts, and efforts typically are accomplished by manipulation of plant species, populations, or communities. Habitat management is generally viewed as an important factor in maintaining stable insect and natural enemy populations in agricultural systems and may have a similar function in increasing weed seed predation. Crop and noncrop habitats provide resources to natural enemies either directly through floral nectar and pollen, indirectly by increased host or prey availability, or through emergent properties of the habitat such as by moderating the microclimate. These critical resources for natural enemies can be provided in agricultural ecosystems at several scales: within fields, at field margins, or as a component of the larger landscape. Because individual natural enemy species may require quite specific resources at different times and spatial scales, not all attempts to manipulate habitat diversity are equally effective. We review the role of plant resources, including weeds, in supporting natural enemy communities and provide case studies of how varying plant diversity at different spatial scales can influence the effectiveness of biological control in agricultural landscapes.

Key words: Biological control, habitat management, natural enemies, plant resources.

In agronomic systems, beneficial arthropods include those species that contribute to maintaining or increasing crop yield or enhance the ecological stability of the cropping system. Herbivores, predators, or parasitoids that act as natural enemies of weed and insect pests, as well as arthropod pollinators, are recognized as beneficial organisms in crop ecosystems. While the importance of plant diversity in maintaining effective pollinator populations is well known (Delaplane and Mayer 2000), the dependence of predators and parasitoids on plant resources is less familiar.

Predators and parasitoids benefit from a variety of plant resources such as nectar, pollen, sap, or seeds, and interact with plant diversity at varying scales (Landis and Menalled 1998; Wilkinson and Landis 2005). Plants provide nonhost resources to natural enemies directly (as above), indirectly (e.g., through support of alternate hosts), or as emergent properties of the habitats they create (e.g., moderated microclimates). The amount, timing, and spatial arrangement of these resources in agricultural landscapes can significantly affect the success or failure of natural enemies in achieving biological control of insect pests and weeds (Menalled et al. 2004).

Given the definition of a weed as “plant growing where it is not wanted” (Roberts et al. 1982), it is not surprising that weed science has been primarily focused on mitigating the negative effects of weeds on crops. Alternatively, when weeds are conceived as “plants that are especially successful at colonizing disturbed, but potentially productive, sites and

at maintaining their abundance under conditions of repeated disturbances” (Mohler 2001), it is possible to assess positive effects that they may exert on the cropping system. Among these benefits is the role of weeds in supporting biodiversity (Marshall et al. 2003).

Because of the tight link between plant resources and insect biology, entomologists have long noted the positive role of weeds in enhancing beneficial insect survivorship in crop ecosystems (van Emden 1963, 1965). In the 1970s, several papers appeared reviewing the positive roles of weeds in integrated pest management systems and their use in manipulating natural enemies (Altieri et al. 1977; Altieri and Whitcomb 1979). This awareness and the growing concern of chemically based insect management sparked a serious exploration of the potential to utilize vegetation management to enhance biological control of crop pests. A review by Altieri and Letourneau (1982) on the importance of plant communities on biological control helped to solidify the concept of habitat management to enhance natural enemy impacts (Barbosa 1998; Gurr et al. 2000; Landis et al. 2000; Pickett and Bugg 1998).

In this article, we outline the role of plant resources in supporting natural enemy communities in agricultural landscapes and provide case studies of how varying plant diversity at different spatial scales can influence the effectiveness of biological control in crop ecosystems. Our goal is to point the reader to the large and growing amount of literature on weed and natural enemy interactions. In doing so, we hope

to encourage collaborations between weed scientists, entomologists, and agronomists in exploring the role of vegetation diversity in supporting sustainable agricultural systems.

Natural Enemies and Plant Resources

Predators and parasitoids of insect pests obtain a significant amount of their nutrition from plant-provided resources (Wäckers et al. 2005). Pollen, floral and extrafloral nectar, and plant sap are directly utilized by parasitoids and predators as energy sources for reproduction, and to enhance survival during periods of prey scarcity. Pemberton and Vandenberg (1993) observed 41 species of lady beetle adults (Coleoptera: Coccinellidae), voracious predators of agricultural pests such as aphids, feeding on extrafloral nectaries of various plants. Parasitoids often require floral resources for survival. *Costia rubecula* (Marshall), a parasitoid of the cabbage white butterfly (*Pieris rapae* (L.)), requires a sugar meal approximately once per day to prevent starvation (Siekmann et al. 2001). Predators may also use plant sap as a water or nutrient source in order to sustain life during times of prey scarcity. For example, female spined soldier bugs (*Podisus maculiventris* (Say)) provided with plant material survived four times longer than starved females (Legaspi and O'Neil 1993, 1994).

Some insects are known to consume large quantities of weed seeds as an important component of their diet, in a process referred to as seed predation. Several empirical studies and modeling analyses suggest that weed seed predation has the potential to reduce seedbank abundance (Davis and Liebman 2003; Davis et al. 2003; Gonzales-Andujar and Fernandez-Quintanilla 1991; Jordan et al. 1995; Liebman et al. 2003) and alter weed community composition (Carroll and Risch 1984; Tooley and Brust 2002). As such, weed seed predation may be an important component of integrated weed management programs that seek to reduce reliance on chemical and mechanical control practices. However, a comprehensive understanding of the ecology, magnitude, and impact of weed seed predation in herbaceous crops is still missing (Menalled et al. 2005).

Due to differences in mechanisms, it is useful to separately analyze predispersal and postdispersal weed seed predation. Predispersal weed seed predation refers to the consumption of seeds on the parent plant before seeds are shed. Small and sedentary specialist feeders belonging to the Diptera, Coleoptera, Hymenoptera, and Lepidoptera insect orders are primarily responsible for predispersal seed predation. Forsyth and Watson (1985) determined that 20 to 85% of Canada thistle (*Cirsium arvense* (L.) Scop.) plants were infested by *Orellia ruficauda* (Fabr.) with 20 to 80% of seeds on the plants damaged by insects. In soybean [*Glycine max* (L.) Merr.] fields, the joint effect of a scentless plant bug (*Niesthrea louisianica* (Sailer)) that feeds on seeds, and fungi of the genera *Fusarium* and *Alternaria* has been proposed as a tool to control velvetleaf (*Abutilon theophrasti* Medik.) (Kremer and Spencer 1989a, 1989b). Finally, Griffiths and Swanton (1999), Nurse et al. (2003), and Swanton et al. (1999a) reported high levels of predispersal seed predation on common agricultural weeds such as common lambsquarters (*Chenopodium album* L.), redroot pigweed (*Amaranthus retroflexus* L.), and Powell amaranth (*A. powellii* S. Wats.).

Vertebrates such as birds and rodents, as well as insects, can consume weed seeds once they have been dispersed from the parent plant. Postdispersal invertebrate seed predators include beetles, crickets, ants, slugs, and earthworms. Tooley and Brust (2002) provided a comprehensive review of granivorous carabid beetles (Coleoptera: Carabidae) that consume weed seeds. In laboratory conditions, female field crickets (*Gryllus pennsylvanicus* Burmeister) have been observed to eat an average of 223 redroot pigweed seeds per day (Carmona et al. 1999). Finally, Seaman and Marino (2003) observed the imported red fire ant (*Solenopsis invicta* Buren) consuming seeds of several agricultural weeds, including redroot pigweed, giant ragweed (*Ambrosia trifida* L.), common lambsquarter, and goldenrod (*Solidago altissima* L.).

Plant Resources in Agroecosystems

Because of the uneven spatial and temporal distribution of insect prey and plant resources within agricultural systems, natural enemies must continuously locate alternative food sources for year-round survival. Predatory mites and their alternative prey utilize forbs and woody plants bordering orchards during part of their life cycle (Coli et al. 1994). Parasitoids may have to leave the crop area to find a host that overwinters in a suitable life stage. For example, *Colpoclypeus florus* (Walker), a parasitoid of several apple leafrollers (Lepidoptera: Tortricidae) is capable of high rates of parasitism but it cannot overwinter on pests and must leave the orchard to find an overwintering host. Pfannenstiel et al. (2000) found *C. florus* overwintering on the strawberry leafroller (*Ancylics comptana* Froelich), which itself overwinters on a wild rose (*Rosa woodsii* Lindl.). Orchards close to riparian areas that support *R. woodsii* are colonized by *C. florus* earlier in the season and achieve higher overall parasitism than orchards far from such habitats.

Noncrop areas often provide habitat needs for natural enemies. Pfiffner and Luka (2000) found that predaceous carabid beetles, rove beetles (Coleoptera: Staphylinidae), and spiders (Araneae) were absent from crop areas and found only in wildflower margins during the overwintering period. Natural enemies may also require access to moderated microclimates in summer months. Dyer and Landis (1996, 1997) demonstrated that *Eriborus terebrans* (Gravenhorst), a parasitoid of the European corn borer (*Ostrinia nubilalis* (Hübner)), required both a source of sugar and a moderated microclimate for maximum survival in corn agroecosystems. While herbaceous field edges likely provided adequate sources of floral nectar and aphid honeydew to sustain *E. terebrans*, the temperature in herbaceous edges was frequently too high for wasp survival. Only wooded field edges provided the right combination of food resources and moderated temperatures to maximize *E. terebrans* survival.

Managing Plant Diversity for Natural Enemies

Modern agricultural production practices frequently lead to the simplification of agricultural landscape (Merriam 1988; Pogue and Schnell 2001). This process has intensified in the last half century due to increased use of mechanization and chemical inputs. As a consequence of both landscape simplification and intensive use of pesticides, natural enemy populations may require specific habitat management

to remain effective within agroecosystems. Habitat management, defined as a set of practices that aim to improve availability of the resources required by natural enemies for optimal performance as biological control agents, appears as a potential approach to mitigate the negative impact of industrialized agriculture (Landis et al. 2000). Rather than increasing plant diversity per se, habitat management seeks to manipulate plants in or around crop ecosystems to provide alternate prey or hosts; nonhost food resources including pollen and nectar; shelter from adverse conditions such as tillage, pesticides, and harvest; as well as favorable microclimates for in-season and overwintering survival (Pickett and Bugg 1998). To provide for such functional diversity at the optimal time or place for natural enemies, habitat management may occur at the within-crop, within-farm, or landscape levels as needed (Landis and Menalled 1998).

Within-Field Plant Diversity

Perhaps the simplest means of increasing plant resources in cultivated areas is to tolerate the presence of some weeds. Although the concept of a threshold level is at the core of integrated arthropod management, it is still unclear whether it can be applied in weed management. On one hand, it is argued that management decisions based on threshold densities and critical periods of interference can help producers reduce herbicide applications (Swanton et al. 1999b). On the other hand, several authors argue that the high reproductive potential of agricultural weeds precludes the implementation of any practice beyond a "no seed threshold level" (Norris 1999). Future research will, one hopes, confirm or reject the suitability of threshold levels in weed management. If threshold levels are implemented, weed seed predation could constitute a viable help to achieve low seed-bank densities.

Providing refuge habitats in crop areas can increase natural enemy population density and effectiveness without the need for tolerating weeds within crop fields. For example, leaving crop residue on the soil surface has increased spider and carabid densities. Halaj et al. (2000) used modular refuges constructed from wire baskets stuffed with straw to increase spider population density, species richness, and reduce arthropod damage in soybean. Grass-legume refuge strips have also been used to increase the population density of predaceous carabid beetles in corn (*Zea mays* L.) and soybean fields (Carmona and Landis 1999; Lee et al. 2001; Menalled et al. 2001).

Establishing polycultures is another technique to increase resource diversity within the crop area. In contrast to monocultures, polycultures can increase natural enemy populations (53% of cases reviewed) (Andow 1991) and result in higher pest mortality (60% of cases reviewed) (Russell 1989). Despite these benefits, current agricultural practices often limit the applicability of polycultures. Cover crops are also a promising approach for enhancing within-field plant diversity (Bugg and Waddington 1994; Hooks et al. 1998). Perennial orchard and vineyard systems frequently employ understory or ground cover vegetation to achieve similar benefits as cover crops. For example, vetch planted in the understory of pecan orchards increased convergent lady beetle (*Hippodamia convergens* Guérin-Meneville) populations in the canopy, resulting in control of pecan aphid (*Melanocallis caryaefoliae* (Davis)) populations (Teddies 1983).

Within-Farm Plant Diversity

Providing less frequently disturbed habitats in close association with crop fields represents a viable approach to conserving beneficial insects while avoiding direct competition and may be easier to manage than increasing within-field diversity. In Great Britain, restricted pesticide applications in "conservation headlands" allowed increased plant diversity and significantly increased carabid abundance in crop fields (Hassall et al. 1992). White et al. (1995) planted strips of phacelia (*Phacelia tanacetifolia* Benth.) along the edges of cabbage (*Brassica oleracea* L.) fields to attract hoverflies (Diptera: Syrphidae), which are important predators of aphid pests. "Insectary hedgerows" comprised of a diversity of flowering shrubs and herbaceous plants have been studied for their ability to provide continuous sources of pollen, nectar, and shelter for natural enemies (Long et al. 1998). Finally, several studies demonstrated that grasslands, hedgerows, field margins, or grassy strips act as undisturbed habitats that can enhance carabid abundance, fecundity, and species diversity by supplying overwintering sites, food, and shelter (Carmona and Landis 1999; Lys and Nentwig 1992; Menalled et al. 2004; Zangger et al. 1994).

Landscape-Level Plant Diversity

Manipulation of crop diversity at larger spatial scales can also affect the potential of natural enemies as biological control agents. Nault and Kennedy (2000) found that populations of the ladybird beetle (*Coleomegilla maculata* (DeGeer)) moved from corn into adjacent potato (*Solanum tuberosum* L.) fields and that corn-potato crop rotations decreased populations of the Colorado potato beetle (*Leptinotarsa decemlineata* (Say)). Certain habitats in the agricultural landscape may act as corridors to enhance population exchange between cultivated and noncultivated areas. For example, connectivity favors dispersal of many natural enemies and enhances their ability to track changing pest populations. Also, the ability of natural enemies to quickly recolonize an agricultural crop can reduce the probability of pest outbreaks (Tscharntke 2000). Nicholls et al. (2001) established corridors consisting of a wide variety of flowering plants from adjacent forest habitats into vineyards. These corridors provided natural enemies with alternative food sources throughout the season and aided in the continuous dispersal of generalist predators and parasitoids, thereby decreasing the numbers of leafhoppers and thrips in the vineyard.

Several studies have evaluated the impact of agricultural landscape structure on weed seed predation. Steffan-Dewenter et al. (2001) assessed the joint effects of agricultural landscape structure on predispersal seed predation and pollination biology of the brown knapweed (*Centaurea jacea* L.). Both the proportion of flower heads damaged by seed predators and the number of flower-visiting pollinating bees increased with landscape complexity. However, the counterbalancing effects of these two processes resulted in the absence of a correlation between the abundance of nonagricultural areas and the number of damaged seeds per flower. Díaz (1992a, 1992b, 1994) and Díaz and Tellería (1994) demonstrated that the magnitude of postdispersal weed seed predation in the cereal crop landscapes of central Spain was

severely limited by the availability of microsites suitable for building nests and lack of refuges from adverse conditions.

Landscape spatial complexity plays an important role in increasing natural enemy abundance and reducing the frequency and severity of insect outbreaks. Thies and Tschamtkke (1999) studied parasitoids of the rape pollen beetle (*Meligethes aeneus* F.) in Germany. They found parasitism was reduced when noncrop habitat fell below 20% of the total landscape and that the amount of noncrop habitat in a 1.5-km radius of the target field was the most important variable in determining parasitism and herbivory (Thies et al. 2003). Similarly, Elliott et al. (2002) found that the amount of grasslands, woods, and other noncrop habitats was the most important factor in determining predator abundance in alfalfa (*Medicago sativa* L.) fields in South Dakota.

Case Studies

Manipulating Plant Diversity to Enhance Carabid Beetles

Carabid beetles are a highly diverse group of generalist natural enemies common in agricultural landscapes. While most carabid beetle adults are predaceous on other arthropods, a subset also feeds on weed seeds. For several years we have been interested in determining whether carabid beetles are important predators of insect pests and weed seeds in Michigan field crop systems and whether their abundance and impact could be enhanced by habitat manipulation.

To determine whether augmenting carabid population density itself was a useful strategy to enhance biological control, Menalled et al. (1999a) utilized selective barriers to augment or reduce the densities of carabid beetles in a corn field. In comparison to unmanipulated plots, carabid population density was increased 54.2% or decreased 83.1%. Insect predation rates were positively correlated with carabid abundance ($r^2 = 0.70$, $P < 0.0001$) and significantly more insect prey were removed in plots with increased carabid population density.

Carmona and Landis (1999) tested the use of within-field refuge habitats as a technique to enhance carabid population density. Refuges consisted of a central 0.5-m strip of three perennial flowering plants within a 3.3-m-wide by 30-m-long strip of orchard grass (*Dactylis glomerata* L.), white clover (*Trifolium repens* L.), and sweet clover (*Melilotus officinalis* L.). Season-long carabid beetle captures were generally higher in refuge strips than in control areas. However, the presence of a refuge strip did not alter carabid populations in the surrounding crop area. In a follow-up study conducted in the same experimental field, Lee et al. (2001) examined the combined effects of refuge habitats and insecticide application in the surrounding corn crop on carabid dispersal from the refuges. Carabid activity-density within crop areas previously treated with insecticide was significantly higher when adjacent to refuge strips. However, the presence of refuge strips did not consistently augment carabid numbers in crop areas where insecticide was not applied. One explanation may be that insecticide use decreased the quality of crop habitat for carabids by the depletion of prey availability and direct mortality. Subsequent rebounds in prey population density and the absence of competing predators may have made these areas more attractive than undisturbed crop habitats, and stimulated carabid coloni-

zation from refuges. This study demonstrated that refuges may interact with insecticide applications in determining carabid populations within fields.

Menalled et al. (2001) studied the impact of herbaceous filter strips on the activity-density and species composition of seed feeding carabids. They found greater species richness and abundance of carabids in filter strips than in the adjacent field and increased seed predation in the filter strips. Finally, Marino et al. (1997) and Menalled et al. (2000) examined weed seed predation at the landscape level. Both studies detected significant seed removal by invertebrates with high variability within fields and Menalled et al. (2000) found a tendency toward higher postdispersal weed seed removal in a highly heterogeneous agricultural area (hereafter, complex landscape) than in a more homogeneous agricultural area (hereafter, simple landscape).

Vegetative and Landscape Diversity Effects on Parasitoids

The effect of vegetative and landscape diversity on the community of generalist parasitoids of the armyworm (*Pseudaletia unipuncta* (Haworth)) was evaluated in a long-term study including five seasons spanning 9 yr. Studies were conducted in a complex landscape and a simple landscape located in Michigan. Deciduous forest vegetation was more abundant in the complex landscape (14.3% of total area) than in the simple landscape (11.2%), whereas the reverse occurred with crops (59.4 and 71.4%, respectively). Fields in the complex landscape were significantly smaller in size, surrounded by more uncultivated borders, and had more wooded perimeter per unit of field area, than those in the simple landscape (Marino and Landis 1996).

In an initial study, Marino and Landis (1996) assessed the percent parasitism of sentinel armyworm larvae released and recovered from three commercial corn fields in each landscape. A significant effect of landscape structure on the percent armyworm parasitism was found in 1993, with overall parasitism significantly higher in the complex landscape (4.2% per day) than in the simple landscape (1.2% per day) (Figure 1). We hypothesized that the more abundant late-successional vegetation of the complex landscape allowed for higher populations of the main parasitoid species collected in the study, *Meteorus communis* (Cresson), which accounted for 72.5% of the parasitism. Moreover, the dominant tree species of field borders in the complex landscape was black cherry (*Prunus serotina* Ehrh.), a primary food plant for five of the seven alternative larval hosts of *M. communis*.

We then expanded this study by replicating the complex and simple landscapes in two additional areas in Ingham and Eaton Counties, Michigan, in 1996 (Menalled et al. 1999b). We obtained the same pattern of higher parasitism in the complex landscape in the original study area, but found no differences in parasitism in the two additional areas (Figure 1), which had very low overall parasitism (<1%). Although analysis of the three landscape pairs proved to be structurally equivalent, the two new areas had a very low proportion of black cherry in the surrounding habitats. This study indicated that the effect of landscape structure on parasitism may depend not only on the presence of diverse vegetation, but also the presence of plant species key to individual parasitoids.

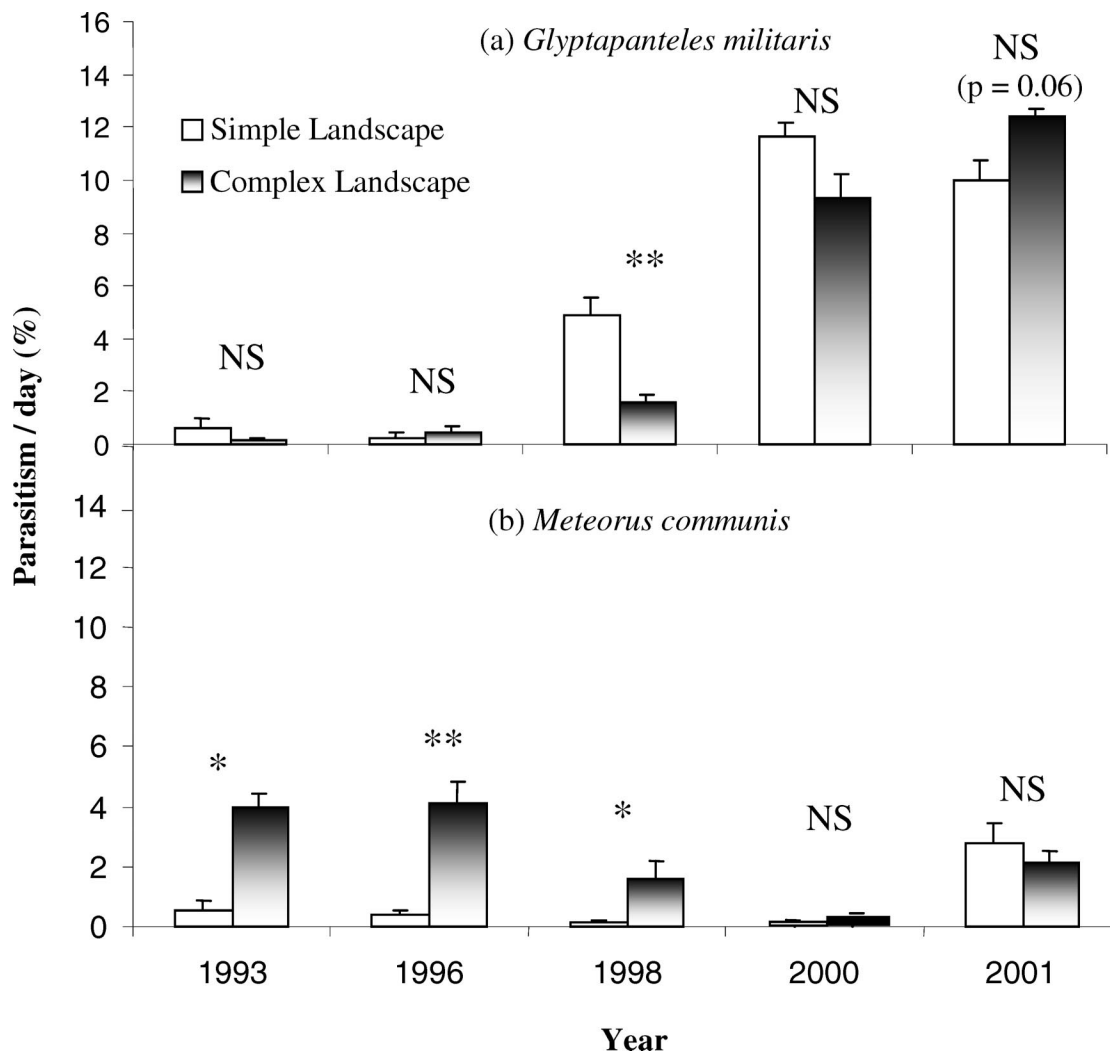


FIGURE 1. Daily percent parasitism (mean \pm SEM) of *Pseudaletia unipuncta* by (a) *Glyptapanteles militaris*, and (b) *Meteorus communis*, in a simple and a complex agricultural landscape in southern Michigan. These two parasitoid species accounted for 96.3% of the parasitism of the study. Daily percentage parasitism was analyzed using a two-factor (landscape and year) ANOVA model. Field effect was modeled as a random effect nested in landscape and year. Landscape by year effects sliced by year are indicated as ** $P < 0.01$, * $P < 0.05$, NS $P > 0.05$. From Menalled et al. 2003.

Menalled et al. (2003) further tested the long-term effect of landscape diversity on the parasitism of the armyworm. In these studies, *Glyptapanteles militaris* (Walsh) became an increasingly important part of the parasitoid community (Figure 1). In the 2000 and 2001 seasons, *G. militaris* was still more abundant than in previous years and equally present in both landscapes. In contrast, to previous years, *M. communis* was almost absent in 2000 but present in both landscapes in 2001, probably attributable to the occurrence of an armyworm outbreak throughout the region (Figure 1). These results indicated that the effect of vegetative and landscape structure varies from one year to the next and for different parasitoid species. These results emphasized the need for long-term studies to fully characterize these relationships.

Implications and Opportunities

Beneficial arthropods take advantage of a diversity of plant resources in their environment. Depending on the resource requirements (daily, seasonal) and the dispersal ca-

pabilities of the insect, resources may need to be provided at the field, farm, or landscape level. Recent integration of techniques from landscape ecology and biological control has allowed detecting the specific spatial scale at which landscape structure influences natural enemies (Thies and Tscharntke 1999; Thies et al. 2003). This approach was used to determine the specific thresholds in habitat fragmentation, which influenced natural enemy abundance (With et al. 2002). One of the more fascinating outcomes is that plant resources may be equally or more important in determining numbers and impacts of beneficial insects than such factors as farming system (organic vs. conventional) (Östman et al. 2001) or prey population density (Elliott et al. 2002). As these concepts mature, there will be increased opportunity for agronomists, entomologists, and weed scientists to collaborate on research exploring ecologically based pest management techniques. Such efforts should be grounded in an appreciation of the ecosystem services that agricultural and natural habitats provide to society and be integrated with regional land use planning and conservation efforts.

Acknowledgments

We thank Robert Norris for the invitation to participate in this symposium and his help in preparing the manuscript for submission. Adam Davis, Karen Renner, Paul Marino, and several anonymous reviewers provided helpful comments on earlier versions of the manuscript. Michigan State University, the Michigan Agricultural Experiment Station, and Project GREEN provided support for this work. F.D.M. thanks the U.S. Department of Agriculture National Research Initiative (projects 2000-35320-9328 and 2002-35320-12175), and A.C.C. acknowledges support from a joint Fulbright-Argentina National Institute of Agricultural Technology (INTA) Fellowship.

Literature Cited

- Altieri, M. A. and D. K. Letourneau. 1982. Vegetation management and biological control in agroecosystems. *Crop Prot.* 1:405–430.
- Altieri, M. A., A. van Schoonhoven, and J. Doll. 1977. The ecological role of weeds in insect pest management systems: a review illustrated by bean (*Phaseolus vulgaris*) cropping systems. *Pest Articles and News Summaries* 23:195–205.
- Altieri, M. A. and W. H. Whitcomb. 1979. The potential use of weeds in manipulation of beneficial insects. *Hort. Sci.* 14:12–18.
- Andow, D. A. 1991. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* 36:561–586.
- Barbosa, P. 1998. *Conservation Biological Control*. San Diego, CA: Academic. 396 p.
- Bugg, R. L. and C. Waddington. 1994. Using cover crops to manage arthropod pests of orchards: a review. *Agric. Ecosyst. Environ.* 50:11–28.
- Carmona, D. M. and D. A. Landis. 1999. Influence of refuge habitats and cover crops on seasonal activity-density of ground beetles (Coleoptera: Carabidae) in field crops. *Environ. Entomol.* 28:1145–1153.
- Carmona, D. M., F. D. Menalled, and D. A. Landis. 1999. Northern field cricket, *Gryllus pennsylvanicus* Burmeister (Orthoptera: Gryllidae): laboratory weed seed predation and within field activity-density. *J. Econ. Entomol.* 92:825–829.
- Carroll, C. R. and S. J. Risch. 1984. The dynamics of seed harvesting in early successional communities by a tropical ant, *Solenopsis geminata*. *Oecologia* 61:388–392.
- Coli, W. M., R. A. Ciurlino, and T. Hosmer. 1994. Effect of understory and border vegetation composition on phytophagous and predatory mites in Massachusetts commercial apple orchards. *Agric. Ecosyst. Environ.* 50:49–60.
- Davis, A. S., P. M. Dixon, and M. Liebman. 2003. Cropping system effects on giant foxtail demography: II. Retrospective perturbation analysis. *Weed Sci.* 51:930–939.
- Davis, A. S. and M. Liebman. 2003. Cropping system effects on giant foxtail (*Setaria faberi*) demography: I. Green manure and tillage timing. *Weed Sci.* 51:921–929.
- Delaplane, K. S. and D. F. Mayer. 2000. *Crop Pollination by Bees*. New York: CABI. 344 p.
- Díaz, M. 1992a. Spatial and temporal patterns of granivorous ant seed predation in patchy cereal crop areas of central Spain. *Oecologia* 91:561–568.
- Díaz, M. 1992b. Rodent seed predation in cereal crop areas of central Spain: effects of physiognomy, food availability, and predation risk. *Ecography* 15:77–85.
- Díaz, M. 1994. Granivory in cereal crop landscapes of central Spain: environmental correlates of rodents, birds, and ants. *Acta Oecologica* 15:739–752.
- Díaz, M. and J. L. Tellería. 1994. Predicting the effects of agricultural changes in central Spain croplands on seed-eating overwintering birds. *Agric. Ecosyst. Environ.* 49:289–298.
- Dyer, L. E. and D. A. Landis. 1996. Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environ. Entomol.* 25:1192–1201.
- Dyer, L. E. and D. A. Landis. 1997. Influence of noncrop habitats on the distribution of *Eriborus terebrans* (Hymenoptera: Ichneumonidae) in cornfields. *Environ. Entomol.* 26:924–932.
- Elliott, N. C., R. W. Kieckhefer, G. J. Michels, and K. L. Giles. 2002. Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. *Environ. Entomol.* 31:253–260.
- Forsyth, S. F. and A. K. Watson. 1985. Predispersal seed predation of Canada thistle. *Can. Entomol.* 117:1075–1071.
- Gonzales-Andujar, J. L. and C. Fernandez-Quintanilla. 1991. Modeling the population dynamics of *Avena sterilis* under dry-land cereal cropping systems. *J. Appl. Ecol.* 28:16–27.
- Griffiths J. T. and C. J. Swanton. 1999. Predispersal seed predation in corn. *Proc. Weed Sci. Soc. Am.* 39:76.
- Gurr, G. M., S. D. Wratten, and P. Barbosa. 2000. Success in conservation biological control of arthropods. Pages 105–132 in G. Gurr and S. Wratten, eds. *Biological control: Measures of success*. Dordrecht: Kluwer Academic.
- Halaj, J., A. B. Cady, and G. W. Uetz. 2000. Modular habitat refugia enhance generalist predators and lower plant damage in soybeans. *Environ. Entomol.* 29:383–393.
- Hassall, M., A. Hawthorne, M. Maudsley, P. White, and C. Cardwell. 1992. Effects of headland management on invertebrate communities in cereal fields. *Agric. Ecosyst. Environ.* 40:155–178.
- Hooks, C. R. R., H. R. Valenzuela, and J. Defrank. 1998. Incidence of pests and arthropod natural enemies in zucchini grown with living mulches. *Agric. Ecosyst. Environ.* 69:217–231.
- Jordan, N., D. A. Mortensen, D. M. Prenzlau, and K. C. Cox. 1995. Simulation analysis of crop rotation effects on weed seedbank. *Am. J. Bot.* 82:390–398.
- Kremer, R. J. and N. R. Spencer. 1989a. Impact of a seed-feeding insect and microorganisms on velvetleaf (*Abutilon theophrasti*) seed viability. *Weed Sci.* 37:211–216.
- Kremer, R. J. and N. R. Spencer. 1989b. Interactions of insects, fungi, and burial on velvetleaf (*Abutilon theophrasti*) seed viability. *Weed Technol.* 3:322–328.
- Landis, D. A. and F. D. Menalled. 1998. Ecological considerations in the conservation of effective parasitoid communities in agriculture systems. Pages 101–121 in P. Barbosa, ed. *Conservation Biological Control*. San Diego: Academic.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45:175–201.
- Lee, J. C., F. D. Menalled, and D. A. Landis. 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *J. Appl. Ecol.* 38:472–483.
- Legaspi, J. C. and R. J. O'Neil. 1993. Life history of *Podisus maculiventris* given low numbers of *Epilachna varivestis* as prey. *Environ. Entomol.* 22:1192–1200.
- Legaspi, J. C. and R. J. O'Neil. 1994. Developmental response of nymphs of *Podisus maculiventris* (Heteroptera: Pentatomidae) reared with low numbers of prey. *Environ. Entomol.* 23:374–380.
- Liebman, M., P. Westerman, F. Menalled, and A. Heggenstaller. 2003. Weed responses to diversified cropping systems. *Proceedings of the Symposium on Beyond Thresholds: Applying Multiple Control Tactics in Integrated Weed Management*. North-Central Weed Science Society meeting, Louisville, KY.
- Long R. F., A. Corbett, C. Lamb, C. Reberg-Horton, J. Chandler, and M. Stimmann. 1998. Beneficial insects move from flowering plants to nearby crops. *Calif. Agr.* 52:23–26.
- 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., K. L. Gross, and D. A. Landis. 1997. Post-dispersal weed seed loss in Michigan maize fields. *Agric. Ecosyst. Environ.* 66:189–196.
- Marino, P. C. and D. A. Landis. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecol. Appl.* 6:276–284.
- Marshall, E.J.P., V. K. Brown, N. D. Boatman, P.J.W. Lutman, G. R. Squire, and L. K. Ward. 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Res.* 43:77–89.
- Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. 2003. Temporal variation in the response of parasitoids to agricultural landscape structure. *Agric. Ecosyst. Environ.* 96:29–35.
- Menalled, F. D., D. A. Landis, and L. Dyer. 2004. Research and extension supporting ecologically based IPM systems. *Journal of Crop Improvement*. 11:153–174.
- Menalled, F., J. Lee, and D. A. Landis. 1999a. Manipulating carabid beetle abundance alters prey removal rates in corn fields. *Biocontrol* 43:441–456.
- Menalled, F. D., J. Lee, and D. A. Landis. 2001. Herbaceous filter strips

- in agroecosystems: implications for ground beetle (Coleoptera: Carabidae) conservation and invertebrate weed seed predation. *Great Lakes Entomol.* 34:77–91.
- Menalled, F. D., M. Liebman, and K. Renner. 2005. The ecology of weed seed predation in herbaceous cropping systems. In H. Singh, D. Batis, and R. Kohli, eds. *Handbook of Sustainable Weed Management*. Binghamton, NY: Haworth.
- Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999b. Does agricultural landscape structure affect parasitism and parasitoid diversity? *Ecol. Appl.* 9:634–641.
- Menalled, F. D., P. C. Marino, K. Renner, and D. A. Landis. 2000. Post-dispersal weed seed predation in Michigan crop fields as a function of agricultural landscape structure. *Agric. Ecosyst. Environ.* 77:193–202.
- Merriam, G. 1988. Landscape dynamics in farmland. *Trends Ecol. Evol.* 3:16–20.
- Mohler, C. L. 2001. Weed life history: identifying vulnerabilities. Pages 40–98 in M. Liebman, C. L. Mohler, and C. P. Staver, eds. *Ecological Management of Agricultural Weeds*. Cambridge, Great Britain: Cambridge University Press.
- Nault, B. A. and G. G. Kennedy. 2000. Seasonal changes in habitat preference by *Coleomegilla maculata*: implications for Colorado potato beetle management in potato. *Biol. Control* 17:164–173.
- 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 Ecol.* 16:133–146.
- Norris, R. F. 1999. Ecological implications of using thresholds for weed management. *J. Crop Prod.* 2:31–58.
- Nurse, R. E., B. D. Booth, and C. J. Swanton. 2003. Predispersal seed predation of *Amaranthus retroflexus* and *Chenopodium album* growing in soyabean fields. *Weed Res.* 43:260–268.
- Östman, O., B. Ekbom, and J. Bengtsson. 2001. Landscape heterogeneity and farming practice influence biological control. *Basic Appl. Ecol.* 2:365–371.
- Pemberton, R. W. and N. J. Vandenberg. 1993. Extrafloral nectar feeding by ladybird beetles (Coleoptera: Coccinellidae). *Proc. Entomol. Soc. Wash.* 95:139–151.
- Pfannenstiel, R. S., T. R. Unruh, and J. F. Brunner. 2000. Biological control of leafrollers: prospects using habitat manipulation. *Washington Hort. Assoc.* 95:144–149.
- Pfiffner, L. and H. Luka. 2000. Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agric. Ecosyst. Environ.* 78:215–222.
- Pickett, C. H. and R. L. Bugg. 1998. *Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agriculture Pests*. Los Angeles: University of California Press. 422 p.
- Pogue, D. W. and G. D. Schnell. 2001. Effects of agriculture on habitat complexity in a prairie-forest ecotone in the southern great plains of North America. *Agric. Ecosyst. Environ.* 87:287–298.
- Roberts, H. A., R. J. Chancellor, and T. A. Hill. 1982. The biology of weeds. Pages 1–36 in H. A. Roberts, ed. *Weed Control Handbook: Principles*. Oxford, Great Britain: Blackwell Scientific.
- Russell, E. P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environ. Entomol.* 18:590–599.
- Seaman, R. E. and P. C. Marino. 2003. Influence of mound building and selective seed predation by the red imported fire ant (*Solenopsis invicta*) on an old-field plant assemblage. *J. Torrey Bot. Soc.* 130:193–201.
- Siekmann, G., B. Tenhumberg, and M. A. Keller. 2001. Feeding and survival in parasitic wasps: sugar concentration and timing matter. *Oikos* 95:425–430.
- Steffan-Dewenter, I., U. Münzenberg, and T. Tscharnkte. 2001. Pollination, seed set and seed predation on a landscape scale. *Proc. Royal Soc. Lond. Series B* 268:1685–1690.
- Swanton, C. J., J. T. Griffiths, H. E. Cromar, and B. D. Booth. 1999a. Pre- and post-dispersal weed seed predation and its implications to agriculture. Pages 829–834 in *The 1999 Brighton Conference—Weeds: Proceedings of an International Conference Held at the Brighton Metropole Hotel, Brighton, U.K., 15–18 November 1999*. Vol. 3. British Crop Protection Council.
- Swanton, C. J., S. Weaver, P. Cowan, R. R. Van Acker, W. Deen, and A. Shreshtha. 1999b. Weed thresholds: theory and applicability. *J. Crop Prod.* 2:9–29.
- Tedders, W. L. 1983. Insect management in deciduous orchard ecosystems: habitat manipulation. *Environ. Manage.* 7:29–34.
- Thies, C., I. Steffan-Dewenter, and T. Tscharnkte. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101:18–25.
- Thies, C. and T. Tscharnkte. 1999. Landscape structure and biological control in agroecosystems. *Science* 285:893–895.
- Tooley, J. and G. Brust. 2002. Weed seed predation by carabid beetles. Pages 215–229 in J. M. Holland, ed. *The Agroecology of Carabid Beetles*. Andover, U.K.: Intercept Ltd.
- Tscharnkte, T. 2000. Parasitoid populations in the agricultural landscape. Pages 235–253 in M. E. Hochberg and A. R. Ives, eds. *Parasitoid Population Biology*. Princeton, NJ: Princeton University Press.
- Wäckers, F. L., P.C.J. van Rijn, and J. Bruin. 2005. *Plant Provided Food and Plant-Carnivore Mutualism*. Cambridge, U.K.: Cambridge University Press.
- Wilkinson, T. K. and D. A. Landis. 2005. Habitat diversification in biological control: The role of plant resources. in F. L. Wäckers, P.C.J. van Rijn, and J. Bruin, eds. *Plant Provided Food and Plant-Carnivore Mutualism*. Cambridge, U.K.: Cambridge University Press.
- van Emden H. F. 1963. Observations of the effects of flowers on the activity of parasitic Hymenoptera. *Entomol. Mon. Mag.* (1962) 265–270.
- van Emden H. F. 1965. The role of uncultivated land in the biology of crop pests and beneficial insects. *Sci. Hort.* 17:121–136.
- White, A. J., S. D. Wratten, N. A. Berry, and U. Weigmann. 1995. Habitat management to enhance biological control of *Brassica* pests by hover flies (Diptera: Syrphidae). *J. Econ. Entomol.* 88:1171–1176.
- With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates, and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecol. Applic.* 12:52–65.
- 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. *Entomol. Exp. Appl.* 71:11–120.

Received March 2, 2004, and approved August 13, 2004.