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The Role and Enhancement of Parasitic Hymenoptera Biodiversity in Agroecosystems

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Introduction

Research on the diversity of parasitic Hymenoptera in agroecosystems has concentrated mostly on the study of parasitoid complexes attacking particular native as well as exotic pest species. Some pest species support a large number of parasitoid species, such as the hessian fly *Mayetiola destructor* (Say) (Gahan, 1933), the wheat-stem sawfly (*Cephus pygmeus* (L.) (Salt, 1931), the coconut beetle *Promecotheca caeruleipennis* Blanchard (Taylor, 1937), the bean gall sawfly *Pontania proxima* (Lepeletier) (Carleton, 1939) and the coffee leaf miner *Perileucoptera coffeella* (Guerin-Meneville) (Parra *et al.*, 1977; Aviles and Cure, 1990). Different crops support particular herbivore species, which, in turn, are attacked by one or several parasitoid species (Table 11.1), although such associations may change according to geographical location, management intensity and crop arrangements. In many cases, only one or two species of such complexes prove vital in the natural biological control of key insect pests. For example, in California's alfalfa fields, the braconid wasp *Apanteles medicaginis* Muesebeck plays a key role in regulating the numbers of the alfalfa caterpillar *Colias eurytheme* Boisduval. Apparently, this pristine butterfly–wasp system moved from native clovers into the new and artificial irrigated alfalfa fields (Hagen *et al.*, 1971). Similarly in North Carolina's tobacco fields, *Campoletis perdistinctus* (Viereck) exerts a high parasitization rate on the budworm *Helio-*

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Table 11.1. Species richness of parasitoid complexes associated with different insect pests in a range of annual cropping systems.

Crop system	Pest species	No. of parasitoid species	Location	Reference
Cotton	*Spodoptera exigua* (Hübner)	11	California	van den Bosch and Hagen (1966)
	Trichoplusia ni (Hübner)	11	California	van den Bosch and Hagen (1966)
	Heliothis zea	14	California	van den Bosch and Hagen (1966)
	Bucculatrix thurberiella Busck	3	California	van den Bosch and Hagen (1966)
	Estigmene acrea (Drury)	3	California	van den Bosch and Hagen (1966)
	Spodoptera praefica (Grote)	13	California	van den Bosch and Hagen (1966)
Sorghum	*Schizaphis graminum* (Rondani)	3	USA	Young and Teetes (1977)
Cassava	*Erinnys ello* L.	4	Brazil, Colombia	Bellotti and Schoonhoven (1978)
	Jatrophobia brasiliensis Rubs.	4	West Indies, Peru	Bellotti and Schoonhoven (1978)
	Saissetia sp.	2	Cuba	Bellotti and Schoonhoven (1978)
Soyabeans	*Plathypena scabra* (F.)	14	Missouri, USA	Turnipseed and Kogan (1976)
	Pseudoplusia includens (Walker)	12	Louisiana, USA	Turnipseed and Kogan (1976)
Potato	*Myzus persicae*	7	Maine, USA	Shands *et al.* (1965)
	Acyrthosiphon solani (Kattenbach)	5	Maine, USA	Shands *et al.* (1965)
	Aphis nasturtii Kattenbach	5	Maine, USA	Shands *et al.* (1965)
Rice	*Nephotettix spp.*	3	Philippines	Reissig *et al.* (1985)
	Chilo suppressalis (Walker)	5	Philippines	Reissig *et al.* (1985)
Alfalfa	*Colias eurytheme* Boisduval	2	California	Hagen *et al.* (1971)
	Spodoptera exigua	11	California	Hagen *et al.* (1971)
	Spodoptera (=*Prodenia*) *praefica* (Grote)	13	California	Hagen *et al.* (1971)
	Heliothis zea	13	California	Hagen *et al.* (1971)
Tobacco	*Heliothis virescens*	2	North Carolina, USA	Rabb (1971)

this virescens (F.), in early summer prior to flowering when plants are most susceptible to budworm injury. After flowering and on post-harvest sucker tobacco, parasitization by *Campoletis perdistinctus* declines and the action of *Cardiochiles nigriceps* becomes an important budworm mortality factor (Rabb, 1971). In other cases, it is a combination of several parasitoid species that exerts regulation on a specific insect pest (Ehler, 1990).

Our knowledge of naturally occurring or already established parasitoid communities in agroecosystems in general is not very sophisticated. One complication is that such communities are hard to define sharply because many parasitoid species enter the parasitoid complexes of more than one host, some of which may not be recognized as belonging to the same community (Askew and Shaw, 1985). Another complication is that Hymenoptera parasitoids are seldom monophagous; on the contrary they are polyphagous and more habitat and/or niche specific than host specific (Vinson, 1977). In fact, many parasitoid species are more likely to attack taxonomically unrelated insects found in one habitat than they are to attack taxonomically related insects occupying different habitats (Vinson, 1981).

In this chapter we discuss the pertinent literature concerned with the community structure, organization and development of parasitic Hymenoptera on agricultural systems, attempting to define trends and perspectives that may be useful to further understand parasitoid communities on crops. Although we know more about the factors that negatively impact parasitoid diversity, abundance and efficacy in agroecosystems (i.e. chemical insecticide applications, monocultures, tillage, etc.), we identify factors important in enhancing Hymenoptera parasitoid diversity, as well as management practices that add environmental resources necessary for improving parasitoid effectiveness in agroecosystems.

The complexity of Hymenoptera parasitoid communities in agroecosystems

Most of the studies on the composition of parasitoid complexes have been conducted on crop monocultures where host populations usually reach abnormal abundance levels (Askew and Shaw, 1985). To some researchers, such records either underestimate species diversity or represent what may be considered 'artificial' parasitoid communities. The relative complexity of Hymenoptera parasitoid communities associated with different cropping systems is determined by biological, environmental and management factors. In large-scale monocultures, diversity is suppressed by pesticides, vegetational simplification and other environmental disturbances. In less disturbed agroecosystems, in addition to the absence of pesticides, parasitoid diversity seems related to crop diversity, ground cover, weeds and native vegetation adjacent to crops. In fact, the few studies conducted on this topic indicate that the vegetational settings associated with particular crops influence the kind, abundance and time of arrival of parasitoids.

Based on the available information, it is possible to define the following

trends of Hymenoptera parasitoid diversity in agroecosystems:

1. *Parasitoid diversity decreases with intensity of agroecosystem management.* Surveys conducted in relatively unmanaged apple orchards revealed a high species richness of parasitic Hymenoptera (Table 11.2). In general, in pesticide-free orchards and/or in unmanaged or abandoned orchards, a wide range of parasitoid species is present. Over the span from unmanaged to intensively managed systems, a dramatic decrease in diversity and species composition occurs, in fact most natural enemies are eliminated (Fig. 11.1) (Croft and Hull, 1983). Although a usual outcome of intensive management is a reduction in the physical heterogeneity within the crop, parasitic Hymenoptera may exhibit a high degree of environmental heterogeneity within the same planted area. Four large plots sampled within the same *Eucalyptus cloeziana* reforested area in Brazil, showed almost 100% dissimilarity values between plots for parasitic Hymenoptera and Bethyloidea (Campos and Cure, 1991; Table 11.3). Sampled areas differed in the types of neighbouring vegetation; reforested plots closer to a natural forest reserve exhibited higher diversity than plots located away from the reserve.
2. *The parasitoid complexes of taxonomically and ecologically related pests found in the same crop but in widely separate areas are similar.* The major parasitoid species associated with the lepidopterous pests *Pieris* and *Plutella* and the

Table 11.2. Species richness of parasitic Hymenoptera inhabiting relatively unmanaged apple orchards in two locations.

	Number of species	
Parasitic Hymenoptera	Indiana	Wisconsin
Dominant families		
Eulophids	24	55
Pteromalids	16	37
Encyrtids	17	14
Braconids	30	36
Ichneumonids	15	34
Total:	**102**	**176**
Dominant genera		
Tetrastichus	7	10
Sympiesis	3	7
Pteromalus	2	6
Apanteles	6	6

Source: After Oatman *et al.* (1964) and Cleveland and Hamilton (1958).

Table 11.3. Dissimilarity measurements (chor distance index, minimum = 0, maximum = 1.41) for Hymenoptera-Parasitica and Bethyloidea between plots in a reforested *Eucalyptus* spp. area in Brazil.

Plot comparisons	Dissimilarity
A1 vs. A2	1.33
A1 vs. B1	1.27
A1 vs. B2	1.39
A2 vs. B1	1.31
A2 vs. B2	1.17
B1 vs. B2	1.31

Source: After Campos and Cure (1991).
The reforested area (approx. 33000 ha) was in contact with a natural forest reserve (approx. 37000 ha). A1 and A2 plots were located about 100 m from the natural reserve. B1 and B2 plots were located 10 km within the reforested area.

aphid *Brevicoryne brassicae* (L.) infesting cabbage in upstate New York and in Minnesota were similar. In both areas, *Diaeretiella rapae* (M'Intosh) was a prominent parasitoid of *B. brassicae*, and *Pieris rapae* (L.) was consistently attacked by *Apanteles glomeratus* (L.) (Pimentel, 1961; Weires and Chiang, 1973). The same parasitoids are prevalent in cole cropping systems throughout South America (Parker and Berry, 1951).

3. *Species diversity of parasitoids associated with hosts on tree crops is higher than with hosts on annual or herbaceous crops.* Orchards are semi-permanent and less disturbed systems than annual monocultures, therefore providing more stable habitats for parasitoid colonization and establishment. Orchards also provide a longer time-frame for the establishment of species associations and/or interactions (MacArthur, 1965). Apple orchards in Wisconsin supported about 176 species of parasitic Hymenoptera whereas in Maine only 22 parasitoid species were associated with the pest complex (mostly aphids) attacking potatoes (Oatman *et al.*, 1964; Shands *et al.*, 1965). Although this comparison may not be totally appropriate, because areas are geographically separate and systems were probably subjected to different management techniques, it highlights the tremendous disparity in parasitoid species diversity associated with a perennial crop versus an annual crop.

Annual monocultures are continuously disturbed and also create unfavourable microclimates for many parasitoids. Ichneumonid species tend to be excluded from systems that lack cool and moist conditions, such as those often prevalent in monocultures in lowland tropical areas and in the Central Valley of California (Townes, 1971).

4. *The colonization of crops by parasitoids is correlated with the pattern of habitat space development in crop systems.* With time, both quantitative and qualitative changes occur in crop habitats which, in turn, affect the structure and organization of the arthropod community. As the season progressed, the

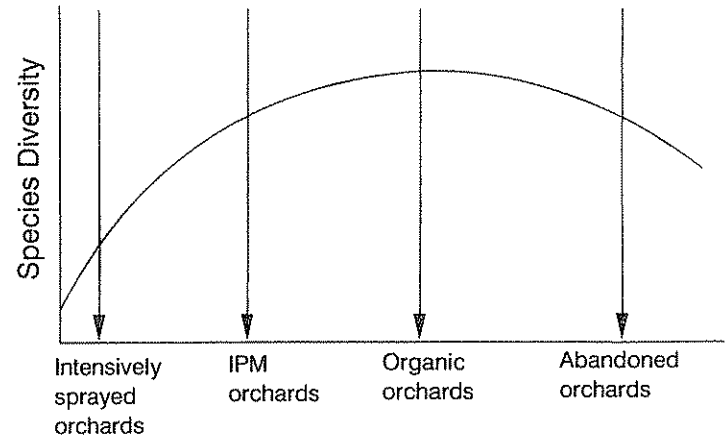

Fig. 11.1. Hypothetical trend in parasitic Hymenoptera species diversity in a range of apple orchards subjected to various degrees of management intensity (based on Croft and Hull, 1983).

complexity of the arthropod food web increased in Illinois soyabean fields (Mayse and Price, 1978). A similar trend was observed in pear orchards as trees developed (Gut, 1985). Over long time periods in tea plantations, species richness increased and guild structure changed with tree age (Banerjee, 1983).

5. *Plant species diversity and plant structural diversity are important in determining parasitoid diversity in agroecosystems.* As plant complexity increases in agroecosystems in the form of intercropping, cover crops, living mulches, windbreaks, etc., insect species diversity also increases. In California, Brussels sprouts monocultures supported only three parasitoid species, whereas Brussels sprouts intercropped with fava beans and/or wild mustards supported five and eight species respectively (Altieri, 1984). In tropical Mexico, malaise trap captures of parasitic Hymenoptera in squash monocultures consisted of fewer individuals and were characterized by a lower parasitoid species richness than those from corn–bean–squash polycultures (Letourneau, 1987; Fig. 11.2). In the polycultures, four braconid species and one ichneumonid species were consistently associated with the main herbivore *Diaphania hyalinata*, exerting higher parasitization rates than in the monoculture. In their survey of soyabean fields, Mayse and Price (1978) found higher numbers of parasitoid species per habitat space in rows located at the edge of a field adjacent to relatively complex vegetation than in the rows located away from the neighbouring vegetation.

Enhancing parasitic Hymenoptera diversity in agroecosystems

There are several environmental factors that influence the diversity, abundance, survival and activity of parasitoids in agroecosystems: microclimatic conditions,

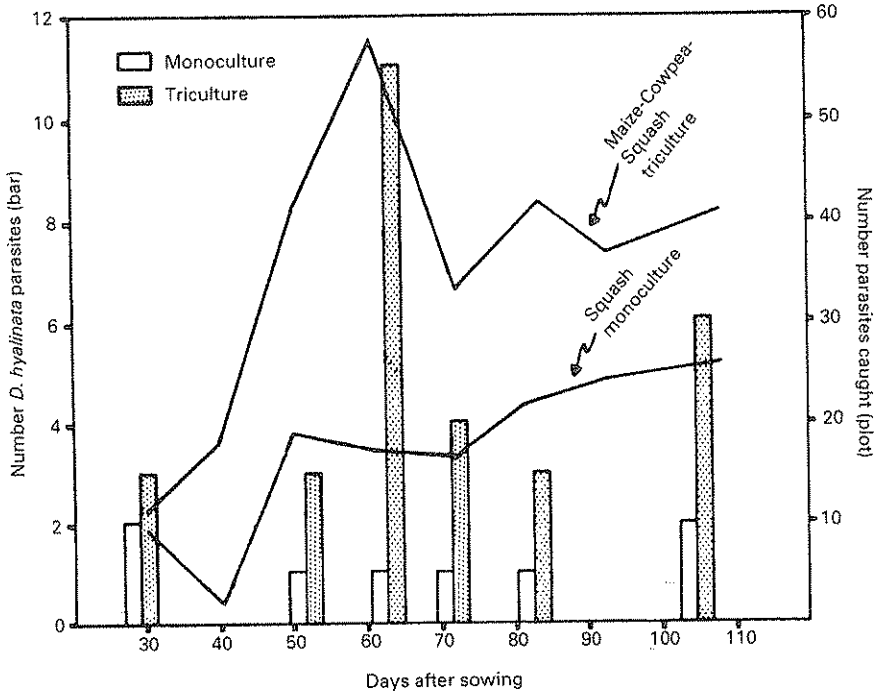

Fig. 11.2. Total number of parasitic Hymenoptera (line plot) and the number of species known to parasitize *Diaphania hyalinata* in squash monocultures and maize–bean–squash tricultures in tropical Mexico (Letourneau, 1987).

availability of food (water, hosts, pollen and nectar), habitat requirements (refuges, nesting and reproduction sites, etc.), intra- and inter-specific competition and other organisms (hyperparasites, predators, humans, etc.). The effect of each of these factors will vary according to the spatial and temporal arrangement of crops and the intensity of crop management. Since agroecosystems are dynamic and subjected to different kinds of management, crop mixes continually change in the face of biological and socio-economic factors. Such landscape variations determine the degree of spatial and temporal heterogeneity characteristic of agroecosystems, which, in turn, may or may not benefit parasitic Hymenoptera diversity in specific cropping systems.

Although parasitoids seem to vary widely in their response to crop distribution, density and dispersion, experimental evidence suggests that structural (i.e. spatial and temporal crop arrangement) and management (i.e. crop diversity, input levels, etc.) attributes of agroecosystems influence parasitoid diversity and dynamics. Based on the available information, parasitoid diversity can be enhanced and effectiveness improved in the following ways (van den Bosch and Telford, 1964; Rabb *et al.*, 1976; Altieri and Letourneau, 1982; Powell, 1986):

Table 11.4. Number of parasitic Hymenoptera species introduced and established as biological control agents for arthropod pests in forests and agroecosystems. The degree of success ranges from zero (no control), to 3 (excellent control) and is based on the arithmetic mean calculated for registered cases classified as: zero = no economic control; 1 = control in a limited part of the distribution range; 2 = control in a substantial part of the distribution range; 3 = excellent control throughout; ? = implies uncertain establishment of the parasite.

Family	Number of species	Number of target species	Number of crop species	Degree of success
Aphelinidae	46	30	13	2.1
Bethylidae	1	1	1	?
Braconidae	66	60	40	1.5
Chalcididae	5	7	13	0.3
Diapriidae	1	1	8	?
Dryinidae	2	1	1	1.0
Encyrtidae	134	44	41	1.0
Eulophidae	25	40	36	1.1
Eupelmidae	2	2	2	1.0
Ibaliidae	1	1	1	0.0
Ichneumonidae	42	30	18	1.2
Mymaridae	7	6	8	1.6
Platygasteridae	5	5	6	2.7
Pteromalidae	13	11	11	1.4
Scelionidae	10	8	8	2.1
Scoliidae	11	6	4	1.3
Sphecidae	1	1	1	3.0
Tiphiidae	4	4	3	1.2
Torymidae	2	3	3	2.0
Trichogrammatidae	9	7	7	0.3

Source: Based on Luck (1981).

1. *Multiple introductions of parasitoids.* Importation of parasitoids has been used since 1906 as a strategy to reach long-term suppression of pests. The practice of classical biological control could be regarded as a global experiment in restoring natural enemy biodiversity in agroecosystems where exotic insects reach pest status because they have been introduced from a geographical distance without their regulating natural enemies. According to Greathead (1986) there are records of 860 successful establishments of 393 species of parasitoids against some 274 pest insects in 99 countries. In many of these cases, introduction of some 250 species of hymenopterous parasitoids have been rated as achieving satisfactory pest suppression in either a limited or substantial part of the pest's distribution range (Table 11.4). Hymenopterous parasitoids were also aided by introduction of other parasitoid or predator species to achieve a useful reduction

Table 11.5. Elimination of Hymenoptera parasitoids by insecticides sprayed to control key pests in a range of cropping systems.

Crop	Location	Pest species	Parasitoid species eliminated	Insecticide
Peach	Ohio	Oriental peach moth	*Macrocentrus ancylivorus* Rohwer	DDT
Apple	Washington State	Woolly apple aphid	*Aphelinus mali* (Haldeman)	DDT
Apple	Washington State	Comstock mealybug	*Pseudaphycus* spp.	DDT
Citrus	Florida	Florida red scale	*Pseudhomalapoda prima* Girault	DDT
Citrus	California	Yellow scale	*Comperiella bifasciata* Howard	DDT
Citrus	California	Brown scale	*Metaphycus luteolus* (Timberlake)	Parathion
Cabbage	England	Cabbageworm	*Cotesia rubecula*	DDT
Citrus	Chile	Whiteflies	*Amitus spiniferus* (Brethes) and *Cales noacki* Howard	Organophosphates
Grapes	Chile	Mealybug	*Pseudaphycus flavidulus* Bohart	Organophosphates

Source: Brown (1978).

in pest numbers (Ehler, 1990). This fact gives support to the multiple-species introduction strategy (MSI) in classical biological control. Long time practitioners such as Huffaker *et al.* (1971) have already argued in favour of MSI and have stated that 'importation of a diverse complex of natural enemies is the only practical manner of obtaining the best species for a given habitat, or the best combination for such habitat, or the best combination for the entire host range'. Clearly, enhancing or restoring natural enemy biodiversity through importation assures a better chance of success than single species introduction; the challenge is determining which species or combination of species to introduce in order to control a given target species in a specific situation (Ehler, 1990).

2. *Reducing direct mortality.* The use of chemical pesticides has often created complex and serious problems by immediate and time-lag effects on natural enemies. Non-selective insecticides have created pest problems by eliminating parasitoids. DDT and parathion have been particularly deleterious to various parasitoids in several agroecosystems (Table 11.5).

Organophosphorus insecticides such as azinphosmethyl, parathion, diazinon, dimethoate and malathion are particularly toxic to hymenopterous parasites of citrus scales and mealybugs (Brown, 1978). Total removal of pesticides can restore parasitoid diversity and lead to renewed biological control of specific pests. Within two years, virtually all banana insect pests in Golfito, Costa Rica dropped to below economic threshold levels, due to enhanced parasitization and predation, after stopping insecticide (dieldrin and carbaryl) sprays (Stephens, 1984). Similarly, in California's walnut orchards, natural biological control of the frosted scale and the calico scale was soon achieved by encyrtid parasitoids after removal of DDT sprays (Hagen *et al.*, 1971).

Some cultural practices can also negatively impact parasitoids. Ploughing and cultivation generally inflict heavy mortality on natural enemies. Pruning, harvesting and crop residue disposal may also have effects on parasitoids. Removal of prunings of apple wood infested by the woolly aphid, but heavily parasitized by *Aphelinus mali* (Haldeman) in Australia, reduced parasitization levels within the orchard (Wilson, 1966). In California, solid harvesting of alfalfa was more devastating to the parasitoid *Aphidius smithii* Sharma and Rao than to its aphid host, *Acyrthosiphon pisum* (Harris). Conversely, strip harvesting resulted in an improved microclimate for the parasite (van den Bosch and Telford, 1964). It is not clear whether burning of sugarcane biomass is negative to the parasites of *Diatraea saccharalis* (F.).

3. *Provision of supplementary resources.* Most parasitoids have resource requirements such as hosts, food other than hosts, water, refuges, etc., which often are not available or found in sufficiency within a given cropping system. Several researchers have demonstrated that manipulating such resources can enhance parasitoid diversity and abundance and also improve their efficacy (Rabb *et al.*, 1976). Addition of host populations proved effective in controlling *Pieris rapae* in cabbage. The continuous release of fertile *Pieris* butterflies increased the pest

population nearly tenfold above normal spring populations, enabling the parasites *Trichogramma evanescens* Westwood and *Cotesia rubecula* (Marshall) to increase early and maintain themselves at an effective level throughout the season (Parker and Pinnell, 1972).

4. *Increasing adjacent vegetational diversity.* Researchers are well aware of the importance of adjacent vegetational settings in determining the diversity of parasitoid species as well as their maintenance and effectiveness within agroecosystems (van den Bosch and Telford, 1964; Altieri and Letourneau, 1982, 1984). Successful colonization by parasites depends upon the presence of the appropriate kind and abundance of primary hosts, alternative hosts, pollen and/or nectar in hedgerows and other neighbouring habitats. For example, in Armenia, scelionid egg parasites of the sunn pest *Eurygaster integriceps* Puton are very efficient in areas with small wheat fields surrounded by diverse vegetation. Under these conditions, the polyvoltine egg parasites have a number of other pentatomid hosts and favourable hibernating places. In California, Doutt and Nakata (1973) found that the egg parasite *Anagrus epos* Girault, was effective in controlling the grape leafhopper *Erythroneura elegantula* Osborn, in vineyards adjacent to wild blackberries which harbour a non-economic leafhopper *Dikrella cruentata* Gillette, whose eggs serve as the only overwintering resource for *Anagrus*. Also in California, Allen and Smith (1958) found that parasitization of the alfalfa caterpillar, *Colias eurytheme*, by *Apanteles medicaginis* was far greater in California's San Joaquin Valley where weeds were in bloom along irrigation canals in contrast to areas where the weeds were destroyed.

In England, the proximity of certain flowering weeds such as *Angelica sylvestris* L., *Urtica dioica* L., *Rumex acetosella* L., *Taraxacum officinale* Weber, *Cirsium vulgare* (Savi) Ten., *Ranunculus repens* L., *Trifolium repens* L., *Chenopodium album* L. and *Anthriscus sylvestris* L. increased the activity of parasitic Hymenoptera in wheat and cabbage fields (Van Emden, 1962).

The high degree of environmental heterogeneity found by Campos and Cure (1991) (Table 11.3) was partly explained by the fact that the 33 000 ha *Eucalyptus* reforested area was adjacent to a 37 000 ha natural forest reserve. Apparently, connections with natural reservoirs are important, and larger repositories can contribute more to species richness than smaller ones, the latter serving mostly as corridors.

5. *Increasing within-field plant diversity.* Considerable work in the former USSR has been devoted to the use of nectar-bearing plants within orchards as a source of adult food for entomophagous insects to increase their effectiveness. Field experiments of Chumakova (1960) in the North Caucasus showed that the growing of *Phacelia* spp. in orchards greatly increased the parasitization of *Quadraspidiotus perniciosus* (Comstock) by its parasite *Aphytis proclia* (Walker). These same plants have been shown to increase the abundance of the wasp *Aphelinus mali* for the control of apple aphids and improve the activity of *Trichogramma* spp. in apple orchards (Chumakova, 1977).

Spectacular parasitism increase was observed in apple orchards with rich undergrowths of wild flowers. Parasitism of tent caterpillar eggs and larvae and codling moth larvae was 18 times greater in those orchards with floral undergrowths than in orchards with sparse floral undergrowth (Leius, 1967).

Mixed cropping can also enhance parasitoids in crops. In Costa Rica, intercrops of corn and sweet potatoes had 75% more species of parasitic Hymenoptera than corresponding monocultures (Carroll, 1978). Parasitism of the leafhopper *Empoasca kraemeri* Ross and Moore by the egg parasitoid *Anagrus* sp. was greater on beans grown associated with corn than on bean monocultures (Altieri *et al.*, 1978). Similarly, artificially placed *Heliothis zea* (Boddie) eggs were more heavily parasitized by *Trichogramma* wasps in corn–soyabean polycultures than in soyabean monocultures (Altieri and Todd, 1981). In Peru, planting rows of corn every fifth or seventh row of cotton favoured the reproduction of many predators and parasitoids (Beingolea, 1957).

It has been suggested that in some cases increased plant diversity could reduce parasitoid efficiency, since certain associated plants may mask cues used by parasitoids for host searching (Price *et al.*, 1980).

6. *Controlling secondary enemies.* The diversity and abundance of primary parasites can be greatly reduced by secondary (hyper) parasites. Several attempts to establish introduced parasites were frustrated by the presence of hyperparasites. In Nova Scotia, hyperparasites destroyed founder colonies of *Aphidius smithii* Sharman and Rao introduced for control of the pea aphid (Mackauer, 1972). In California, the effectiveness of *Diaeretiella rapae* against cabbage aphids in cole crops is negatively affected by species of *Asaphes* and *Pachyneuron.* In potato fields in Maine, 17 species of primary parasites and 18 species of hyperparasites were reared from the aphid complex. At times the hyperparasites *Asaphes lucens* (Provancher) and *Coruna clavata* Walker substantially reduced the abundance of the primary parasite *Aphidius nigripes* Ashmead, allowing populations of the potato aphid to flourish (Shands *et al.*, 1965). As pointed out by Greathead, (1986), the highly effective genus *Aphytis* is the only one among the successful parasitoids of Coccoidea that develops as an external parasitoid, thus avoiding hyperparasitism.

7. *Manipulating host plant attributes.* Several chemical, genetic and architectural attributes of plants can influence parasitoid action on insect pests. Rabb and Bradley (1968) found that parasitization of *Manduca sexta* (L.) eggs by *Trichogramma minutum* Riley and *Telenomus sphingis* (Ashmead) was inhibited by sticky exudates of tobacco leaves. *Encarsia formosa* Gahan, a normally effective parasitoid of the greenhouse whitefly, is greatly hindered by the hairs produced by cucumber (Price *et al.*, 1980).

It is also known that the nature of the host plant habitat affects the degree of parasitization obtained from certain parasitoids. In northern Florida, parasitization rates of *Heliothis* spp. and Plusiinae eggs by *Trichogramma pretiosum* Riley showed considerable variation in various crops grown in the same field (Martin

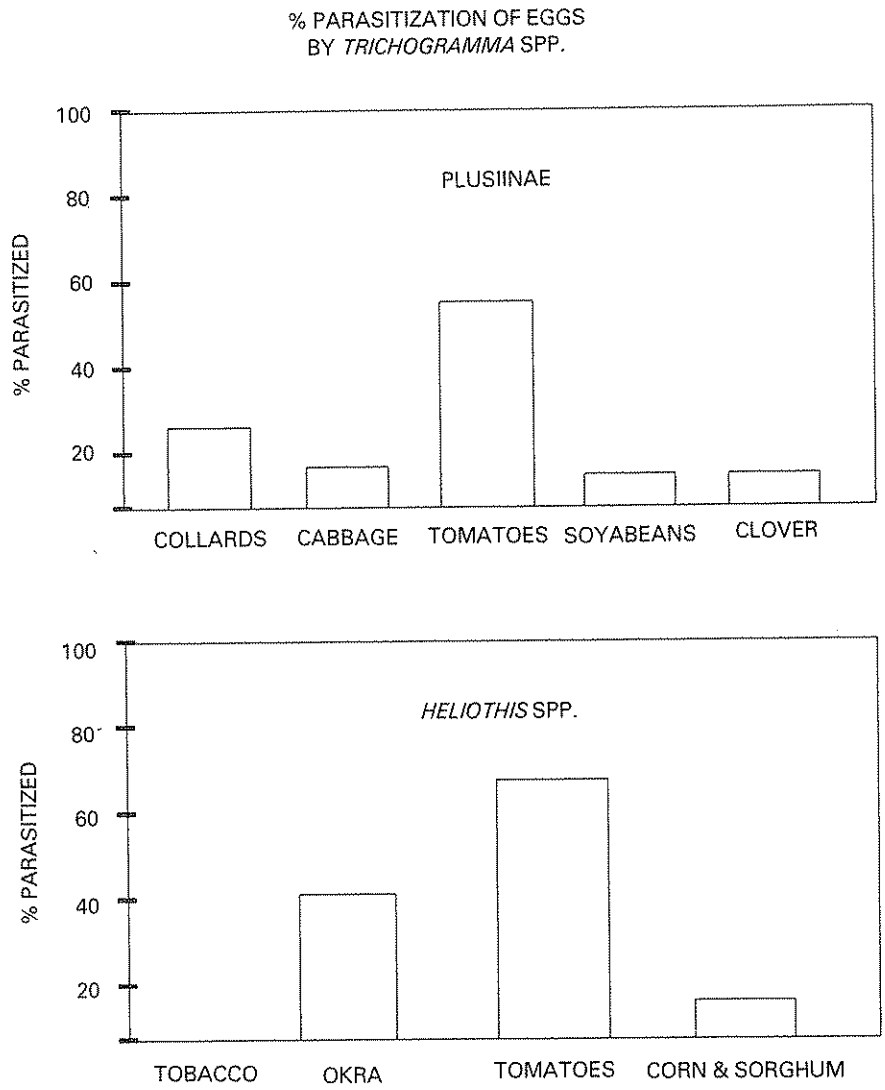

Fig. 11.3. Parasitization of Plusiinae eggs and *Heliothis* spp. by *Trichogramma* spp. populations in various crop systems in north Florida (Martin *et al.*, 1976).

et al., 1976). Moderate to high rates of parasitization were attained in tomatoes, collards and okra. The released parasites were ineffective against the target pests in tobacco (Fig. 11.3). Although these differences could have been due to differences in host egg densities, various chemical and physical cues emitted by the different crops were significant in affecting the location of the host habitat by *Trichogramma* wasps. Similar results were obtained in New York State where para-

sitism by *Diaeretiella rapae* was much higher when the aphid *Myzus persicae* (Sulzer) was on collard than when it was on beet (Read *et al.*, 1970).

Some parasitoids specialize their search to specific plant organs or even parts of an organ. For example, Gold *et al.* (1989) found significantly lower rates of parasitism of cassava hornworm eggs by *T. sphingis* on lower leaf surfaces than on the upper leaf surfaces. Other parasitoids will have differential rates of attack on the same host but inhabiting different plant species. Apple maggots that feed on apples are less often parasitized by *Biosteres melleus* (Gahan) than when they feed on hawthorn fruits (Porter, 1928).

Alkaloids and other allelochemicals involved in plant resistance can be toxic to parasitoids within hosts. The effects of tomatine on the larval development of the ichneumonid *Hyposoter exiguae* (Viereck) illustrates how toxins derived from plants by herbivores can affect parasitoid survivorship (Campbell and Duffy, 1979). Smith (1957) found high larval mortality of two parasitoids of the California red scale, when the scale fed on sago palm compared to when it fed on citrus.

Resistant varieties can have negative effects on natural enemies. The smaller sized hosts on resistant varieties can lead to the emergence of smaller parasitoids having reduced fecundity. According to Van Emden (1991) these disadvantages disappear at low levels of plant resistance.

8. *Manipulations with semiochemicals.* Chemicals which stimulate host-searching behaviour in parasitoids have been identified for a number of Hymenoptera species: *Cardiochiles nigriceps, Trichogramma evanescens, T. pretiosum, Trissolcus* sp., *Telenomus* sp., *Microplitis croceips* and *Aphidius nigripes* (Nordlund *et al.*, 1981). Hexane extracts sprayed in field trials have consistently improved parasitization rates of *H. zea* eggs by *T. pretiosum*. The greatest utility of such kairomonal applications appears to be for aggregating or retaining released parasites in target locations (Lewis and Nordlund, 1985).

Taking advantage of the fact that many parasitoids seek out particular habitats and are guided by volatiles emanating from plants, some researchers have applied certain plant extracts on crop plants to reinforce the host location behaviour of parasitoids and have improved parasitization rates (Altieri *et al.*, 1981). Spraying of plant-produced synomones attracted ovipositioning female parasitoids, enhancing the parasitization of *H. zea* and *Anagasta kuehniella* (Zeller) by *Trichogramma* wasps under soyabean field and greenhouse conditions respectively (Altieri *et al.*, 1981; Altieri and Letourneau, 1982). Similar results were obtained by Titayavan and Altieri (1990) in broccoli plots. Direct application of an allylisothiocyanate emulsion at a rate of 0.25 ml per broccoli plant consistently gave higher parasitization rates of the cabbage aphid and/or number of *Diaeretiella rapae* wasps per plant, than those observed on plants treated with 0.25 ml of water or with 0.25 ml of wild mustard extract.

Conclusions

Agroecosystems are complex and dynamic systems subjected to a whole range of vegetational designs and management intensities depending on farmers' preferences, environmental factors and socio-economic constraints. Changes in plant diversity, plant density, crop dispersion and patch size will increase or reduce resources for natural enemies. Therefore, the size and structure of parasite Hymenoptera communities should be expected to vary according to the heterogeneity of specific agroecosystems.

When considering ways of enhancing parasitoid diversity and efficiency, what is difficult is that each agricultural situation must be assessed separately. Diversified vegetational settings will generally result in enhanced diversity and abundance of parasitoids, although specifically which species will be enhanced will vary depending on the diversity and availability of primary and alternative hosts, location and size of the field, plant composition, floral diversity and phenology, surrounding environments and management technologies. One can only hope to elucidate the basic ecology of parasitoids, their relationships with other components of the agroecosystem and the ecological principles governing parasitoid diversity in crop fields. In this regard, manipulating agroecosystem components (habitat diversity, pesticide-free space, alternative food, semiochemicals, etc.) to provide the basic requirements needed by parasitoids (hosts, pollen and nectar, refuges, reproduction and nesting sites, etc.) is an effective way to apply ecological theory to improve parasitoid diversity and efficiency in agriculture.

References

Allen, W.W. and Smith, R.F. (1958) Some factors influencing the efficiency of *Apanteles medicaginis* Muesebeck (Hymenoptera: Braconidae) as a parasite of the alfalfa caterpillar *Colias eurytheme* Boisduval. *Hilgardia* 28, 1–42.

Altieri, M.A. (1984) Patterns of insect diversity in monocultures and polycultures of Brussels sprouts. *Protection Ecology* 6, 227–232.

Altieri, M.A. and Letourneau, D.K. (1982) Vegetation management and biological control in agroecosystems. *Crop Protection* 1, 405–430.

Altieri, M.A. and Letourneau, D.K. (1984) Vegetation diversity and insect pest outbreaks. *CRC Critical Reviews in Plant Sciences* 2, 131–169.

Aliteri, M.A. and Todd, J.W. (1981) Some influences of vegetational diversity on insect communities of Georgia soybean fields. *Protection Ecology* 3, 333–338.

Altieri, M.A., Francis, C.A, van Schoonhoven, A. and Doll, J. (1978) A review of insect prevalence in maize (*Zea mays* L.) and bean (*Phaseolus vulgaris* L.) polycultural systems. *Field Crops Research* 1, 33–49.

Altieri, M.A., Lewis, W.J., Nordlund, D.A., Gueldner, R.C. and Todd, J.W. (1981) Chemical interactions between plants and *Trichogramma* wasps in Georgia soybean fields. *Protection Ecology* 3, 259–263.

Askew, R.R. and Shaw, M.R. (1985) Parasitoid communities: their size, structure and development. In Waage, J. and Greathead, D. (eds), *Insect Parasitoids*. Academic Press, London, pp. 225–259.

Aviles, D.P. and Cure, J.R. (1990) Guilda de parasitoides de *Perileucoptera coffeela* (Guerin-Meneville) na regiao de Paula Candido, estado de Minas Gerais. In: *17th Congresso Brasileiro de Pesquisas Cafeeiras*. Mines Gerais, Brazil.

Banerjee, B. (1983) Arthropod accumulation on tea in young and old habitats. *Ecological Entomology* 8, 117–123.

Beingolea, O. (1957) El sembrio del maiz y la fauna benefica del algodonero. *Estacion Experimental Agricola*. La Molina, Lima.

Bellotti, A. and van Schoonhoven, A. (1978) Mite and insect pests of cassava. *Annual Review of Entomology* 23, 39–68.

Brown, A.W.A. (1978) *Ecology of Pesticides*. John Wiley & Sons, New York. 525pp.

Campbell, B.C. and Duffy, S.S. (1979) Tomatine and parasitic wasps: potential incompatibility of plant antibiosis with biological control *Science* 205, 700–702.

Campos W.G. de and Cure, J.R. (1991) Estrutura e composicao da fauna de insecta, especialmente Hymenoptera, em diferentes areas de um reflorestamento de *Eucalyptus cloeziana*. *Revista Brasileira de Entomologia* (submitted).

Carleton, M. (1939) The biology of *Pontania proxima* Lep., the bean gall sawfly of willows. *Journal of the Linnean Society (Zoology)* 40, 575–624.

Carroll, C.R. (1978) Beetles, parasitoids and tropical morning glories: a study in host discrimination. *Ecological Entomology* 3, 79–85.

Chumakova, B.M. (1960) Supplementary feeding as a factor increasing the activity of parasites of harmful insects. *Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Instituta Zashchity Rastenii* 15, 57–70.

Chumakova, B.M. (1977) Ecological principles associated with augmentation of natural enemies. In: Ridgway, R.L. and Vinson, S.B. (eds), *Biological Control by Augmentation of Natural Enemies*, Plenum Press, New York, pp. 39–78.

Cleveland, M.L. and Hamilton, D.W. (1958) The insect fauna of apple trees in southern Indiana. *Proceedings of the Indiana Academy of Science* 68, 205–217.

Croft, B.A. and Hull, S.C. (1983) *Integrated Management of Insect Pests of Pome and Stone Fruits*. John Wiley & Sons, New York, 454pp.

Doutt, R.L. and Nakata, J. (1973) The *Rubus* leafhopper and its egg parasitoid: an endemic biotic system useful in grape-pest management. *Environmental Entomology* 2, 381–386.

Ehler, L.E. (1990) Introduction strategies in biological control of insects. In: Mackauer, M., Ehler, L.E. and Roland, J. (eds), *Critical Issues in Biological Control*. Intercept, Andover, UK, pp. 111–134.

Gahan, A.B. (1933) The serphoid and chalcidoid parasites of the Hessian fly. *United States Department of Agriculture, Miscellaneous Publication* 174, 1–147.

Gold, C.S., Altieri, M.A. and Bellotti, A.C. (1989) Relative oviposition rates of the cassava hornworn, *Erinnys ello* (Lep.: Sphingidae) and accompanying parasitism by *Telenomus sphingis* (Hym.: Scelionidae) on upper and lower surfaces of cassava. *Entomophaga* 34, 73–76.

Greathead, D.J. (1986) Parasitoids in classical biological control. In: Waage, J. and Greathead, D. (eds), *Insect Parasitoids*. Academic Press, London, pp. 290–318.

Gut, L.J. (1985) Arthropod community organization and development in pear. PhD thesis. Oregon State University, Corvallis.

Hagen, K.S., van den Bosch, R. and Dahlsten, D.L. (1971) The importance of naturally-occurring biological control in the Western United States. In: Huffaker, C.B. (ed.), *Biological Control.* Plenum Press, New York, pp. 253–287.

Huffaker, C.B., Messenger, P.S. and DeBach, P. (1971) The natural enemy component in natural control and the theory of biological control In: Huffaker, C.B. (ed.), *Biological Control.* Plenum Press, New York, pp. 16–67.

Leius, K. (1967) Influence of wild flowers on parasitism of tent caterpillar and codling moth. *Canadian Entomologist* 99, 444–446.

Letourneau, D.K. (1987) The enemies hypothesis: tritrophic interactions and vegetational diversity in tropical agroecosystems. *Ecology* 68, 1616–1622.

Lewis, W.J. and Nordlund, D.A. (1985) Behavior-modifying chemicals to enhance natural enemy effectiveness. In: Hoy, M.A. and Herzog, D.C. (eds), *Biological Control in Agricultural Integrated Pest Management Systems.* Academic Press, New York, pp. 89–101.

Luck, R.F. (1981) Parasitic insects introduced as biological control agents for arthropod pests. In: Pimentel, D. (ed.), *Handbook of Pest Management in Agriculture.* CRC Press, Florida, pp. 125–284.

MacArthur, R.H. (1965) Patterns of species diversity. *Biological Review* 40, 510–533.

Mackauer, M. (1972) Genetic aspects of insect production. *Entomophaga* 17, 24–48.

Martin, P.B., Lingren, P.D., Greene, G.L. and Ridgway, R.L. (1976) Parasitization of two species of Plusiinae and *Heliothis* spp. after releases of *Trichogramma pretiosum* in seven crops. *Environmental Entomology* 5, 991–995.

Mayse, M.A. and Price, P.W. (1978) Seasonal development of soybean arthropod communities in east central Illinois. *Agroecosystems* 4, 387–405.

Nordlund, D.A., Lewis, W.J. and Gross, H.R. (1981) Elucidation and employment of semiochemicals in the manipulation of entomophagous insects. In: Mitchell, E.R. (ed.), *Management of Insect Pests with Semiochemicals Concepts and Practice.* Plenum Press, New York, pp. 463–475.

Oatman, E.R., Legner, E.F. and Brodes, R.F. (1964) An ecological study of arthropod population on apple in northeastern Wisconsin. *Journal of Economic Entomology* 57, 978–983.

Parker, F.D. and Pinnell, R.E. (1972) Further studies of the biological control of *Pieris rapae* using supplemental host and parasite releases. *Environmental Entomology* 1, 150–157.

Parker, H.L. and Berry, P.A. (1951) Host–parasite and parasite–host lists of insects reared in the South American parasite laboratory during the period 1940–1946. *Revista de la Asociacion de Ingenieros Agricolas* No. 92 (Enero-Junio). Montevideo, Uruguay.

Parra, J.R.P., Goncalves, W., Gravena, S. and Marconato, A.R. (1977) Parasitos e predatores do bichomineiro do cafeeiro *Perileucoptera coffeella* (Guerin-Meneville) em Sao Paulo *Anais de Sociedade Entomologica do Brasil* 6, 138–143.

Pimentel, D. (1961) Species diversity and insect population outbreaks. *Annals of the Entomological Society of America* 54, 76–86.

Porter, B.A. (1928) The apple maggot. *United States Department of Agriculture Technical Bulletin* 66, 1–48.

Powell, W. (1986) Enhancing parasitoid activity in crops. In: Waage, J. and Greathead, D. (eds), *Insect Parasitoids.* Academic Press, London. pp. 319–335.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. and Weise, A.E. (1980) Interactions among three trophic levels: influence of plants on interaction

between insect herbivores and natural enemies. *Annual Review of Ecological Systems* 2, 41–65.

Rabb, R.L. (1971) Naturally-occurring biological control in the Eastern United States, with particular reference to tobacco insects. In: Huffaker, C.B. (ed.), *Biological Control.* Plenum Press, New York, pp. 294–309.

Rabb, R.L. and Bradley, J.R. Jr (1968) The influence of host plants on parasitism of eggs of the tobacco hornworm. *Journal of Economic Entomology* 61, 1249–1252.

Rabb, R.L., Stinner, R.E. and van den Bosch, R. (1976) Conservation and augmentation of natural enemies. In: Huffaker, C.B. and Messenger, P. (eds), *Theory and Practice of Biological Control.* Academic Press, New York, pp. 233–254.

Read, D.P., Feeny, P.P. and Root, R.B. (1970) Habitat selection by the aphid parasite *Diaeretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassica* (Hymenoptera: Cynipidae). *Canadian Entomologist* 102, 1567–1578.

Reissig, W.H., Heinrichs, E.A., Litsinger, J.A., Moody, K., Fiedler, L., Mew, T.W. and Barrios, A.T. (1985) *Illustrated Guide to Integrated Pest Management in Rice in Tropical Asia.* International Rice Research Institute, Manila, Philippines.

Salt, G. (1931) Parasites of the wheat-stem sawfly. *Cephus pygmaeus* L., in England. *Bulletin of Entomological Research* 22, 479–545.

Shands, W.A., Simpson, G.W., Muesebeck, C.F.W. and Wave, H.E. (1965) Parasites of potato-infesting aphids in northeastern Maine. *University of Maine Agricultural Experiment Station Bulletin* T19, 77pp.

Smith, J.M. (1957) Effects of the food plant of California red scale, *Aonidiella aurantii* (Mask.), on reproduction of its hymenopterous parasites. *Canadian Entomologist* 89, 219–230.

Stephens, C.S. (1984) Ecological upset and recuperation of natural control of insect pests in some Costa Rican banana plantations. *Turrialba* 34, 101–105.

Taylor, T.H.C. (1937) *The Biological Control of an Insect in Fiji: an Account of the Coconut Leaf-mining Beetle and its Parasite Complex.* Imperial Institute of Entomology, London. 239pp.

Titayavan, M. and Altieri, M.A. (1990) Synomone-mediated interactions between the parasitoid *Diaeretiella rapae* and *Brevicoryne brassica* under field conditions. *Entomophaga* 35, 499–507.

Townes, H.T. (1971) Ichneumonidae as biological control agents. *Proceedings Tall Timbers Conference on Ecological Animal Control by Habitat Management.* Tallahassee, Florida. pp. 235–248.

Turnipseed, S.G. and Kogan, M. (1976) Soybean entomology. *Annual Review of Entomology* 21, 247–282.

van den Bosch, R. and Hagen, K.S. (1966) Predaceous and parasitic arthropods in California cotton fields. *California Agricultural Experimentation Bulletin* 820, 32pp.

van den Bosch, R. and Telford, A.D. (1964) Environmental modification and biological control. In: DeBach, P. (ed.), *Biological Control of Insect Pests and Weeds.* Chapman and Hall, London, pp. 459–488.

Van Emden, H.F. (1962) Observations on the effects of flowers on the activity of parasitic Hymenoptera. *Entomologist's Monthly Magazine* 98, 225–236.

Van Emden, H.F. (1991) The role of host plant resistance in insect pest mis-management. *Bulletin of Entomological Research* 81, 123–126.

Vinson, S.G. (1977) Behavioral chemicals in the augmentation of natural enemies. In: Ridgway, R.L. and Vinson, S.B. (eds), *Biological Control by Augmentation of Natural*

Enemies. Plenum Press, New York, pp. 237–279.

Vinson, S.B. (1981) Habitat location. In: Nordlund, D.A., Jones, R.L. and Lewis, W.J. (eds), *Semiochemicals: Their Role in Pest Control.* John Wiley & Sons, New York, pp. 51–77.

Weires, R.W. and Chiang, H.J. (1973) Integrated control prospects of major cabbage pests in Minnesota. *University of Minnesota Experiment Station Technical Bulletin* 241, 42pp.

Wilson, F. (1966) The conservation and augmentation of natural enemies. *Proceedings of the Food and Agriculture Organization Symposium on Integrated Pest Control* 3, 21–26.

Young, W.R. and Teetes, G.L. (1977) Sorghum entomology. *Annual Review of Entomology* 72, 193–218.