



Agriculture and
Agri-Food Canada

Agriculture et
Agroalimentaire Canada



Agricultural Practices that Promote Crop Pest Suppression by Natural Predators

Elsa Étilé, Ph.D.

Agricultural Practices that Promote Crop Pest Suppression by Natural Predators

Review of the Literature Submitted to Agriculture and Agri-Food Canada on August 6, 2012
Montreal, QC
Contract 01B46-2011-0257

© Her Majesty the Queen in Right of Canada, represented by the Minister of Agriculture and Agri-Food (2013).

Opinions and statements in the publication attributed to named author do not necessarily reflect the policy of Agriculture and Agri-Food Canada or the Government of Canada.

AAFC Number: AAFC 12189E
Catalogue Number: A59-13/2014E-PDF
ISBN Number: 978-1-100-23304-8

*Paru également en français sous le titre
Pratiques agricoles favorisant la répression des ravageurs des cultures par leurs prédateurs*

Cover page: pepper plant being visited by a lady beetle. Photo credit: M.E. Bartolo, Bugwood.org.

TABLE OF CONTENTS

I.	INTRODUCTION	1
II.	ROLE OF SEMI-NATURAL HABITATS AND NON-CROP AREAS FOR NATURAL ENEMIES	4
A.	Intermediate hosts and alternative prey	5
B.	Plant food resources.....	7
C.	Shelter and overwintering and breeding sites.....	8
D.	Landscape.....	10
III.	MANAGEMENT PRACTICES THAT OPTIMIZE NATURAL ENEMY ACTIVITY ..	12
A.	Non-crop areas on the edges of fields	12
B.	Promoting biodiversity within crop areas	13
C.	Practical considerations.....	15
	Cultural practices and possible agricultural systems.....	15
	Choosing cultural strategies	16
	Plant species selection for polyculture and habitat management	17
D.	Other cultural practices that affect natural enemies	19
	Tillage.....	19
	Herbicide and pesticide use.....	20
	Nitrogen fertilization.....	20
	Seeding and harvesting dates.....	20
	Food spray	21
IV.	CONCLUSION.....	22
	APPENDIX I.....	24
	APPENDIX II.....	26
V.	BIBLIOGRAPHY	29

I. INTRODUCTION

Modern agriculture, whose development has been driven by the goal of increasing productivity and meeting the growing need for food and textile fibres, has led to considerable simplification of cropping systems in terms of the diversity of the species grown and cultural practices in agricultural landscapes (Altieri, 1999; Altieri and Nicholls, 2004). Today, agricultural environments are the most striking example of the consequences of the massive loss of biodiversity (Altieri and Nicholls, 2004). In Canada, the development of intensive agriculture has been accompanied by the steady loss of natural habitats. More than half of the wetlands in southern Canada have been lost, 70% of which were located in southern Ontario (Mineau and McLaughlin, 1996).

The simplification of the agricultural environment has weakened the natural defences of agricultural ecosystems, which in turn has led to the intensive use of petrochemical inputs to provide a fast and effective response to the rising incidence of pest, weed and disease infestations (Matson et al., 1997). In 2008, worldwide production losses caused by arthropod pests were estimated at 15% (Pimentel, 2008). There is no longer any doubt about the adverse impacts of the intensive use of synthetic pesticides. Pesticide use has negative effects on both the environment and human health, while the pesticides themselves are becoming less effective as a result of the development of resistance in insects, resulting in economic losses (Ekström and Ekbom, 2011). In 2005, 2.4 million hectares of Canadian farmland were treated with insecticides (Statistics Canada, 2006). In 2007, worldwide use of active agents was estimated at more than 2.3 million tonnes, and associated expenses at more than US\$39 billion (Grube et al., 2011). The loss of biodiversity and associated ecosystem services, including pollination and pest suppression, continues to be one of the main consequences of intensive agriculture and the use of chemical pesticides (Bianchi et al., 2006; Denys and Tscharrntke, 2002).

It is currently widely accepted that the development of more sustainable agricultural production systems depends on a reduction in the use of pesticides and, consequently, the introduction of cropping systems that promote biodiversity and make use of the natural services provided by agroecosystems (Altieri and Nicholls, 2004; Dinter, 2002; Gurr et al., 2003; Landis et al., 2000; Madsen et al., 2004; Östman and Ives, 2003;

Ratnadass et al., 2012). The focus of modern agroecology is not only on the adoption of new agricultural techniques, but also on the adaptation of traditional agricultural practices or practices used in developing countries that are based on promoting biodiversity and implementing methods that mimic natural ecological processes (Altieri and Nicholls, 2004). However, because modern agricultural and socio-economic contexts are totally different, effective implementation of these practices is a major challenge.



Figure 1. Herbicide application in a field under no-till cropping system

Photo credit: Jack Dykinga, USDA-ARS.

Of the various services provided by ecosystems, natural pest suppression is considered one of the most important (Médiène et al., 2011; Östman and Ives, 2003). The annual value of this ecosystem service was estimated at more than US\$400 billion worldwide in 1997 (Jones and Sieving, 2006) and approximately US\$5 billion in Canada in 2010. Diversity in agroecosystems can enhance the activity of the natural enemies of crop pests and thus reduce pressure from pests and associated costs.

However, several authors have pointed out the importance of identifying and enhancing the key functional ecosystem traits, rather than “encouraging diversification per se” (Landis et al., 2000). Indeed, it has been shown that simply increasing diversity may possibly exacerbate pest problems (Gurr et al., 1998). It is therefore important to carefully examine the underlying ecological mechanisms that are responsible for the benefits of biodiversity in agricultural environments before considering the question of which cultural practices will be most effective in ensuring the optimum contribution of natural crop allies/enemies.

“Conservation biological control” is defined as the management of agricultural environments in a way that promotes pest suppression by natural enemies. Although

conservation biological control was one of the earliest documented insect pest suppression measures (Coll, 2009), it was initially overlooked by researchers in favour of other forms of biological control. However, the trend has clearly been reversed in the last two decades, since the number of publications on this subject has increased significantly (Landis, Wratten and Gurr, 2000). Today, it is generally accepted that conservation biological control must constitute the basis of any crop pest control program, whether biological or integrated (Coll, 2009).

The present review of the literature first provides some general background information to help understand the role of biodiversity in the ecological services provided by natural enemies in controlling agricultural pests, and then examines the agricultural practices that promote these services in agroecosystems and the implementation of conservation biological control. The review highlights the results of studies that are useful for the main crops grown in eastern Canada, excluding field vegetable production.

**Figure 2. Willow
hedgerow in
Prince Edward
Island, Canada.**

**Photo credit:
Victoria
MacPhail, 2012.**



II. ROLE OF SEMI-NATURAL HABITATS AND NON-CROP AREAS FOR NATURAL ENEMIES

Crop monocultures are difficult environments in which to induce efficient biological pest suppression because these systems lack adequate resources to allow populations of natural enemies of crop pests to contribute in an optimal way to pest control efforts (Altieri and Nicholls, 2004; Rusch et al., 2012). Semi-natural habitats, such as forests, hedgerows, field margins, fallows and meadows, contain numerous species of beneficial arthropods, because these habitats provide a more stable environment than annually-cropped monocultures (Altieri and Nicholls, 2004; Bianchi, Booij and Tscharntke, 2006; Médiène et al., 2011; Rusch et al., 2010). This stability is attributable to the greater complexity and biodiversity of these habitats compared to monocultures, weakened by several centuries of simplification (Altieri and Nicholls, 2004) and regular disturbance.

Although it was long believed that semi-natural habitats were a source of harmful organisms, it is now known that they generally contain more beneficial than harmful organisms (Denys and Tscharntke, 2002; Marshall, 2004). The conservation or establishment of such habitats is therefore essential to the development of sustainable agriculture.

To provide guidance for conservation efforts, it is very important to understand precisely how these habitats provide essential resources for maintaining natural enemy populations and what factors optimize their pest suppression function (Landis, Wratten and Gurr, 2000). According to Landis et al. (2000), the goal is to provide the “right diversity.” This process can be guided by studying the resources required by beneficial insects. Semi-natural habitats provide insect predators and parasitoids with prey and intermediate hosts of target pests, nutritional plant resources, as well as shelter and overwintering sites (Landis, Wratten and Gurr, 2000; Médiène et al., 2011; Rusch et al., 2012).

A. Intermediate hosts and alternative prey

Non-crop habitats contain populations of intermediate hosts and alternative prey that are useful to pest parasitoids and predators (Bianchi, Booij and Tscharntke, 2006; Denys and Tscharntke, 2002; Landis, Wratten and Gurr, 2000). According to Landis and Menalled (1998), more than 60% of the intermediate hosts of parasitoids that attack populations of phytophagous caterpillars in corn, soybeans, wheat and alfalfa are also present in trees and shrubs.

Today, it is widely accepted that the presence of accessible alternative prey or intermediate hosts is essential to optimal control of pests by generalist insect predators (that have several alternative prey or intermediate hosts). The consumption of secondary resources by insect predators becomes disadvantageous only if this comes at the expense of consumption of the target pest (Huffaker and Flaherty, 1966). Secondary animal resources are useful to the survival of the predator in the event of a low density of prey following a drop in population, or a lag between the availability of prey and the natural enemies of interest (van Emden, 1990). Because of their more varied diet, generalist predators are more dependent on alternative prey or intermediate hosts than specialist predators (Rusch et al., 2010).

Östman and Ives (2003) observed that the presence of large populations of pea aphids (*Acyrtosiphon pisum*) attracted predatory damsel bugs (*Nabis* spp.) in alfalfa fields. The increase in damsel bug populations then resulted in better control of the potato leafhopper (*Empoasca fabae*), a major alfalfa pest (Östman and Ives, 2003). When both the alternative prey and the target pest are crop enemies, as is the case with the pea aphid and the potato leafhopper, this is referred to as “negative prey-prey interaction.”



Figure 3. Common damsel bug (species *Nabis americana*), a generalist predator, feeding on aphid.

Photo credit : MAPAQ, IRIS phytoprotection ([http:// www.iriisphytoprotection.qc.ca/](http://www.iriisphytoprotection.qc.ca/)), 2013.



Figure 4. Larva and adults of the ground beetle species *Agonum muelleri* prey on slugs, caterpillars, aphids and other soft-bodied insects.

Photo credit : MAPAQ, IRIIS
 phytoprotection (<http://www.iriisphytoprotection.qc.ca/>), 2013.

In some cases, the presence of alternative prey may even increase the size of beneficial insect populations. The population density of the parasitoid *Anagrus erpos* increased significantly where semi-natural habitats that provide alternative prey were available (Corbett and Rosenheim, 1996).

Many species of parasitoids can feed on the honeydew secreted by numerous sap-sucking insect species such as aphids (Wäckers et al., 2008). Their presence in non-crop areas can therefore promote pest suppression in fields. Evans and England (1996) reported higher levels of parasitism of the alfalfa weevil (*Hypera postica*) by the wasp *Bathyplectes curculionis* in the presence of pea aphids (Evans and England, 1996). Access to aphid honeydew significantly increased the fecundity as well as the longevity of adult parasitoids. Similarly, Fuschberg et al. (2007) observed that the rate of parasitism of the eggs of the European corn borer was approximately twice as high by females of the parasitoid *Trichogramma ostriniae* that had access to honeydew secreted by the corn leaf aphid (*Rhopalosiphum maidis*). The size of the progeny and the proportion of females of the parasitoids also increased under these conditions (Fuchsberg et al., 2007).

It has also been demonstrated that the presence of alternative prey can facilitate biological pest suppression by reducing potential intraguild predation between different predators. Dinter (2002) reported better control of the cereal aphid *Sitobion avenae*, an insect belonging to the family Aphididae in the suborder Homoptera, when there was a combination of lacewing and spider larvae in the presence of alternative prey. The introduction of springtails and fruit flies into the system visibly reduced intraguild predation between spiders and lacewings that had been observed in the absence of these alternative prey (Dinter, 2002).

However, it is important to note that the presence of alternative prey does not always have a positive effect on insect pest suppression, the success of which depends in part on the specificity of each predator-prey interaction and predator-predator interaction and on the feeding behaviour of the various protagonists (Gavish-Regev et al., 2009; Lucas and Rosenheim, 2011; Madsen, Terkildsen and Toft, 2004; Ratnadass et al., 2012).

B. Plant food resources

Numerous studies, including Bianchi, Booij and Tscharntke (2006), Lundgren et al. (2009) and Wäckers, van Rijn and Heimpel (2008), mention vegetation as a secondary food source for predators and parasitoids. Consumption of pollen, floral and extrafloral nectar, sap or seeds is observed in a large variety of insect orders, including Hymenoptera, Diptera, Coleoptera, Heteroptera, Thysanoptera, Neuroptera and Lepidoptera, as well as in certain arachnids such as predatory spiders and mites (Hagen, 1986; Wäckers, van Rijn and Heimpel, 2008). Only 25% of the 163 families of insect parasites and predators studied by Hagen (1987) were strictly carnivorous. The remaining proportion fed on plant resources during at least one life stage (Hagen, 1986).

For these insects, these sources of sugar, proteins and sometimes water constitute sources of energy for reproduction and survival in the event of a shortage of prey, and are also a way of balancing their diet (Landis et al., 2005; Lundgren, 2009; Rusch et al., 2010). Several studies have shown that greater phytodiversity results in greater availability of pollen and nectar, leading, for example, to a higher density of ground beetles in wheat (Zangger et al., 1994), hoverflies in barley (Sutherland et al., 2001) and lady beetles in orchards (Brown, 2012). Other studies have shown that many species of parasitoids feed on floral nectar (Jervis et al., 1993; Wäckers, 2001) and that their rate of parasitism, the size of their population, their distribution or their diversity varies depending on the availability of nectar (Berndt et al., 2006; Marino et al., 2006).

Many species of parasitoids and predators use the plant resources of the semi-natural habitats located outside fields. According to Lundgren (2009), migration from fields to adjacent habitats is even obligatory for certain natural allies whose survival depends on the availability of plant resources which is often more stable in space and time than animal resources. Consequently, in addition to improving the survival of natural enemies, these food resources influence their movements within and outside crop areas (Lundgren, 2009).



Figure 5. In the United Kingdom, a flower strip in margin of a crop provides many predator species with the plant resources they need at one or more stages of their life, such as pollen and nectar.

Photo credit : © Copyright Living Countryside, www.ukagriculture.com.

C. Shelter and overwintering and breeding sites

Because of their more complex structure compared to crop areas, non-crop habitats can be beneficial to arthropod populations by providing shelter and breeding or overwintering sites (Altieri and Nicholls, 2004). According to several studies, herbaceous and wooded areas provide a more moderate microclimate than crop fields, thus protecting the natural enemies from extreme temperature variations (Rahim et al., 1991). For example, in corn, access to the microclimate of non-crop areas and field margins improved the longevity and rate of parasitism of major parasitoids of the European corn borer (Dyer and Landis, 1996; Landis and Haas, 1992; Orr et al., 1997). In alfalfa, strip harvesting preserved refuge areas for natural enemies and maintained populations of various species of predatory lacewings, lady beetles and damsel bugs (Landis, Wratten and Gurr, 2000).

Figure 6. Adult syrphid flies feed on pollen and nectar, but the larva are predators who feed on aphids, scale insects and other small, soft-bodied insects.

Photo credit : MAPAQ, IRIIS phytoprotection (<http://www.iriisphytoprotection.qc.ca/>), 2013.



In annual crops, refuge areas also serve as overwintering habitats for natural enemies. In the Canadian context, it is important to point out the importance of these overwintering areas. Indeed, few insect predators survive the Canadian winter in open agricultural environments (McLaughlin and Mineau, 1995). The population density of beneficial insects in the spring is highly dependent on the availability of semi-natural habitats during the preceding winter (McLaughlin and Mineau, 1995).

The diversity and distribution of overwintering areas are also decisive factors in the spatial and temporal distribution of beneficial insects the following spring. For example, the hoverfly *Episyrphus balteatus*, a major predator of aphids in eastern Canada, overwinters in adult or larval form, depending on the types of winter shelters available to it and their geographic orientation (Sarhou et al., 2005). Because the winter survival of natural enemies is crucial to the effectiveness of the control that they will provide during the following season, several studies have endeavoured to identify the habitats that will help optimize the overwintering conditions of natural enemies (Landis, Wratten and Gurr, 2000). For example, in England, a study conducted in grain fields found that the perennial herbs *Dactylis glomerata* and *Hoculus lanatus* were the preferred species when establishing beetle banks, since they meet the needs of a larger number of predators (Thomas et al., 1992).

Non-crop vegetation can also provide oviposition sites for many species of beneficial insects (Landis, Wratten and Gurr, 2000). For example, it was reported that the twelve-spotted lady beetle (*Coleomegilla maculata*), a beetle of the Coccinellidae family and a highly generalist predator that is present in many herbaceous crops and in orchards of eastern Canada (Coderre and Tourneur, 1986), laid more eggs on the weed *Acalypha ostryaefolia* than on sweet corn despite the fact that this weed harboured fewer prey than corn. Corn plots surrounded by this weed contained significantly more lady beetles than the plots without weed strips, and the rate of predation on the corn earworm (*Helicoverpa zea*) was also higher in these plots (Cottrell and Yeargan, 1998).

According to Keller and Häni (2000), nine out of ten species of beneficial insects need a non-crop environment during at least one stage of their life cycle, whereas this is the case for only half of insect pests (Keller and Häni, 2000).

D. Landscape

The importance of the landscape context on the dynamics of pests and their natural enemies is increasingly well documented (Bianchi, Booij and Tscharntke, 2006; Veres et al., 2011). The reviews by Bianchi et al. (2006) and Veres et al. (2011) found that, in most cases, more complex landscapes containing more semi-natural habitats are associated with a higher abundance and greater diversity of natural enemies. Unfortunately, few studies have endeavoured to determine the actual impact of these changes on pest populations and the damage they cause. For this reason, the direct links of pest suppression with the landscape are less clear (Veres et al., 2011).

Of the ten studies mentioned in the review by Bianchi et al. (2006), five reported a reduction in pest pressure in complex landscapes. In these five studies, differences of 5% to 60% in pest pressure were measured between complex and non-diversified landscapes (one of these studies measured a significant positive effect in half of the observations only). The pests concerned were mainly species of aphids, thrips and pollen beetles. These studies mentioned effects such an increase in oviposition rate or parasitism rate of natural enemies to explain these results (Bianchi, Booij and Tscharntke, 2006).

Several recent studies have also highlighted the importance of studying biological interactions on larger spatial scales than habitat or field when implementing conservation biological control programs; the proportion of crop and non-crop habitats as well as their distribution in the landscape are important factors for natural enemy dynamics (Médiène et al., 2011, Veres et al., 2011).



Figure 7. Heterogeneous agricultural landscape composed of numerous natural and semi-natural habitats.

Photo credit: Ron Garnett, AirScapes.ca.

In eastern Canada, very few studies have examined the effect of the landscape context on pests and their natural enemies. In Quebec, a study published in 2010 sought to determine whether the landscape influenced the assemblage of insect predators (ground beetles) found in ditches bordering grain corn fields. It was found that non-crop areas and landscape heterogeneity generally had a positive effect on beetle abundance and diversity, which corroborates current thinking (Maisonhaute et al., 2010).

In soybeans, American studies have shown that simplification of the agricultural landscape has resulted in a 24% reduction in the control of the soybean aphid by its natural enemies (Landis et al., 2008). Another study currently being conducted in Quebec aims to determine which landscape elements promote soybean aphid infestations and establishment in fields, as well as control of this aphid by natural enemies (study under way at the University of Quebec at Montreal). The ultimate goal of this study is to provide data that can serve as a basis for formulating recommendations for agricultural producers. Indeed, research is still in the very early stages in terms of developing and applying landscape management criteria aimed at producers. It is first necessary to determine the spatial scale at which species respond to landscape effects (Médiène et al., 2011).

Figure 8. Braconid wasp – species *Aphidius colemani* – near an aphid mummy (parasitized aphid).

Photo credit: David Cappaert, Michigan State University, Bugwood.org.



III. MANAGEMENT PRACTICES THAT OPTIMIZE NATURAL ENEMY ACTIVITY

A. Non-crop areas on the edges of fields

The agroecological functions of semi-natural habitats illustrate the importance of non-crop areas for natural enemies, which underlines the need to conserve these areas or establish new ones in agricultural environments. The diversity of the resources available in these non-crop areas promotes the development of beneficial arthropods that subsequently migrate to the fields (Duelli et al., 1990; Tscharntke et al., 2007). In fact, it has been demonstrated that the quantity and quality of non-crop habitat patches adjacent to fields can influence the effectiveness of pest suppression (Olson and Wäckers, 2007). Establishing buffer zones (field margin strips, hedgerows, beetle banks, conservation strips, windbreaks) are practical methods for using the natural functions of non-crop habitats for the benefit of crops (Médiène et al., 2011).

There are many cases where establishing or preserving buffer zones have helped improve biological pest suppression by natural enemies (Altieri and Nicholls, 2004). However, according to these authors, there are still many questions that need further research in order to draw clearer conclusions about how to provide non-crop borders for beneficial insect species:



Figure 9. Broad herbaceous field margin, in United Kingdom, that provide ground beetle with a refuge (beetle bank).

Photo credit : © Copyright Living Countryside, www.ukagriculture.com.

1. To what extent do natural enemies depend on hedgerows, ditch banks and forests for their continued existence in agricultural areas, particularly during winter?
2. Do these borders influence the species diversity and abundance of entomophagous insects in adjacent crop fields?
3. Which attributes of the boundary are important for the natural enemies?
4. Can existing natural refuges within boundaries be improved or can new ones be created?

These are still very relevant questions in Canada, since very few studies have endeavoured to answer them. In 1996, Mineau and McLaughlin claimed that Canadian ecologists still had much work to do before being able to formulate specific management recommendations that optimize the services provided by ecosystems. In eastern Canada, very few studies have examined the impact of non-crop areas on the abundance and activity of beneficial organisms (Boutin et al., 2003; Boutin et al., 2009; Maisonhaute, Peres-Neto and Lucas, 2010). Internationally, a growing number of studies have examined the effect of peripheral habitats on arthropod populations (Asteraki et al., 2004; Blake et al., 2011; Cole et al., 2007; Denys and Tscharntke, 2002; Eyre and Leifert, 2011; Frampton and Dorne, 2007; Olson and Wäckers, 2007; Reeves et al., 2010; Thomas and Marshall, 1999; Thomas et al., 2001). However, only a few of these studies compared the various techniques for establishing, managing or preserving non-crop areas to draw conclusions that could serve as a basis for formulating recommendations aimed at producers (Fritch et al., 2011; Olson and Wäckers, 2007; Thomas and Marshall, 1999). Our review of the literature found no studies of this type in eastern Canada.

B. Promoting biodiversity within crop areas

Diversity within an agricultural landscape is directly linked to the size of natural enemy populations and to the control of pests in this landscape context (Landis et al., 2005). Perhaps the best way of promoting beneficial insects is to provide them directly, within fields, with the resources that they depend on (Andow, 1991; Lundgren, 2009). Indeed, not all entomophagous species are sufficiently mobile to travel outside fields in search of resources. For many predators, the larval stage is relatively or entirely immobile, and consequently, only the resources available within the field are accessible to them (Lundgren, 2009). In addition, many parasitoids, as well as some predators, are highly

dependent on the wind for their dispersal, which can make their migration outside the field and return to the field quite difficult. Providing resources directly in the fields therefore minimizes the need of these beneficial insects to emigrate from the fields (Lundgren, 2009).

Polyculture, defined as a type of cropping system in which at least two useful plants are grown simultaneously (Ruthenberg, 1971), promotes the activity of natural enemies by providing them with various resources, such as secondary food resources, breeding sites, shelters and overwintering sites, within the fields that require protection (Altieri and Nicholls, 2004). The results of the review published by Andow (1991) indicate that the benefits associated with polyculture systems outweigh the negative effects. Of the 287 phytophagous species listed by Andow, 52% were less abundant in diversified agroecosystems than in monocultures, while only 15% were more abundant in polycultures. One of the main hypotheses advanced to explain these results is the “natural enemy hypothesis,” initially proposed by Root (1973), according to which generalist natural enemies (including lacewings and lady beetles) and specialist natural enemies (especially parasitoids) are more abundant in polycultures and, consequently, are more effective in controlling phytophagous populations (Altieri and Nicholls, 2004; Root, 1973). It is also thought that generalists are more abundant mainly for the following reasons: they can diversify their diet with the various types of arthropods present in polycultures at various times during the growing season; they may have access to plant resources (pollen, nectar) provided by polycultures; prey and hosts are more abundant and diversified in polycultures; and they maintain their breeding populations (Smith and McSorley, 2000). Specialist natural enemies are believed to be more abundant mainly because the refuges provided by polycultures to their prey or hosts prevent extinction of their populations, which has a stabilizing effect on predator-prey and parasitoid-host relationships (Altieri and Nicholls, 2004).

However, some authors have suggested that diversification may have a negative effect on specialist natural enemies, by inducing a more heterogeneous distribution of prey, which hinders their ability to locate these prey (Sheehan, 1986). These opposing theories attest to the complexity of agroecological systems and illustrate why formulating practical recommendations is a complicated task.

C. Practical considerations

We have highlighted the importance of biodiversity in fields and adjacent areas to promote pest suppression ecosystem services. Various factors must be considered before taking any action to modify a habitat. Once again, it is not a matter of “encouraging diversification per se,” but rather of implementing optimal diversification strategies that take into consideration the biology of the organisms concerned in the various trophic levels as well the ecological principles that determine their interactions. In concrete terms, the challenge is to find optimal ways of increasing biodiversity without sacrificing the primary goal of agriculture, i.e. the sustainable and profitable production of crops.

Another challenge is to motivate producers to adopt these pest suppression methods. Many producers are still reluctant to adopt these practices, because ecological pest suppression methods do not produce equally reliable results, and because the agricultural practices involved are more complicated to implement. A habitat management approach is often more complex than conventional pest control methods and it runs contrary to the simplification of agricultural practices that was widely advocated in the last century (Gurr, van Emden and Wratten, 1998). This poses a major challenge for researchers, and the unique characteristics of each agricultural system make this task even more complicated.

Cultural practices and possible agricultural systems

Various agronomic practices have been tested in the last few decades, often modelled on traditional agricultural principles (Altieri and Nicholls, 2004). These practices include mixed cropping, strip cropping, intercropping, cover crops and agroforestry. The table in Appendix I, based on Gurr (2003), Altieri and Nicholls (2004) and Lundgren (2009), lists all of these practices and provides a brief description of their applications, with references to the authors that presented or mentioned them in reviews.

Altieri and Nicholls (2004) suggest that the decision as to which of these various options to use should be based on whether the crop to be protected is an annual or perennial. For instance, for annual crops such as corn, soybeans, grains and certain forage plants, producers should adopt techniques such as crop rotation, intercropping, strip cropping, weed cover crops, managed fallows and windbreaks along field edges. For perennial crops such as orchards, vineyards and certain forage plants (including alfalfa), the

authors recommend cover crops, living mulches, perennial polycultures, mixed orchards, intercropping with annual crops and manipulation of surrounding vegetation.

In addition to promoting pest suppression by natural enemies, these techniques provide other ecosystem services that contribute to the development of sustainable cropping systems, such as minimizing pest outbreaks and improving soil health, where applicable. These services are not addressed in this review.

Choosing cultural strategies

Choosing the best strategies for providing species of beneficial crop insects with the resources that they need and optimizing their activities can be complicated. Concerning access to secondary plant resources, Lundgren (2009) suggests that the best solution may be a combination of the various practices listed in Appendix 1.

It is virtually impossible to apply pest management solutions to large geographic areas because the soil, climate, pest populations and site management history are all factors that affect ecological interactions (Shennan, 2008). Each agroecosystem is unique. It is very important to make a careful study of the pest suppression context specific to the agricultural environment in question to make an informed choice among the various cultural practices. Combining antagonistic practices that could lead to undesirable results must be avoided.



Figure 10. Corn crop intercropped with flax.

Photo credit: © Copyright Living Countryside,
www.ukagriculture.com.

Take, for example, lepidopteron pests of corn. The larval stage of the fall army worm (*Spodoptera frugiperda*) can cause serious damage to corn crops, particularly in eastern Canada. It has been demonstrated that these larvae are generally more common in weed-free corn fields than in fields where complex populations of natural or selected weeds grow (Altieri and Nicholls, 2004). Pavuk and Stinner (1992) reported that the parasitoid *Eriborus terebrans* has a greater tendency to parasitize the European corn borer (*Ostrinia nubilalis*) in weed-infested fields than in weed-free fields (Pavuk and Stinner, 1991). However, the corn earworm (*Helicoverpa zea*), another major corn pest in eastern Canada, causes as much damage in weed-infested fields as in weed-free fields. The latter observation suggests that all species are not equally affected by the presence of weeds, or, more generally, by the management systems that may be used in fields (Altieri and Nicholls, 2004).

Tables 1 and 2 of Appendix II list a few authors who have studied the effects of these practices on natural enemies, the target pest and the crop. The most relevant studies for eastern Canada have been selected.

These tables show that the study of the effects of cultural practices and habitat management on natural enemies is still in the very early stages in eastern Canada. The crops for which the most information was found are corn, soybeans, grains and apple orchards. According to Boiteau (2010), no methods promoting natural enemies through cultural practices have been tested in the potato crop. A study conducted in New Brunswick has nevertheless shown that opening up the crop canopy and the absence of litter limit the migration of natural enemies from non-crop habitats to crops (Boiteau, 2010). A recent study conducted in blueberry fields in Nova Scotia examined the potential of compost in the fields as a source of predators of the blueberry maggot (*Rhagoletis mendax*), a pest whose larvae can cause serious damage (Renkema et al., 2012). This study showed that the ground beetle *Pterostichus melanarius* is an effective predator of this pest when it has few alternative prey. However, although the compost attracted ground beetles, it did not lead to a reduction in *R. mendax* populations (Renkema et al., 2012).

Plant species selection for polyculture and habitat management

The choice of which plant species to introduce in a field can prove to be fairly complicated. Annual plants may require several production cycles or cuttings to promote regrowth of flower buds (Irvin et al., 1999). These practices can be very time-consuming and labour-intensive and may interfere with producers' routine practices.

To make an informed choice in a given cropping system, Lundgren (2009) suggests that the decision be based on the findings of previous studies, while Fiedler and Landis recommend giving preference to native plants over exotic plants (Fiedler and Landis, 2007). The advantage of annuals is that there is no persistence of the vegetation into the next growing season (Landis, Wratten and Gurr, 2000). For perennial crops, the ideal plant may be a species that is a good competitor with weeds for the following year (Landis, Wratten and Gurr, 2000). Other factors to consider include the attractiveness of these plants to natural enemies, the predators of these natural enemies or potentially harmful pathogens to the crop of interest (Bottrell et al., 1998). Other authors also mention flowering period, seed cost and availability, as well as the competitiveness of the plant as important factors (Gurr, van Emden and Wratten, 1998).

Pearson (1990) suggested an approach to selection based on various plant criteria (Table 1). His approach consists in evaluating the potential of a plant based on the following criteria: biological factors, risks to the main crop and economic considerations. A weighting is assigned to each factor based on the producer's agroenvironmental context and a score is awarded to the plant for each of its factors on the basis of knowledge about its ecological and economic properties. This approach yields a score by plant species for comparison and selection purposes (Gurr, van Emden and Wratten, 1998; Pearson, 1990).



Figure 11. *Phacelia tanacetifolia* is a plant often grown by European producers for conservation purposes.

Photo credit: © Copyright Living Countryside,
www.ukagriculture.com.

Table 1. Approach using a list based on the classification and weighting of control criteria for evaluating the potential of *Phacelia tanacetifolia* as a food source in the context of habitat management in an alfalfa (*Medicago sativa*) field in New South Wales, Australia*

Criteria	Weighting (1 = unimportant 5 = important)	Estimated value	Final value (weighting X estimated value)
RISKS (1=high risk 5=low risk)			
Weed potential	3	3	9
Intermediate host of a crop pathogen	3	4	12
Toxicity to livestock	5	5	25
Potential contamination of products	4	5	20
ECONOMIC FACTORS (1=poor 5=good)			
Possibility of a second crop	2	3	6
Affordable price and availability of seed	2	1	2
Establishment costs	2	4	6
BIOLOGICAL FACTORS (1=poor 5=good)			
Pollen production (total and spread over time)	4	4	16
Nectar production (total and spread over time)	4	5	12
Agronomic compatibility with the crop	5	4	20
Vigor or competitiveness with weeds	3	3	9
Perennials or self-reseeding annuals	1	2	2
TOTAL			139**

* Table adapted from Pearson (1990) – refer to the author’s original text for discussion purposes.

**Compare the plant’s final value to that of other potential plants evaluated in the same way.

D. Other cultural practices that affect natural enemies

Tillage

Tillage can have a major impact on soil organisms and on the relationships between organisms of different trophic levels (El Titi, 2003). Tillage intensity, the method used, the frequency of tillage operations and the dates of crop planting and harvesting are all factors that can affect natural enemies. Generally, reduced tillage promotes a more stable environment, which in turn promotes a diversity of species (Altieri, 1999). Less tillage is associated with greater abundance and diversity of the fauna. However, the effects vary from one species to another, depending on their specific ecological characteristics. For example, species with a soil-dwelling larval or pupal stage are particularly sensitive to tillage (Kendall, 2003). A study carried out with canola demonstrated that post-harvest tillage led to a reduction the next spring in the rate of emergence of parasitoids overwintering in the soil (Ferguson et al., 2003).



Figure 12. Tillage can have a major impact on soil organisms and on the relationships between organisms of different trophic level.

Photo credit: © Copyright Living Countryside, www.ukagriculture.com.

Herbicide and pesticide use

Numerous studies have demonstrated the negative effects of pesticides on natural enemy communities. The effects on predators and parasitoids can be direct (e.g. direct effects on their biological functions) or indirect (e.g. effects on their secondary resources). To cite a few examples, Ulber et al. (2010) demonstrated that many species of parasitoids of canola pests are directly affected by pesticide treatments during flowering, a period when they are particularly active (Ulber et al., 2010). The indirect effects of herbicides on certain arthropods was demonstrated by Heard et al. (2006) in corn: weed control using herbicides also suppressed the resources that the weeds provided to beneficial insect species (Heard et al., 2006).

Nitrogen fertilization

In addition to having an effect on pests, fertilization can also impact their natural enemies (Rusch et al., 2010). Safraz et al. (2009) studied the effects of fertilization on the diamond back moth (*Plutella xylostella*) and its parasitoid *Diadegma insulare* in canola. They demonstrated that the parasitoid was more effective on plants that received high doses of fertilizer and that the proportion of diamond back moths that were able to evade the parasitoid was higher on the less fertilized plants (Safraz et al., 2009).

Seeding and harvesting dates

Although this topic has received little attention, some studies note that seeding and harvesting dates could have an impact on both pests and natural enemy communities (Rusch et al., 2010). According to Riechert and Lockley, harvesting constitutes a massive

disturbance which may have a greater impact on spiders than pesticide use (Riechert and Lockley, 1984). The actual effects on the suppression of pests remain to be proven.

Food spray

The management of plant food resources directly targeting natural enemies in the field is an increasingly popular solution. In Chapter 16 of the book *Relationships of Natural Enemies and Non-Prey Foods*, Lundgren (2009) provides a detailed review of the practice of food spray. He describes the optimal application techniques and discusses the difficulties and disadvantages of the practice. Although providing a detailed description of this practice is beyond the scope of the present review, it is nonetheless important to point out that this practice is widely used and considered very promising for the development of integrated pest control programs (Lundgren, 2009). We have provided an example of this in Table 2 of Appendix II.

IV. CONCLUSION

In this review of the literature, we explored the principles and practical applications of habitat management, the goal of which is to promote the control of agricultural pests by their natural enemies. This requires increasing populations of natural enemies in fields. However, this is not necessarily sufficient to achieve a satisfactory level of biological control. These natural enemies must also achieve a sufficient reduction in pest populations below economic threshold for controls. Study authors generally focus on the effects of agricultural practices on the abundance of beneficial insect species, but neglect to measure the concrete effects on crop yields and quality.

To encourage producers to adopt conservation biological control practices, it is necessary to suggest strategies that are both effective and economically viable. Unfortunately, study findings are highly variable. The level of uncertainty is still too high to make definite recommendations for controlling a given phytophagous species in a particular set of conditions (Letourneau et al., 2009).

According to Landis et al. (2000), most of the factors that limit the effectiveness of natural enemies in agricultural systems (including pesticides, lack of food or lack of intermediate hosts) are direct results of the disturbance regimes imposed on these systems. Efforts to conserve and promote the natural enemies of crop pests should target not only the immediate limiting factors, but also the disturbances that cause them. Conservation should therefore encompass interventions at various spatial scales. For example, while eliminating pesticides in a field may create more favourable conditions for the establishment of natural enemy populations, if viable metapopulations do not exist at the landscape level to provide immigrants, the within-field effort may be ineffective in the medium to long term (Landis, Wratten and Gurr, 2000).

As mentioned earlier, the scientific community is increasingly aware of the importance of the scale of intervention in establishing viable pest control strategies. However, in eastern Canada, work in this area is only just beginning. In Canada, the issue of geographic scale is particularly important. Re-establishing the self-regulating character of natural communities, which is the foundational principle of conservation biological control, can be difficult in ultrasimplified modern agricultural systems. The average size

of Canadian fields is steadily increasing (Canada Grains Council 2004-), while field size poses another obstacle to the establishment of natural enemy communities (Mineau and McLaughlin, 1996).

From an economic perspective, convincing producers of the cost-effectiveness of the suggested practices continues to be a major challenge. According to Cullen et al. (2008), conservation biological control can be economically worthwhile, although, unfortunately, too few studies have been conducted with the specific goal of assessing this economic benefit, one of the few examples being Schmidt et al. (2007). These authors studied the effect of alfalfa living mulch on the natural enemies of soybeans. They observed that this practice reduced the populations of soybean aphids (*Aphis glycines* Matsumura) to below the economic damage threshold. However, they concluded that this practice was not economically cost-effective, since competition between alfalfa and soybeans reduced soybean yield by 26%. It will be essential to conduct more exhaustive studies of this type in order to ensure that the strategies suggested to producers interested in adopting biological control practices are in fact cost-effective.

Major research efforts are still required to make the adoption of conservation biological control practices a practical proposition and, in particular, to identify the most effective ways to conserve the natural habitats that promote the self-regulation of agricultural production systems. However, given the encouraging results provided by agricultural communities, it seems clear that this approach is destined to become a paradigm of the 21st century (Kassam, 2011).

APPENDIX I

Agronomic practices that promote diversity within and outside fields

Table based on Gurr (2003), Altieri and Nicholls (2004) and Lundgren (2009).

Scale		Practice	Description	Reference
Field	Weeds: a. Tolerance	Reduce herbicide applications	Tolerate some weeds in fields by reducing the dose or frequency of herbicide applications. Base herbicide application decisions on economic threshold criteria (i.e. refrain from applying herbicides until the weed population has reached a stage where the impact on the final crop yield is sufficient to justify the costs associated with herbicide application).	(Altieri and Letourneau, 1982; Zandstra and Motooka, 1978)
		Directed herbicide applications	Target only the most competitive weeds, leaving the others as a source of biodiversity.	(Zandstra and Motooka, 1978)
		Modify the spatial and temporal distribution of weeds	Do not apply herbicide to certain plots distributed throughout the field. Apply herbicides in strips so that some weeds are present in portions of the field throughout the season.	(Altieri and Nicholls, 2004; Bugg and Waddington, 1994; Lys, 1994)
	b. Introduction	Sown weed strips	Selected weed species sown along strips throughout the field	(Hausamann, 1996; Landis, Wratten and Gurr, 2000; Nentwig et al., 1998; Zandstra and Motooka, 1978)
	Mixed cropping	Simultaneous intercropping and strip cropping	Traditional polyculture	(Altieri and Letourneau, 1982; Coll, 1998; Wilkinson and Landis, 2005)
		Relay intercropping or overseeding	Planting the next crop directly into the standing crop, never leaving bare soil.	(Altieri and Letourneau, 1982; Coll, 1998; Landis, Wratten and Gurr, 2000)

Scale		Practice	Description	Reference
	Cover crops	Fall planting	Planting the cover crop in the fall and destroying it before development of the main crop the next year (this ensures that natural enemies are present before the crop becomes established).	(Clark, 1998; Wilkinson and Landis, 2005)
		Living mulch	Planting an understory crop that will be left in place when the primary crop is planted (mainly in orchards).	(Altieri and Letourneau, 1982; Landis et al., 2000; O'Neal et al., 2005; Prasifka et al., 2006; Wilkinson and Landis, 2005)
	Diversification within monoculture	Varietal diversification	Planting several varieties of the same crop with different characteristics.	(Lundgren, 2009)
		Species diversification: Relax the monoculture	Planting several closely related crop species	(Gurr et al., 2003)
		Structural diversification	Make the crop structure more complex, for example by harvesting different strips in staggered rows, which ensures that a refuge is always maintained for natural enemies	(Gurr, Wratten and Michael Luna, 2003; Hossain et al., 2001)
	Within-field cultivated areas	Beetle banks		(Landis, Wratten and Gurr, 2000; MacLeod et al., 2004)
Farm	Uncultivated areas outside fields	Diversification of vegetation beyond field borders	Natural or planted fallows around fields	(Gurr, Wratten and Michael Luna, 2003; Thies and Tscharntke, 1999)
Landscape	Landscape management	Heterogeneous landscapes Landscapes with woodlands		(Gurr, Wratten and Michael Luna, 2003; Marino, Landis and Hawkins, 2006)

APPENDIX II

Examples of management strategies and their effects on pest suppression in field crops, forage crops, apple orchards, vineyards and berry crops

NB: The effects on pests and crops do not necessarily indicate a direct link with natural enemies.

CULTURAL PRACTICE	TARGETED PEST	EFFECTS ON BENEFICIAL INSECTS	IMPACT ON PEST AND/OR CROP	OTHER EFFECTS OBSERVED	LOCATION	REFERENCE
Strip cropping (18 m or 36 m) of corn, soybeans, wheat and vetch	Soybean aphid (<i>Aphis glycines</i>)	More numerous in monoculture generally More numerous in the strips during infestation peak	Half as many aphids as in soybean monoculture	Better natural enemy-pest synchronization in the strips	Quebec	(Labrie, 2010)
Strip cropping (18 m or 36 m) of corn, soybeans, wheat and vetch	European corn borer (<i>Ostrinia nubilalis</i>)	More diversified in the strips	More aphids in the 18 m strips		Quebec	(Labrie, 2010)
Soybeans intercropped with corn	European corn borer (<i>Ostrinia nubilalis</i>)	Not identified	- 40% reduction in damage compared to corn monoculture - No change in yield	Competition between soybeans and corn which affected corn yields	Ontario	(Martin et al., 1989)
Corn intercropped with soybeans	Soybean aphid (<i>Aphis glycines</i>)	Twice as many natural enemies as in monoculture	Aphid control of more than 80%		China	(Wang and Ba, 1998)
Alfalfa as cover crop in soybeans	Soybean aphid (<i>Aphis glycines</i>)	45% more natural enemies than in monoculture	- Later arrival of aphids in the plots with cover crop - Aphid populations kept below the economic damage threshold	Alfalfa reduced the growth rate of the aphid population (less nitrogen in the soybeans associated with the alfalfa)	Iowa, US	(Schmidt et al., 2007)

CULTURAL PRACTICE	TARGETED PEST	EFFECTS ON BENEFICIAL INSECTS	IMPACT ON PEST AND/OR CROP	OTHER EFFECTS OBSERVED	LOCATION	REFERENCE
Alfalfa and clover Kura clover as cover crop in corn and soybeans	European corn borer (<i>Ostrinia nubilalis</i>)	Increase in the abundance of ground beetles in correlation with the consumption of <i>O. nubilalis</i> pupae	Not specified		Iowa, US	(Prasifka et al., 2006)
Application of mustard seed meal (as food source) in canola	<i>Delia radicum</i>	Rate of parasitism of <i>A. bipustulata</i> higher in the meal-treated plots	No effect on the population of <i>D. radicum</i> or on the damage caused by the larvae		Switzerland/ Canada	(Riley et al., 2007)
Agroforestry system of alley cropped walnut with alfalfa	Several	Twice as many arthropod predators and parasites than in alfalfa monoculture	Half as many herbivores as in alfalfa monoculture	Minor impact on the growth of walnut trees and nut yield	Missouri	(Stamps et al., 2002)
Flowering hedges along the edges of apple orchards	Tarnished plant bug, sawflies, white apple leafhopper, aphids, mites	More numerous near the flower borders (spiders, lady beetles, hoverflies, lacewings)	- Fewer sawflies in the plots with flower borders - Less sawfly damage	No effect beyond 10 m from the flowering hedges	Quebec	(De Almeida, 2012)
Flowering cover crops (phacelia, buckwheat) in apple orchards	Apple aphids: - <i>Aphis pomi</i> - <i>Aphis spiraecola</i>	- No effect on the abundance of beneficial insects - No cover crop: 1) negative effect on oviposition of gall midges 2) positive effect on adult lady beetles	No effect on the abundance of aphids	The effects on natural enemies are variable depending on the apple cultivar	Quebec	(Fréchette et al., 2008)
Floral strips within apple orchards	Codling moth (<i>Cydia pomonella</i>)	Higher abundance and diversity of parasitoids in the flower borders	The parasitoids found in the codling moths were not the same as those found in the flower borders		France	(Dib et al., 2012)

CULTURAL PRACTICE	TARGETED PEST	EFFECTS ON BENEFICIAL INSECTS	IMPACT ON PEST AND/OR CROP	OTHER EFFECTS OBSERVED	LOCATION	REFERENCE
Establishment of a vegetational corridor between the riparian forest and vineyard	Leafhoppers and thrips	Increase in the populations of lady beetles, hoverflies, predatory damsel bugs and lacewings	Significant decrease in the populations of leafhoppers and thrips near the corridors		California	(Nicholls et al., 2008)
Cover crops (clover, buckwheat or ryegrass) in aisles within blueberry fields	Onion maggot (<i>Delia antiqua</i>)	Increase in the relative abundance of ground beetles	Not specified		Michigan	(O'Neal et al., 2005)

V. BIBLIOGRAPHY

- Altieri, M.A.** 1999. The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment* 74:19-31.
- Altieri, M.A., and D.K. Letourneau.** 1982. Vegetation management and biological control in agroecosystems. *Crop Protection* 1:405-430.
- Altieri, M.A., and C.I. Nicholls.** 2004. *Biodiversity and pest management in agroecosystems*, 2nd ed. New York: Food Products Press.
- Andow, D.A.** 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36:561-586.
- Asteraki, E.J., B.J. Hart, T.C. Ings, and W.J. Manley.** 2004. Factors influencing the plant and invertebrate diversity of arable field margins. *Agriculture, Ecosystems & Environment* 102:219-231.
- Berndt, L.A., S.D. Wratten, and S.L. Scarratt.** 2006. The influence of floral resource subsidies on parasitism rates of leafrollers (Lepidoptera: Tortricidae) in New Zealand vineyards. *Biological Control* 37:50-55.
- Bianchi, F.J., C.J. Booij, and T. Tscharntke.** 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings. Biological Sciences/The Royal Society* 273:1715-1727.
- Blake, R.J., B.A. Woodcock, A.J. Ramsay, E.S. Pilgrim, V.K. Brown, J.R. Tallowin, and S.G. Potts.** 2011. Novel margin management to enhance Auchenorrhyncha biodiversity in intensive grasslands. *Agriculture, Ecosystems & Environment* 140:506-513.
- Boiteau, G.** 2010. Insect pest control on potato: Harmonization of alternative and conventional control methods. *American Journal of Potato Research* 87:412-419.
- Bottrell, D.G., P. Barbosa, and F. Gould.** 1998. Manipulating natural enemies by plant variety selection and modification: A realistic strategy? Pp. 347-367.
- Boutin, C., B. Jobin, and L. Bélanger.** 2003. Importance of riparian habitats to flora conservation in farming landscapes of southern Quebec, Canada. *Agriculture, Ecosystems & Environment* 94:73-87.
- Boutin, C., P.A. Martin, and A. Baril.** 2009. Arthropod diversity as affected by agricultural management (organic and conventional farming), plant species, and landscape context. *Ecoscience* 16:492-501.
- Brown, M.W.** 2012. Role of biodiversity in integrated fruit production in eastern North American orchards. *Agricultural and Forest Entomology* 14:89-99.
- Bugg, R.L., and C. Waddington.** 1994. Using cover crops to manage arthropod pests of orchards: A review. *Agriculture, Ecosystems & Environment*, 50:11-28.
- Canada Grains Council.** 2004-. Online Statistical Handbook [electronic resource].
- Clark, A.** 1998. *Managing Cover Crops Profitably*, 2nd ed. Beltsville, MD.

- Coderre, D.L., and J.C. Tourneur.** 1986. Synchronization and voracity of aphidophagous insects on maize in Quebec, Canada. In *Ecology of Aphidophaga*. I. Hodek, ed. Dordrecht, The Netherlands: Dr. W. Junk. Pp. 363-368.
- Cole, L.J., D.I. McCracken, L. Baker, and D. Parish.** 2007. Grassland conservation headlands: Their impact on invertebrate assemblages in intensively managed grassland. *Agriculture, Ecosystems & Environment* 122:252-258.
- Coll, M.** 1998. Parasitoid activity and plant species composition in intercropped systems. In *Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pests*. C.H. Pickett and R.L. Bugg, eds. Berkeley, CA: University of California Press. Pp. 85-120.
- Coll, M.** 2009. Conservation biological control and the management of biological control services: Are they the same? *Phytoparasitica* 37:205-208.
- Corbett, A., and J.A. Rosenheim.** 1996. Quantifying movement of a minute parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), using fluorescent dust marking and recapture. *Biological Control* 6:35-44.
- Cottrell, T.E., and K.V. Yeargan.** 1998. Influence of a native weed, *Acalypha ostryaefolia* (Euphorbiaceae), on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology* 27:1375-1385.
- De Almeida, J.** (2012) Aménagement d'une haie composite pour favoriser l'établissement et le maintien de la faune auxiliaire dans les vergers de pommiers. Montreal, Canada: University of Quebec at Montreal.
- Denys, C., and T. Tscharntke.** 2002. Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia* 130:315-324.
- Dib, H., G. Libourel, and F. Warlop.** 2012. Entomological and functional role of floral strips in an organic apple orchard: Hymenopteran parasitoids as a case study. *Journal of Insect Conservation* 16:315-318.
- Dinter, A.** 2002. Microcosm studies on intraguild predation between female erigonid spiders and lacewing larvae and influence of single versus multiple predators on cereal aphids. *Journal of Applied Entomology* 126:249-257.
- Duelli, P., M. Studer, I. Marchand and S. Jakob.** 1990. Population movements of arthropods between natural and cultivated areas. *Biological Conservation* 54:193-207.
- Dyer, L.E., and D.A. Landis.** 1996. Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environmental Entomology* 25:1192-1201.
- Ekström, G., and B. Ekbom.** 2011. Pest control in agro-ecosystems: An ecological approach. *Critical Reviews in Plant Sciences* 30:74-94.
- Evans, E.W., and S. England.** 1996. Indirect interactions in biological control of insects: Pests and natural enemies in alfalfa. *Ecological Applications* 6:920-930.
- Eyre, M.D., and C. Leifert.** 2011. Crop and field boundary influences on the activity of a wide range of beneficial invertebrate groups on a split conventional/organic farm in northern England. *Bulletin of Entomological Research* 101:135-144.

- Ferguson, A.W., J.M. Campbell, D.J. Warner, N.P. Watts, J.E.U. Schmidt, and I.H. Williams.** 2003. Spatio-temporal distributions of *Meligethes aeneus* and its parasitoids in an oilseed rape crop and their significance for crop protection. In *11th International Rapeseed Congress*. Pp. 1057–1059.
- Fiedler, A.K., and D.A. Landis.** 2007. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. *Environmental Entomology* 36:751-765.
- Frampton, G.K., and J.L.C.M. Dorne.** 2007. The effects on terrestrial invertebrates of reducing pesticide inputs in arable crop edges: A meta-analysis. *Journal of Applied Ecology* 44:362-373.
- Fréchette, B., D. Cormier, G. Chouinard, F. Vanoosthuyse, and É. Lucas.** 2008. Apple aphid, *Aphis* spp. (Hemiptera: Aphididae), and predator populations in an apple orchard at the non-bearing stage: The impact of ground cover and cultivar. *European Journal of Entomology* 105:521-529.
- Fritch, R.A., H. Sheridan, J.A. Finn, L. Kirwan, and D.Ó. hUallacháin.** 2011. Methods of enhancing botanical diversity within field margins of intensively managed grassland: A 7-year field experiment. *Journal of Applied Ecology* 48:551-560.
- Fuchsberg, J.R., T.-H. Yong, J.E. Losey, M.E. Carter, and M.P. Hoffmann.** 2007. Evaluation of corn leaf aphid (*Rhopalosiphum maidis*; Homoptera: Aphididae) honeydew as a food source for the egg parasitoid *Trichogramma ostrinae* (Hymenoptera: Trichogrammatidae). *Biological Control* 40:230-236.
- Gavish-Regev, E., R. Rotkopf, Y. Lubin, and M. Coll.** 2009. Consumption of aphids by spiders and the effect of additional prey: evidence from microcosm experiments. *BioControl* 54:341-350.
- Grube, A., D. Donaldson, T. Kiely, and L. Wu.** 2011. Pesticides Industry Sales and Usage: 2006 and 2007 Market Estimates. U.S. Environmental Protection Agency, OCSPP. Washington, DC.
- Gurr, G.M., H.F. van Emden, and S.D. Wratten.** 1998. Chapter 9 - Habitat manipulation and natural enemy efficiency: Implications for the control of pests. In *Conservation Biological Control*. B. Pedro, ed., San Diego: Academic Press. Pp. 155-183.
- Gurr, G.M., S.D. Wratten, and J. Michael Luna.** 2003. Multi-function agricultural biodiversity: Pest management and other benefits. *Basic and Applied Ecology* 4:107-116.
- Hagen, K.S.** 1986. Nutritional ecology of terrestrial predators. In *Nutritional ecology of insects, mites, spiders, and related invertebrates*. F. Slansky and J.G. Rodriguez, eds. New York: Wiley. Pp. 533-577.
- Hausammann, A.** 1996. Strip-management in rape crop: is winter rape endangered by negative impacts of sown weed strips? *Journal of Applied Entomology* 120:505-512.
- Heard, M.S., S.J. Clark, P. Rothery, J.N. Perry, D.A. Bohan, D.R. Brooks, G.T. Champion, A.M. Dewar, C. Hawes, A.J. Haughton, M.J. May, R.J. Scott, R.S. Stuart, G.R. Squire, and L.G. Firbank.** 2006. Effects of successive seasons of genetically modified herbicide-tolerant maize cropping on weeds and invertebrates. *Annals of Applied Biology* 149:249-254.
- Hossain, Z., G.M. Gurr, and S.D. Wratten.** 2001. Habitat manipulation in lucerne (*Medicago sativa* L.): Strip harvesting to enhance biological control of insect pests. *International Journal of Pest Management* 47:81-88.

- Huffaker, C.B., and D.L. Flaherty.** 1966. Potential of biological control of two-spotted spider mites on strawberries in California. *Journal of Economic Entomology* 59:786-792.
- Irvin, N.A., S.D. Wratten, R.B. Chapman, and M.C. Frampton.** 1999. The effects of floral resources on longevity, populations and efficacy of the leafroller parasitoid (*Dolichogenidea tasmanica* (Cameron) in apples. In *New Zealand Plant Protection Conference*, NZPP Society, ed. Wellington, New Zealand. Pp. 84-88.
- Jervis, M.A., N.A.C. Kidd, M.G. Fitton, T. Huddleston, and H.A. Dawah.** 1993. Flower-visiting by hymenopteran parasitoids. *Journal of Natural History* 27:67-105.
- Jones, G.A., and K.E. Sieving.** 2006. Intercropping sunflower in organic vegetables to augment bird predators of arthropods. *Agriculture, Ecosystems & Environment* 117:171-177.
- Keller, S., and F. Häni.** 2000 Ansprüche von Nützlingen und Schädlingen an den Lebensraum. In *Streifenförmige ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrache, Feldränder*. W. Nentwig, ed. Switzerland: Verlag Agrarökologie. Pp. 199-217.
- Kendall, D.A.** 2003. Soil tillage and epigeal predatory arthropods. In *Soil Tillage in Agroecosystems*. A. El Titi, ed. US: CRC Press.
- Labrie, G.** 2010. Synthèse de la littérature scientifique sur le puceron du soya, *Aphis glycines* Matsumura: CEROM.
- Landis, D.A., M.M. Gardiner, W. Van Der Werf, and S.M. Swinton.** 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 105:20552-20557.
- Landis, D.A., and M.J. Haas.** 1992. Influence of landscape structure on abundance and within-field distribution of European corn borer (Lepidoptera: Pyralidae) larval parasitoids in Michigan. *Environmental Entomology* 21:409-416.
- Landis, D.A., F.D. Menalled, A.C. Costamagna, and T.K. Wilkinson.** 2005. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science* 53:902-908.
- 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.
- Letourneau, D.K., J.A. Jedlicka, S.G. Bothwell, and C.R. Moreno.** 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 40:573-592.
- Lucas, É., and J.A. Rosenheim.** 2011. Influence of extraguild prey density on intraguild predation by heteropteran predators: A review of the evidence and a case study. *Biological Control* 59:61-67.
- Lundgren, J.G.** 2009. Relationships of Natural Enemies and Non-Prey Foods: Springer Netherlands.
- Lundgren, J.G., K.A.G. Wyckhuys, and N. Desneux.** 2009. Population responses by *Orius insidiosus* to vegetational diversity. *BioControl* 54:135-142.
- Lys, J.-A.** 1994. The positive influence of strip-management on ground beetles in a cereal field: increase, migration and overwintering. *Series Entomologica* 51:451.
- MacLeod, A., S.D. Wratten, N.W. Sotherton, and M.B. Thomas.** 2004. 'Beetle banks' as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. *Agricultural and Forest Entomology* 6:147-154.

- Madsen, M., S. Terkildsen, and S. Toft.** 2004. Microcosm studies on control of aphids by generalist arthropod predators: Effects of alternative prey. *BioControl* 49:483-504.
- Maisonhaute, J.-É., P. Peres-Neto, and É. Lucas.** 2010. Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage. *Agriculture, Ecosystems & Environment* 139:500–507.
- Marino, P.C., D.A. Landis, and B.A. Hawkins.** 2006. Conserving parasitoid assemblages of North American pest Lepidoptera: Does biological control by native parasitoids depend on landscape complexity? *Biological Control* 37:173-185.
- Marshall, E.J.P.** 2004. Agricultural landscapes: Field margin habitats and their interaction with crop production. *Journal of Crop Improvement* 12:365-404.
- Martin, R.C., T.J. Arnason, J.D.H. Lambert, P. Isabelle, H.D. Voldeng, and D.L. Smith.** 1989. Reduction of European corn borer (Lepidoptera: Pyralidae) damage by intercropping corn with soybean. *Journal of Economic Entomology* 82:1455-1459.
- Matson, P.A., W.J. Parton, A.G. Power, and M.J. Swift.** 1997. Agricultural intensification and ecosystem properties. *Science* 277:504-509.
- McLaughlin, A., and P. Mineau.** 1995. The impact of agricultural practices on biodiversity. *Agriculture, Ecosystems & Environment* 55:201-212.
- Médiène, S., M. Valantin-Morison, J.P. Sarthou, S. De Tourdonnet, M. Gosme, M. Bertrand, J. Roger-Estrade, J.N. Aubertot, A. Rusch, N. Motisi, C. Pelosi, and T. Doré.** 2011. Agroecosystem management and biotic interactions: A review. *Agronomy for Sustainable Development* 31:491-514.
- Mineau, P., and A. McLaughlin.** 1996. Conservation of biodiversity within Canadian agricultural landscapes: Integrating habitat for wildlife. *Journal of Agricultural and Environmental Ethics* 9:93-113.
- 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*. San Diego, Calif., USA: Academic Press. Pp. 133-153.
- O'Neal, M.E., E.I. Zontek, Z. Szendrei, D.A. Landis, and R. Isaacs.** 2005. Ground predator abundance affects prey removal in highbush blueberry (*Vaccinium corymbosum*) fields and can be altered by aisle ground covers. *BioControl* 50:205-222.
- Olson, D.M., and F.L. Wäckers.** 2007. Management of field margins to maximize multiple ecological services. *Journal of Applied Ecology* 44:13-21.
- Orr, D.B., D.A. Landis, D.R. Mutch, G.V. Manley, A.A. Stuby, and R.I. King.** 1997. Ground cover influence on microclimate and Trichogramma (Hymenoptera: Trichogrammatidae) augmentation in seed corn production. *Environmental Entomology* 26:433-438.
- Östman, Ö., and A.R. Ives.** 2003. Scale-dependent indirect interactions between two prey species through a shared predator. *Oikos* 102:505-514.
- Pavuk, D.M., and B.R. Stinner.** 1991. Influence of weeds in corn plantings on population densities of and damage by second-generation *Ostrinia nubilalis* (Hubner) (Lepidoptera: Pyralidae) larvae. *Environmental Entomology* 20:276-281.
- Pearson, A.W.** 1990. The management of research and development. In *Technology and Management*. R. Wild, R. ed. New York, NY: Nichols. Pp. 28-41.
- Pimentel, D.** 2008. Preface Special Issue: Conservation biological control. *Biological Control* 45:171.

- Prasifka, J.R., N.P. Schmidt, K.A. Kohler, M.E. O'Neal, R.L. Hellmich, and J.W. Singer.** 2006. Effects of living mulches on predator abundance and sentinel prey in a corn–soybean–forage rotation. *Environmental Entomology* 35:1423-1431.
- Rahim, A., A.A. Hashmi, and N.A. Khan.** 1991. Effects of temperature and relative humidity on longevity and development of *Ooencyrtus papilionis* Ashmead (Hymenoptera: Eulophidae), a parasite of the sugarcane pest, *Pyrilla perpusilla* Walker (Homoptera: Cicadellidae). *Environmental Entomology* 20:774-775.
- Ratnadass, A., P. Fernandes, J. Avelino, and R. Habib.** 2012. Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. *Agronomy for Sustainable Development* 32:273-303.
- Reeves, R.B., J.K. Greene, F.P.F. Reay-Jones, M.D. Toews, and P.D. Gerard.** 2010. Effects of adjacent habitat on populations of stink bugs (Heteroptera: Pentatomidae) in cotton as part of a variable agricultural landscape in South Carolina. *Environmental Entomology* 39:1420-1427.
- Renkema, J.M., D.H. Lynch, G.C. Cutler, K. Mackenzie, and S.J. Walde.** 2012. Emergence of blueberry maggot flies (Diptera: Tephritidae) from mulches and soil at various depths. *Environmental Entomology* 41:370-376.
- Riechert, S.E., and T. Lockley.** 1984. Spiders as biological control agents. *Annual Review of Entomology* 29:299-320.
- Riley, K.J., U. Kuhlmann, P.G. Mason, J. Whistlecraft, L.J. Donald, and N.J. Holliday.** 2007. Can mustard seed meal increase attacks by *Aleochara* spp. on *Delia radicum* in oilseed rape? *Biocontrol Science and Technology* 17:273-284.
- Root, R.B.** 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124.
- Rusch, A., M. Valantin-Morison, J. Roger-Estrade, and J.-P. Sarthou.** 2012. Using landscape indicators to predict high pest infestations and successful natural pest control at the regional scale. *Landscape and Urban Planning*.
- Rusch, A., M. Valantin-Morison, J.-P. Sarthou, and J. Roger-Estrade.** 2010. Chapter Six - Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming Systems, and Seminatural Habitats at the Landscape Scale: A Review. In *Advances in Agronomy*. L.S. Donald, ed. Academic Press. Pp. 219-259.
- Ruthenberg, H.** 1971. *Farming Systems in the Tropics*. London: Clarendon Press.
- Sarfraz, M., L.M. Dosdall, and B.A. Keddie.** 2009. Fitness of the parasitoid *Diadegma insulare* is affected by its host's food plants. *Basic and Applied Ecology* 10:563-572.
- Sarthou, J.P., A. Ouin, F. Arrignon, G. Barreau, B. and Bouyjou.** 2005. Landscape parameters explain the distribution and abundance of *Episyrphus balteatus* (Diptera: Syrphidae). *European Journal of Entomology* 102:539-545.
- Schmidt, N.P., M.E. O'Neal, and J.W. Singer.** 2007. Alfalfa living mulch advances biological control of soybean aphid. *Environmental Entomology* 36:416-424.
- Sheehan, W.** 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: A selective review. *Environmental Entomology* 15:456-461.
- Shennan, C.** 2008. Biotic interactions, ecological knowledge and agriculture. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:717-739.

- Smith, H.A., and R. McSorley.** 2000. Intercropping and pest management: A review of major concepts. *American Entomologist* 46:154-161.
- Stamps, W., T. Woods, M. Linit, and H. Garrett.** 2002. Arthropod diversity in alley cropped black walnut (*Juglans nigra* L.) stands in eastern Missouri, USA. *Agroforestry Systems* 56:167-175.
- Sutherland, J.P., M.S. Sullivan, and G.M. Poppy.** 2001. Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agricultural and Forest Entomology* 3:57-64.
- Thies, C., and T. Tscharntke.** 1999. Landscape Structure and Biological Control in Agroecosystems. *Science* 285:893-895.
- Thomas, C.F.G., and E.J.P. Marshall.** 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems & Environment* 72:131-144.
- Thomas, C.F.G., L. Parkinson, G.J.K. Griffiths, A.F. Garcia, and E.J.P. Marshall.** 2001. Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. *Journal of Applied Ecology* 38:100-116.
- Thomas, M.B., N.W. Sotherton, D.S. Coombes, and S.D. Wratten.** 1992. Habitat factors influencing the distribution of polyphagous predatory insects between field boundaries. *Annals of Applied Biology* 120:197-202.
- Tscharntke, T., R. Bommarco, Y. Clough, T.O. Crist, D. Kleijn, T.A. Rand, J.M. Tylianakis, S.V. Nouhuys, and S. Vidal.** 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control* 43:294-309.
- Ulber, B., I.H. Williams, Z. Klukowski, A. Luik, and C. Nilsson.** 2010. Parasitoids of Oilseed Rape Pests in Europe: Key Species for Conservation Biocontrol-Based Integrated Management of Oilseed Rape Pests. I.H. Williams, ed. Springer: Netherlands. Pp. 45-76.
- van Emden, H.F.** 1990 Plant diversity and natural enemy efficiency in agroecosystems. In *Critical Issues in Biological Control*. M. Mackauer, L.E. Ehler and J. Roland, eds. Andover, UK: Intercept Press. Pp. 63-80.
- Veres, A., S. Petit, C. Conord, and C. Lavigne.** 2011. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems & Environment*.
- Wäckers, F.L.** 2001. A comparison of nectar and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *Journal of Insect Physiology* 47:1077-1084.
- Wäckers, F.L., P.C.J. van Rijn, and G.E. Heimpel.** 2008. Honeydew as a food source for natural enemies: Making the best of a bad meal? *Biological Control* 45:176-184.
- Wang, Z., and F. Ba.** 1998. Study of the optimum control of soybean aphid. *Acta Phytophylacica Sinica* 151-155.
- Wilkinson, T.K., and D.A. Landis.** 2005. Habitat diversification in biological control: the role of plant resources. In *Plant Provided Food and Plant-Carnivore Mutualism*. F.L. Wäckers, P.C.J. van Rijn and J. Bruin, eds. Cambridge, UK: Cambridge University Press. Pp. 305-325.
- Zandstra, B.H., and P.S. Motooka.** 1978. Beneficial effects of weeds in pest management — A review. *Tropical Pest Management* 24:333-338.

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 and Applicata* 71:111-120.