Journal of Applied Ecology 2001 **38**, 557–570

Pest damage and arthropod community structure in organic vs. conventional tomato production in California

D.K. LETOURNEAU and B. GOLDSTEIN*

Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA

Summary

1. To test common assumptions that the reduction in agrochemicals on organic farms allows (i) the conservation of biodiversity but (ii) has some cost in terms of increased pest damage, we compared arthropod communities and pest damage levels to fresh market tomato *Lycopersicon esculentum* on 18 commercial farms. These farms represented a range of management practices, with half of them operating as certified organic production systems and half as conventional operations.

2. Purported drawbacks to the adoption of organic farming include an increased incidence of pest damage and higher risk of pest outbreaks. Although insect pest damage levels varied across the spectrum of farm management practices, they were not associated with whether the farming operation was organic or conventional; organic and conventional farms did not differ significantly for any type of damage to tomato foliage or fruit.

3. Although conventional and organic farms shared a similar range of arthropod damage levels to tomato, we detected a significant difference between the actual community structures of arthropods associated with the crop. Using canonical discriminant analysis, we found that whereas herbivore abundance did not differ, higher natural enemy abundance and greater species richness of all functional groups of arthropods (herbivores, predators, parasitoids and other) distinguished organic from conventional tomato. Thus, any particular pest species would have been associated with a greater variety of herbivore species (diluted) and subject, on average, to a wider variety and greater abundance of potential parasitoids and predators, if it occurred in organically grown tomato.

4. Trophically based community parameters, specifically species richness and relative abundance of functional guilds, were clearly associated with farm management category (organic vs. conventional). However, the abundance patterns of prominent pests and natural enemies were associated with specific on-farm practices or landscape features. Fallow management, surrounding habitat and transplant date of the crop field were strongly associated with arthropod species that explained the major variability among farms. Insecticide intensity was a weaker factor. Other factors, such as distance to riparian habitats and tissue nitrogen levels, did not emerge as indicators of pest or natural enemy abundance.

5. This comparative study of active commercial farms does not support predictions of increased crop loss in California tomato when synthetic insecticides are withdrawn. It highlights the importance of large-scale on-farm comparisons for testing hypotheses about the sustainability of agro-ecosystem management schemes and their effects on crop productivity and associated biodiversity.

Key-words: biodiversity, biological control, farm management practices, GIS, insect pests, landscape patterns, multivariate analysis, natural enemies.

Journal of Applied Ecology (2001) 38, 557-570

Introduction

Negative social and environmental consequences of chemical-intensive agriculture have prompted vigorous debates about the sustainability of modern agriculture (Reganold 1989; Adams 1990; Pimentel et al. 1991; Avery 1995; McCann et al. 1997) and have inspired comparative research programmes in many parts of the world (Basedow 1998; Chamberlain, Wilson & Fuller 1999; Hald 1999; Ryan 1999; Ulen 1999; Chamberlain et al. 2000). The most prominent alternatives to conventional agriculture in the United States and Europe fall within the purview of 'organic' agriculture, which stresses biological processes and allows no synthetic chemical inputs for crop or pest management (National Research Council 1989; EEC Council Regulation 2092/9, Annex II B). Whereas natural and biological suppression of insects and diseases is likely to pose fewer human health risks and to reduce environmental disruption compared with chemical intensive pest controls, losses due to pests are expected to rise in the absence of synthetic pesticides. On the other hand, organic practices are designed to promote beneficial biotic processes; organically managed agroecosystems comprise a suite of community and ecosystem characteristics that may compensate for synthetic chemical inputs (Lampkin 1990). Organic management systems have recently caught the attention of conservation biologists as well, who remind us that the large proportion of our lands managed for agricultural production is indeed a source of important biodiversity (Ryszkowski et al. 1993; Roth, Perfecto & Rathcke 1996; Feber et al. 1997; Omerod & Watkinson 2000).

We compared organic (ORG) and conventional (CNV) tomato production systems in California to assess these alternative modes of crop production in terms of pest damage to the crop, pest abundance and arthropod community structure. We used fresh market tomato Lycopersicon esculentum L. as a model system for several reasons. First, tomato is a relatively highinput crop in terms of pesticide and fertilizer use for California agriculture. Of the top 15 vegetable crops, 11 field crops and 11 fruit/nut crops produced in the USA, Pimentel et al. (1981) listed tomato as having the highest percentage of acreage treated with insecticides (93%) and fungicides (98%) and the ninth highest for acreage treated with herbicides (67%). A 36% yield reduction was predicted if pesticides (insecticides and fungicides) were not applied to the tomato crop (Agricultural Issues Center 1988). Secondly, organic and conventional tomato growers use a wide range of management practices (from high to low input on a range of farm sizes) in the region. This allows for both a representative spectrum of actual commercial farming practices, and the variability needed to begin to identify particular practices that affect pest management. Finally, this region is facing problems typical of agricultural areas with high levels of pesticide use, from groundwater contamination to worker health problems,

© 2001 British Ecological Society, Journal of Applied Ecology, **38**, 557–570 to the loss of biodiversity (Agricultural Issues Center 1988; National Research Council 1989). These issues have led to the introduction of legislation in California aimed at restricting the use of some agricultural chemicals relied upon by conventional vegetable growers.

Our initial comparisons of organic and conventional tomato production in California indicated fundamental contrasts between these broad categories of farm management practices, but these differences were not defined by a simple absence of synthetic chemical inputs leading to lower yields for organic tomato (Drinkwater et al. 1995). In this study, we examined specifically the various types of pest damage incurred on organic and conventional tomato, and tested the assumption that organic farms will experience greater levels of damage from insect species that reduce yields in California tomato production. We used a hierarchical approach to compare arthropod community structure among the range of farming practices within the management categories: organic and conventional. First, community-level attributes (patterns of species richness and abundance of trophic guilds) of arthropods associated with organic and conventional tomato were measured to examine the evidence for greater biodiversity, compensatory biological control and herbivore pest/non-pest complementarily on organic farms compared with conventional farms. Secondly, we analysed pest and natural enemy population abundance patterns with respect to a number of factors (management practices, landscape features) that are known or purported to directly or inadvertently affect pest damage or biological control (Kromp & Meindl 1997; Barbosa 1998; Pickett & Bugg 1998; Altieri 1999). These included crop transplant dates, distance to the nearest riparian habitat, insecticide use intensity, percentage of uncultivated lands within 1 km of the crop field, winter fallow practices, and crop tissue nitrogen levels. We predicted that some or all of these factors, which overlapped to different degrees with our management categories, would contribute as mechanisms underlying different arthropod community structures in organic and conventional farms.

Methods

STUDY SITES

During the 1990 growing season, pest damage levels on the tomato crop and crop-associated arthropod communities were sampled on 18 commercial organic and conventional farms in a 600-km² area encompassing five counties in the Central Valley of California (Fig. 1). In this mediterranean climate, rains are primarily between the months of September and April, with summer vegetables depending on irrigation. The mean annual rainfall in the study area decreased over a north–south climatic gradient from 500 to 300 mm, and local variations in mean daily maximum temperatures during the growing season ranged from 29 to 32 °C.



Fig. 1. Location of tomato field study sites in the Central Valley of California, with open circles signifying organic farms and triangles signifying conventionally managed farms.

Nine organic and nine conventional farms were selected for this comparative study from an initial survey of 60 farms, using criteria described in Shennan et al. (1991). The 18 commercial tomato fields comprised the on-farm study system, with a majority of organic tomato producers in the region and a subset of the conventional tomato growers. Whereas organic farms comprised only 1-2% of California agriculture, commercial organic growers were common enough in the region for a sufficient sample size. Conventional farms were then selected to represent both the variety of conventional tomato producers in the region (e.g. conventional farms ranging from small to very large) yet to be similar to the organic farms with respect to environmental characteristics (soil texture, climate and surrounding vegetation) and properties related to farm scale (field size, crops produced and marketing approach) (Table 1). Thus, we used two methods of reducing the likelihood that confounding variables would obscure real differences due to management schemes (ORG vs. CNV). We either minimized the variation between and within management categories (e.g. the majority of CNV and ORG farms had similar soil texture and a moderate presence of weeds around the fields) or we included the whole range of variation in both categories (e.g. early and late transplant dates and small and large fields were included for both ORG and CNV farms). Farms classified as organic were managed with an emphasis on biological processes: nutrients were supplied at rates similar to those on conventional tomatoes through leguminous green manures and/or organic soil amendments, and pests were treated with microbials and other alternative controls; no synthetic fertilizers or pesticides were applied. Farms that used synthetic fertilizers and/or pesticides and did not add organic soil amendments (other than crop residues) were classified as conventional.

An insecticide intensity index, ranging from 0 to 8, was calculated for each farm using the frequency of applications of each compound, its relative breadth of susceptible arthropods, especially natural enemies, and its persistence. For example, given a single treatment of each, a persistent and broad-spectrum organochlorine would have a higher index than a more specific less persistent pyrethroid, and the pyrethroid would have a higher index than the lepidopteran-specific formulated Bacillus thuringiensis (Bt) spores and crystals, which break down quickly. Farms with a rating over 3.2 were considered high for categorical analyses. Thus, in the category of low insecticide intensity were tomato fields with one application of a pyrethroid or a carbamate, single applications of Bt, sulphur and soap, and all the fields with no insecticide applications. Farms designated high insecticide intensity used either multiple sprays with carbamates or applications of

Table 1. Scale, soil management and pest management characteristics of organic and conventional farms. The number in parentheses denotes the number of farms using a particular practice or input

Characteristics	Organic	Conventional		
Farm size	4–325 ha			
Tomato field	< 0·4–2 ha	0·4–65 ha		
Winter fallow	Cover crops (4) or annual weeds (5)	Cover crops (2), weeds (2), bare fallow (5)		
Nitrogen inputs	$72-258 \text{ kg ha}^{-1}$	$78-303 \text{ kg ha}^{-1}$		
Nitrogen forms	Legume residues, manure, compost, worm castings	Legume residue (1) and synthetic fertilizers		
Arthropod control	None (6), insectary plants (4), Bt (4), sulphur (1), Safer soap (1)	None (1), Bt (2), Sevin (1), Asana (4), Disyston (2), Diazinon (1), Monitor (1), 7XLR (1), sulphur (1), soap (1)		
Weed control	Cultivation	Cultivation (3), herbicide (6)		
Pathogen control	None	None, Ridomil (2)		

Six organic growers applied no pesticides; one applied *Bacillus thuringiensis* as formulated Dipel (Bt) at 2·24 kg ha⁻¹; one applied sulphur dust at 33·6 kg ha⁻¹; and one applied Javelin (Bt) at 2·336 l ha⁻¹ and Safer soap at 1·171 ha⁻¹. Conventional farmers applied the following pesticides (rates given when known) during the growing season: Devrinol DE at 9·344 l ha⁻¹; Asana XL at 0·71 ha⁻¹; Copper Count N at 4·71 ha⁻¹ (twice); Treflan at 1·171 ha⁻¹; Ridamil at 0·951 ha⁻¹; Treflan at 0·58 l ha⁻¹; Eptam at 4·11 ha⁻¹; sulphur dust at 67·2 kg ha⁻¹; Safer soap at 11·21 ha⁻¹ and Bt at 1·171 ha⁻¹; Tillam at 2·336 l ha⁻¹; Asana XL at 0·511 l ha⁻¹; Disyston 8 at 1·171 ha⁻¹; Monitor, Asana, Ridomil at 0·44 l ha⁻¹; Dipel 2X at 2·24 kg ha⁻¹; Sevin Bait at 28 kg ha⁻¹; Roundup, Treflan, 7XLR Plus and Devernol at 71 ha⁻¹; Tillam at 6·42 l ha⁻¹; 7XLR Plus at 3·51 ha⁻¹; Disyston at 2·341 ha⁻¹; Asana XL at 0·58 l ha⁻¹; Disyston AG 400 at 1·171 ha⁻¹ (twice).

more persistent broad-spectrum organophosphates (Table 1).

All 18 farms had soils of alluvial origins typical of sites commonly used for tomato production in the area (Drinkwater et al. 1995). Farms in both ORG and CNV management categories included sites bordered by various combinations of annual crop fields, orchards, oak woodland and riparian habitats. All fields were maintained reasonably weed-free within the beds during the growing season, but annual weeds were abundant along roadsides and field edges, especially where sufficient moisture was available. Thus, all tomato fields had weedy areas in the vicinity of the crop field. The cropping history of the fields, however, was not independent of management category. The majority of conventional farms were maintained as bare ground fallows over winter through initial tillage and subsequent herbicide applications, whereas organically managed fields had a vegetative cover with annual weeds and/or cover crops (different species or varieties of rye Secale cereale L., vetch Vicia spp., oats Avena sativa L., barley Hordeum vulgare L., mustards Brassica spp., Austrian winter pea Pisum sativum ssp. arvense L. or a combination). For our categorical analysis of winter ground cover, we categorized farms as having either vegetative cover or bare fallow.

CROP ESTABLISHMENT

Transplants of fresh market tomato, variety Blazer®, were grown in a peat moss–vermiculite mix amended with nitrogen and phosphorus fertilizer for conventional farms and with fishmeal for organic farms. Seedlings were transplanted 5–6 weeks after emergence in April, May or June, depending upon the grower's marketing strategy.

SAMPLING

Each of 20 sampling subplots consisted of a 1.5-m² area of the tomato crop, located in a stratified-random pattern within a centrally located sampling area in each field. These sampling areas varied in size from 0.04 to 0.1 ha, depending on the dimensions and shape of the field, and were located near the centre of the field. In comparisons of arthropod fauna in wheat, sampling in the centre of the field maximized differences between organic and conventional fields (Reddersen 1997). However, we used interior field samples to avoid edge effects and to represent the arthropod community associated with the majority of tomato plants, those occurring in the field interior. Because transplant dates for the crop differed among fields, foliar damage, fruit damage, nitrogen analyses and arthropod samples were timed to the phenology of the crop. Thus, all samples were taken at harvest time for that particular field (the stage at which 10% of the fruit is pink, and the mature green fruit is harvested for shipping fresh market tomatoes). Whereas the time between transplant dates and sample dates (harvest) was approximately 3 months, it varied among fields from 11 to 16 weeks,

depending on abiotic conditions in the field. Pest damage samples from all 20 subplots consisted of insect damage measurements, calculated as the proportion of leaflets or fruit damaged by different pest taxa. Each of these leaflets and each of 20 fruits per subplot (1600– 4000 leaflets and 400 tomatoes per farm) were collected haphazardly from throughout the canopy and inspected for insect damage according to characteristic feeding by thrips, flea beetles, lepidopteran larvae, sucking insects and leafminers (Flint 1985). Shoot nitrogen (Kjeldahl method) was determined on shoot biomass (subsample taken from total above-ground tissue, after drying and grinding stems plus leaves) for each of the 20 subplots on each farm (for details on these methods see Letourneau, Drinkwater & Shennan 1996).

Arthropods were sampled on a randomly selected subset of five subplots per farm by extracting them from the vegetation with a vacuum machine (Allen, Coville & Osborne 1988; Osborne & Allen 1999) before the vegetation was harvested for the samples listed above. The 10.5-cm diameter cylinder of the gas-powered suction apparatus was passed over and into the tomato foliage, moving along the bed and from the tops of plants to near the soil level for a single 30-second sample in each of five subplots per farm. This technique was shown to be an efficient means of sampling representatives of all trophic levels from the vegetation at this stage of crop canopy development. Arthropods from these samples were separated from the foliage, sorted and identified to species (pests and common insects) or morphospecies (Vandermeer 1972), and categorized trophically as herbivore, predator, parasitoid or other.

GEOGRAPHIC INFORMATION SYSTEMS ANALYSES

Geographic information systems (GIS) analyses were done using ArcInfo version 6 and ArcView version 2 (Environmental Systems Research Inst. 380 New York Str, Redlands, CA) on a Sun Solaris 7 workstation. USGS National Aerial Photography program (United State Geological Survey, 12201 Sun Valley Drive, Reston, VA USA) aerial photographs (1:40 000) were visually edgematched to create a photomontage with a 5-km radius around each of the tomato fields sampled for damage and arthropods. Using acetate overlays, boundaries were drawn surrounding (i) contiguous areas of similar row crops or orchards; (ii) uncultivated natural habitats; (iii) rivers and streams; (iv) urban areas. Each photomontage was digitized using six to eight ground control points from USGS topoquad sheets. Cumulative root mean square errors (photographic distortion) ranged from 15 to 37 m. All polygon vertices that fell within 30 m of one another were merged. Two additional layers were created for each site by removing the area that lay beyond a radius of 1 km. Total area and perimeter were measured for agricultural (crop fields, orchards) and wildland (uncultivated areas) patches within 1 km from the centre of each tomato field. The measurements of

individual patch area and perimeter were estimated by eliminating all polygons that did not have at least one half of their area inside the 1-km radius. The shortest distance from the centre of each field to a waterway was also measured, to indicate its distance from a riparian habitat.

STATISTICAL ANALYSES

Nested ANOVAS on data from field subplots (pest damage, arthropod abundance) or ANOVAS with one value per field (off-farm parameters) were used on raw data, unless transformation was necessary to meet the assumptions of the model, to compare organic and conventional crop and landscape features. For nested ANOVAS, we used the type III mean squares for farm, nested in treatment, as the error term. We used the term species richness for the number of species or morphospecies; and abundance was the number of individual arthropods. Principal components analysis (PCA) was used to determine which of the community-level arthropod profile parameters (herbivore abundance, predator richness, etc.) to include in a canonical discriminant analysis for comparing arthropod community patterns between management types. This process reduced the number of variables from a total of eight to the five variables that explained the majority of the variance. We report the pooled within-canonical structure correlations, and standardized pooled within-class canonical coefficients, and considered those coefficients of at least 0.3 as significant.

In a separate analysis, we used a data set of abundances per subsample (n = 5) per farm of particular species of arthropods that were relatively common within an order, and represented both pests and natural enemies. Abundances of the most common potential pests and natural enemies (21 species) were examined first with PCA (using the default analysis on correlation matrices to standardize abundances through a common variance) to determine which arthropod groups were associated with each other, and how much of the total variability was contributed by each principal component. Subsequent nested ANOVAS were conducted on the first four principal components (73% of the total variation) to identify measured factors that may have been associated with the major sources of variability in these arthropod abundance patterns. Thus, each of the first four principal components was tested for significant effects of the following categorical independent factors: management, crop tissue nitrogen, insecticide spray intensity, percentage wildlands and distance to riparian habitats. Analyses were conducted using PC-SAS for Windows, version 6.12 (SAS Institute 1993).

Results

© 2001 British Ecological Society, Journal of Applied Ecology, **38**, 557–570

PEST DAMAGE LEVELS

Crop damage levels by thrips [Frankliniella occidentalis (Perg.) and others], flea beetles [primarily Epitrix

hirtipennis (Melsheimer)], leaf-eating caterpillars [including Manduca sexta (L.), Trichopulsia ni (Hubner), Spodoptera exigua (Hubner), Autographa spp. and many others], leafminers (including Liriomyza spp.), fruiteating caterpillars [including Helicoverpa (Heliothis) zea (Boddie) and Keiferia lycopersicella (Walsingham)] and fruit-piercing insects (including Nezara viridula L., Lygus spp., tomato bugs Cyrtopeltis modesta Van Duzee and Empoasca spp.) varied from twofold to 100-fold among farms with detectable damage, but did not differ significantly between organic and conventional farms [(Fig. 2; nested ANOVA, n = 20 subplots per farm, and d.f. = 1 for management category and d.f. = 16 for farm nested in farming category; thrips damage (F = 0.08, d.f. = 1,16, P = 0.7862), flea beetle damage (F = 0.44, d.f. = 1,16, P = 0.5170), caterpillar damage on leaves (F = 0.12, d.f. = 1,16, P = 0.7297), leafminer damage (F = 1.4, d.f. = 1, 16, P = 0.2535), caterpillar damage on fruit (F = 0.94, d.f. = 1,16, P = 0.3466) and piercing insect damage on fruit (F = 0.07, d.f. = 1,16, P = 0.7792)]. Average damage levels (n = 20 subplots per farm)accrued over the season were significantly correlated with the mean abundance of the most common species of that pest in vacuum samples (n = 5 subplots per farm). That is, western flower thrip Frankliniella occidentalis abundance correlated directly with percentage tomato leaflets damaged by thrips (r = 0.66, P = 0.0027); flea beetle Epitrix hirtipennis abundance was correlated with percentage tomato leaflets damaged by pitfeeders (r = 0.71, P = 0.0010); and tomato fruitworm Helicoverpa zea abundance and percentage of fruits with deep wounds typical of fruitworm damage were significantly correlated (r = 0.81, P = 0.0001).

COMMUNITY STRUCTURE

Community-level profiles (richness and abundance of herbivores and natural enemies) in commercial tomato fields under organic and conventional management were significantly different despite the wide range of specific farming practices and conditions represented within these management categories. The first principal component explained 53% of the variance among farms, with the highest loadings on species richness of all functional categories (herbivores, predators, parasitoids and other arthropods) and abundance of parasitoids. These species richness and abundance patterns differed significantly between organic and conventional farms (canonical discriminant analysis, Wilks' lambda *F*-value = 3.37, d.f. = 6,11, *P* = 0.0394; Fig. 3), indicating fundamentally different arthropod community structures. Organic farms had a more diverse arthropod fauna, on average, than conventional farms, with the average for five 30-second vacuum samples per farm yielding approximately 40 arthropod morphospecies in conventional tomato and 66 morphospecies in organically managed tomato (Table 2), and natural enemies (parasitoids plus predators) were more abundant on organic farms ($\overline{X}_{CNV} = 177.0 \pm 70.2 \text{ SE vs.}$

562 D. K. Letourneau & B. Goldstein



Fig. 2. Average (\pm SE) percentage of damaged leaves and fruits harvested from 201.5-m² subplots of tomato, located centrally in a field in a stratified random arrangement, on each farm, with conventional or organic management schemes. Determinations of damage types were based on those described by Flint (1985) for the common pests of tomato in the region. These damage types were distinct for various thrips (including western flower thrip *Frankliniella occidentalis*), flea beetles such as *Epitrix hirtipennis*, caterpillars (hornworms *Manduca* spp., loopers *Trichoplusia ni* and *Autographa* spp., tomato fruitworm *Helicoverpa zea*, tobacco budworm *Heliothis virescens*, armyworms *Spodoptera* spp., and tomato pinworm *Keiferia lycopersicella*), leafminers *Liriomyza* spp. and sucking bugs (stinkbugs *Euschistus conspersus* and *Nezara viridula*, *Lygus* bugs *Lygus hesperus*, leafhoppers *Empoasca* spp. and tomato bugs *Cyrtopeltis modesta*).

 $X_{\text{ORG}} = 318 \cdot 8 \pm 37 \cdot 4 \text{ SE}$) while herbivore abundance was similar on conventional and organic farms ($\overline{X}_{\text{CNV}} = 1178 \pm 362 \text{ SE}$ vs. $\overline{X}_{\text{ORG}} = 1241 \pm 243 \text{ SE}$).

Separate canonical discriminant analyses on the abundance of relatively prominent pests and natural enemies showed no significant difference between organic and conventional farms for pests (canonical discriminant analysis, Wilks' lambda F-value = 1.65, d.f. = 6,11, P = 0.2226) (Fig. 4a) but a significant difference for natural enemies (Wilks' lambda F-value = 4.09, d.f. = 6,11, P = 0.0211) (Fig. 4b). The relative densities of pests and potential pests were variable, either being evenly distributed among farm management categories or occurring more prominently on individual conventional farms or on individual organic farms (Fig. 5). The densities of prominent natural enemies tended, instead, to be more abundant on organic farms (Fig. 6). The western flower thrip Frankliniella occidentalis was common on many farms in both

categories (Fig. 5). High abundance of leafhoppers in the Empoasca complex tended to occur on organic farms, whereas high levels of other pests, the prominent aphid species [green peach aphids Myzus persicae (Sulzer) and bean aphids Aphis fabae Scopoli] or flea beetles Epitrix hirtipennis, occurred on some conventional farms (Fig. 5). The tomato fruitworm Helicoverpa zea was collected in vacuum samples at a mean abundance of 5.2 ± 3.5 SE per organic farm and 0.4 ± 0.2 SE per conventional farm (nested ANOVA, F = 1.81, d.f. = 1,16, P = 0.1977). The tobacco budworm *Heliothis virescens* Fabricius showed the opposite trend, with a mean abundance of 2.4 ± 2.2 SE on organic farms and 7.4 ± 3.9 SE on conventional farms (nested ANOVA, F = 1.25, d.f. = 1,16, P = 0.2795). For each of the common natural enemies, specifically the spined stilt bug Jalysus wickhami (Say), the minute pirate bug Orius tristicolor (White), the predatory mirid bug Engytatus modestus (Distant), the crab spider Misumenops sp.



Fig. 3. Species richness (number of species collected per five 30-second vacuum samples, per farm) of all groups (predators, parasitoids, herbivores and other) and abundance of parasitoids (number of individuals per five 30-second vacuum samples, per farm) (combined as canonical function 1) vs. herbivore abundance per five 30-second vacuum sample of 1.5-m² tomato plant per farm at harvest, with open circles signifying organic farms and closed circles signifying conventionally managed farms.

and the total complex of parasitic Hymenoptera, however, the highest abundances occurred on one or more individual organic farms (Fig. 6).

LANDSCAPE-LEVEL COMPARISONS

Whereas some management practices such as insecticide spray intensity ($\overline{X}_{CNV} = 3.8 \pm 0.8$ SE vs. $\overline{X}_{ORG} =$ 0.5 ± 0.2 SE; anova, F 1,18 = 20.4, P = 0.0003), shoot nitrogen content ($\overline{X}_{CNV} = 2.7 \pm 0.1$ SE vs. $\overline{X}_{ORG} = 2.1 \pm$ 0.1 SE; nested ANOVA, P = 0.02, n = 20 samples on 17 farms) and type of fallow (Table 1) differed between organic and conventional farms, there was no difference in average transplant date. None of the landscape variables differed significantly for organic vs. conventional farms, such as the mean percentage natural lands within a 1-km radius of the tomato field ($\overline{X}_{CNV} = 9.2 \pm 6.7\%$ SE vs. $\overline{X}_{ORG} = -23.6 \pm 7.0\%$ SE; anova, d.f. = 1,16, F = 2.2, P = 0.1583), the perimeter to area ratio of the field $\bar{X}_{CNV} = 83.6 \pm 14.9\%$ SE vs. $\bar{X}_{ORG} = 84.6 \pm 19.3\%$ SE) and the distance to the nearest stream or river $(\bar{X}_{CNV} = 1.5 \pm 0.6 \text{ km SE vs. } \bar{X}_{ORG} = 0.7 \pm 0.1 \text{ km SE};$ ANOVA, d.f. = 1,16, F = 2.9, P = 0.1078).



Fig. 4. Abundances of pest insects (a) vs. the abundance of leafhoppers, aphids and noctuid caterpillars (canonical function 1) and (b) the abundance of known or potential natural enemies vs. the abundance of predatory mirids, berytids, spiders and scelionid parasitoids (canonical function 1), with open circles signifying organic farms and closed circles signifying conventionally managed farms. All abundance values are the total number of arthropods in the specified group (leafhoppers, predatory mirids, etc.) per 30-second vacuum sample in each of five $1.5-m^2$ randomly selected subplots of the tomato crop in each farm.

SPECIES-LEVEL PATTERNS

When all 21 species/morphospecies of arthropods that represented either known tomato pests, natural enemies of those pests or particularly abundant potential pests or natural enemies were analysed together, the general management category (organic vs. conventional)

Table 2. Community-level parameters cosntributing significantly (standardized coefficient ≥ 0.3) to classification of the observations in management categories (conventional and organic) by canonical discriminant analysis, and mean values per management category

	Canonical function 1		Management category	
Community profile variables	Pooled within class correlations	Standard coefficients	Conventional (mean ± 1 SE)	Organic (mean ± 1 SE)
Species richness: herbivores	0.9	0.8	15.6 ± 1.0	22.4 ± 1.3
Species richness: parasitoids	0.6	0.5	12.7 ± 2.7	24.9 ± 4.1
Species richness: predators	0.4	-0.0	8.6 ± 1.4	12.6 ± 1.7
Species richness: others	0.5	0.2	2.9 ± 0.4	6.4 ± 1.8
Abundance: parasitoids	0.3	-0.4	119.1 ± 64.5	222.7 ± 89.4



Fig. 5. Ranked abundances of tomato pests captured from five vacuum samples per farm (mean \pm SE) showing patterns between conventional and organic management schemes for thrips (western flower thrip *Frankliniella occidentalis*), leafhoppers *Empoasca* spp., aphids (green peach aphid *Myzus persicae* and bean aphid *Aphis fabae*) and flea beetles *Epitrix hirtipennis*.

did not clearly distinguish the patterns of relative abundance among farms. For individual species groups that sorted together in the PCA, we found that a series of factors emerged to explain the variability of their abundance among farms. Three parasitic wasps of leafminers (Hymenoptera: Eulophidae) and the common flea beetle had significant loadings for the first principal component, and this component was significantly associated with whether the farm had used vegetative or bare fallow the previous winter (Table 1 and Table 3). Fields managed with cover crops or annual weeds over the winter wet season had at least a magnitude higher abundance of all four species than fields that were kept in bare fallow (no vegetation) (Table 4). Insecticide use intensity was a marginally significant factor for explaining the first principal component (F = 3.86, d.f. = 1,16, P = 0.07), so may have interacted with fallow practices to promote these patterns. Flea beetles and all three wasps were much more abundant on farms in the low category of insecticide use intensity than on farms in the high category (mean abundances of flea beetles: 199.6 vs. 15.3; Chrysocharis avia Hansson: 40.0 vs. 1.0; *Diglyphus begini* Ashmead: 57.8 vs. 3.5; *Chrysocharis liriomyzae* Delucchi: 8.6 vs. 0.0 per farm).

The relative amount of surrounding natural vegetation (vs. row crops and orchards or urban development) was the best parameter for explaining the second principal component, which featured aphids, a mymarid egg parasitoid and a mirid predator (Table 4). Both bean aphids Aphis fabae and green peach aphids Myzus persicae were rare on farms with a high proportion of natural areas nearby, and although aphid mummies followed this trend directly, a greater proportion of aphids were found parasitized on farms near natural areas. Principal component 2 was associated to a lesser degree with management category (conventional vs. organic, F = 4.67, d.f. = 1,16, P = 0.046), with all aphids and the parasitic wasp being more abundant on conventional farms and the predatory mirid being much more abundant, on average, on organic farms than on conventional farms (Figs 5 and 6).

A smaller amount of the total variance was explained by crop phenology (principal component 3; Table 3).



Fig. 6. Ranked abundances of potential natural enemies captured from five vacuum samples per farm (mean \pm SE) showing patterns between conventional and organic management schemes for the spined stilt bug *Jalysus wickhami*, minute pirate bugs *Orius tristicolor*, omnivorous plant bugs *Engytatus modestus*, a common crab spider *Misumenops* sp. and the parasitic hymenopterans as a group.

Western flower thrip *Frankliniella occidentalis* were ubiquitous in arthropod samples, but their abundance was determined by transplant date, with high levels on tomato when transplanted early in the season (Table 4). A common web spider *Erigone* sp. followed this trend as well. An unidentified pterymalid wasp (parasitoid) also exhibited abundance patterns related to transplant date, but with higher levels on late-season transplants.

The fourth principal component showed an association of four natural enemies and two herbivores and, as with principal component 2, this component was significantly affected by the amount of natural lands surrounding the farm. Farms that had greater than 25% natural lands within 1 km of the tomato were characterized by high levels of leafhoppers *Empoasca* spp., grain thrips *Limothrips cerealium* (Haliday) (which is not known to be a pest of tomato) and elevated levels of predatory stilt bugs *Jalysus wickhami* (Table 4). Two parasitic wasps, one a parasitoid of scale insects (*Atropates* sp.) and one (*Gryon* sp.) parasitizing hemipterans, and a major thrips predator *Orius* tristicolor were more abundant on farms surrounded by cultivated areas. Neither the distance from a riparian habitat nor crop tissue nitrogen level was a useful factor for explaining abundance patterns as reflected by the PCA for prominent species in our study.

Discussion

Despite predictions that the removal of insecticides would cause a substantial increase in the average pest damage in California tomato crops (Agricultural Issues Center 1988), the variability in insect damage to the foliage and fruit among 18 commercial farms was not explained by management category. Indeed, organic farms, which allow only a small subset of conventional pest control options, experienced no significant difference from conventional farms for any individual category of pest-feeding damage (leaf grazers, foliage pitfeeders, fruit punctures, etc.) and no difference in

conventional tomato fields. Percentages following each principal component show the proportion of total variance explained, with PC1 explaining the most variance, and PC 1-4 explaining a total of 57%. For each PC, the significant categorical source of variation is given along with the values of significance from nested anovas on the PCs. For each PC only variables (groupings of arthropod species) that had a sufficiently Jalysus wickhami/-0.32 Species/EV Berytid bug Limothrips cerealium/-0.32 Engytatus modestus/0.30 Species/EV Grain thrip Mirid bug Chrysocharis liriomyzael 0.33 Polynema sp. 31/0·36 Empoasca spp./0.35 Eulophid wasp Mymarid wasp Leafhoppers Species/EV high loading to be considered significant (eigenvectors ≥ 0·3) are included. Eigenvector values (EV) are listed after each species Epitrix hirtipennis/0.33 Orius tristicolor/0.36 Erigone sp. 2/0·36 Minute pirate bug mumnies/0·43 Aphis fabae Species/EV Web spider Flea beetle Halticoptera sp. 37/-0.44 Diglyphus begini/0.34 Atropates sp. 54/0.49 Myzus persicae/0.40 Green peach aphid Pteromalid wasp Eulophid wasp Encyrtid wasp Species/EV Frankliniella occidentalis/0·57 Chrysocharis avia/0.38 Western flower thrip Gyron sp. 54/0·45 Aphis fabae/0·49 Eulophid wasp Scelionid wasp Species/EV Bean aphid $F_{1,16} = 9.25, P = 0.008$ $F_{1,16} = 5.52, P = 0.016$ $F_{1,16} = 5.47, P = 0.033$ $F_{1,16} = 4.93, P = 0.041$ PC/source PC1 (26%) PC2 (13%) PC3 (10%) Phenology Wildlands Wildlands PC4 (8%) Fallow

Table 3. Coefficients for the first four principal components (PC) for the 21 arthropod morphospecies collected in vacuum samples and classified as known or potential pests and natural enemies in organic and

overall insect damage (Drinkwater *et al.* 1995). In fact, the average abundance of phytophagous insects was extremely similar on organic andonventional tomato at the time of crop harvest. On the other hand, arthropod biodiversity, as measured by morphospecies species richness, was, on average, one-third greater on organic farms than on conventional farms, suggesting that, at least for tomato in the Sacramento Valley, commercial production using organic management techniques is both practical and beneficial.

The broad scope of our arthropod and damage comparisons on organic vs. conventional farms was designed to assess arthropod community structure (biodiversity, abundance in different trophic levels, impact of herbivore feeding guilds) and to provide a comparative measure of particular pests and natural enemies at crop harvest. Although the resolution required for detecting the dynamics of particular pest species was exchanged for higher order assessments, our samples included snapshot comparisons of both the major pests of tomato in California [flea beetles Epitrix hirtipennis, green peach aphid Myzus persicae, potato aphid Macrosiphum euphorbiae (Thomas), tomato russet mite Aculops lycopersici (Massee), cabbage looper Trichoplusia ni, vegetable leafminers Liriomyza spp., tomato fruitworm Helicoverpa zea, beet armyworm Spodoptera exigua, tomato pinworm Keiferia lycopersicella and stink bugs Euschistus conspersus Conchuela and Nezara viridula] and the minor or occasional pests, such as tomato hornworm Manduca sexta Pupa or tobacco budworm Manduca quinquemaculata (Haworth), which are patchy in occurrence, or thrips, which can damage the crop early in the season if plants are water stressed (Strand 1998). Cutworms, which damage transplants, were the only major insect pests that were not assessed in our damage or vacuum samples. Our finding of overlap in damage and herbivore levels but higher biodiversity on organic tomato compared with conventional tomato is similar to a comparison of Holland & Fahrig (2000) who also found habitat factors (in this case woody borders within a 1-km radius) influencing the diversity of herbivores but not the density. Feber et al. (1997) measured similar levels of pest butterflies in organic vs. conventional farmland, but also found significantly more non-pest butterflies in organic farmland. A broader faunal comparison by Reddersen (1997) revealed a higher arthropod abundance in conventional cereal fields and a higher diversity of arthropods in organic cereal fields, with higher abundance in conventional fields depending only on two major cereal herbivores, and only in one of two years.

Plant tissue nitrogen has been shown to be a critical limiting nutrient for herbivores (Jones 1976; Slansky & Rodriguez 1987). Although tissue nitrogen levels were significantly higher in conventionally managed tomato, on average bottom-up effects caused by low nitrogen availability on organic farms did not seem to be an important limiting factor for herbivores in those fields (Letourneau, Drinkwater & Shennan 1996). Finding

Table 4. Mean ± 1 SE abundance of arthropods in five 30-second vacuum samples in five subsamples of tomato crop per farm (n = number of farms) with respect to significant sources of variation as shown by nested ANOVAS on the principal components

PC1 (source: winter fallow)	Farms with heavy vegetative cover $(n = 13)$		Farms with bare ground fallow $(n = 5)$	
Chrysocharis avia parasitoid	36·1 ± 12·9		$2 \cdot 0 \pm 0$.9
Diglyphus begini parasitoid	62.0 ± 28.3		3.4 ± 2.4	
Epitrix hirtipennis flea beetle	211.2 ± 77.5		22.0 ± 9	·8
Chrysocharis liriomyzae parasit	oid $9 \cdot 2 \pm 4 \cdot 3$		0.0 ± 0	·0
	Farms with > 2	5% natural	Fai	rms with < 25% natural lands,
PC2 (source: % wildlands)	lands in 1 km radius $(n = 7)$		1 km radius $(n = 11)$	
Aphis fabae bean aphid	17·7 ± 5·4		129	0.4 ± 62.1
Aphis fabae mummies	7.3 ± 3.0		40.6 ± 34.3	
Myzus persicae peach aphid	20.3 ± 9.9		215.6 ± 116.1	
Polynema sp. 31 egg parasitoid	2.0 ± 1.3		4.9 ± 3.0	
Engytatus modestus predator	$271 \cdot 4 \pm 79 \cdot 4$		157	$1 + 121 \cdot 1$
PC3 (source: crop phenology)	April transplant farms $(n = 6)$	May transplant farm	ms (n = 6)	June transplant farms $(n = 6)$
Frankliniella occidentalis thrip	458.5 ± 120.8	341.5 ± 56.8		125·8 ± 90·5
Halticoptera sp. 37 parasitoid	0.3 ± 0.2	5.3 ± 4.3		41.7 ± 22.5
Erigone sp. 2 spider	23.0 ± 11.0	6.0 ± 1.6		1.5 ± 0.4
	Farms with > 259	% natural	Fa	rms with < 25% natural lands,
PC4 (source: % wildlands)	e: % wildlands) lands in 1 km radius (= 7) 1 km radius ($n = 11$)	
<i>Gyron</i> sp. 83 parasitoid 0.0 ± 0.0			1	1 ± 0.6
Atropates sp. 54 parasitoid	9.7 ± 7.0		24	$\cdot 5 \pm 10.0$
Orius tristicolor predator	28.1 ± 7.0		56	$\cdot 0 \pm 24 \cdot 4$
Empoasca spp. leafhoppers	83.7 ± 45.3		18	$\cdot 7 \pm 7 \cdot 1$
Limothrips cerealium thrips	348.7 ± 65.9		26	$\cdot 2 \pm 21 \cdot 4$
Jalysus wickhami predator	1.7 ± 0.5		0	$\cdot 2 \pm 0.2$

no relationship between plant nitrogen levels and herbivore damage or herbivore abundance is a surprising result given the strong basis of theory and supporting studies (Scriber 1984). However, if our expectations of herbivore release with high nitrogen are based mainly on comparisons with potted plant and/or with a subset of herbivores (aphids and mites), then they may not be effective predictors of other types of pest damage in the field (Letourneau 1997). Large-scale field comparisons with a broad range of herbivores may show more variable responses to crop nitrogen levels.

Although abundance patterns of prominent pests did not differ significantly among organic and conventional farms, an examination of abundant herbivores in a wide range of taxa showed that different species were either similar in abundance (such as thrips), tended to be abundant on some conventional farms (such as aphids and tobacco budworm), or tended to be abundant on some organically grown tomato (such as leafhoppers and tomato fruitworm). Teasing out the reasons for high abundances of a particular arthropod on specific farms is beyond the scope of this empirical analysis, but certain expected patterns were observed. For example, there was an order of magnitude higher mean level of tobacco budworm on farms in the high spray intensity category than in the low spray intensity category, and this species is known to be a secondary

pest exacerbated by broad-spectrum sprays. Known natural enemies of tomato pests (Strand 1998) captured in our samples showed distinct community-level differences in abundance between organic and conventional farms, with a tendency, even at the species level, for higher abundances on organic farms. We assume that the pattern of greater abundance and richness of natural enemies was indicative of a real difference between organic and conventional fields. First, the magnitude of the difference was great despite the wide range of management practices within each of the general management categories. Secondly, the pattern from this snapshot comparison was even stronger when data from an early season sample (6 weeks after transplanting) were included in the analysis (Drinkwater et al. 1995). Thirdly, increased abundance or diversity was also found recently in comparative studies of other crops, particularly organic wheat (Moreby et al. 1994; Basedow 1995; Pfiffner & Niggli 1996) and carrot (Berry et al. 1996).

Variable outcomes among farms for relative abundances of particular arthropod taxa may reflect the unique conditions of a particular farm against a background of the larger management category. For example, source pools for particular pests or enemies may be large because of a certain winter fallow practice or more distant landscape factor. Whether or not such a spatial or temporal source pool resulted in high

abundances at harvest would probably be modified by on-farm management practices for the tomato crop. Thus, our analysis of all relatively common species of potential pests and natural enemies showed that overall management strategy was no longer as powerful an explanatory factor as it was for community-level arthropod abundance and richness. For particular groups of arthropod species, other characteristics of the farms (e.g. surrounding lands) and farming practices (e.g. winter fallow) across the spectrum of organic and conventional farms emerged as significant factors.

To explore some of these factors in more depth, it is reasonable to suggest that vegetative fallow practices, which maintain vegetative cover during the wet season, may act to perennialize the crop habitat and allow continuity of certain arthropod populations through the year. Natural enemies are often enhanced in perennial crop habitats and in vegetative fallow compared with annual crops disrupted by bare fallow (Honek 1997). However, insecticide treatments could disrupt the potential stability gained by local vegetational cover. In this study, the ubiquitous flea beetles and several parasitoids attacking leafminers were more common on farms using vegetative fallow practices, suggesting that alternative hosts and/or refugia were provided to maintain these local populations through the winter. These leafminer parasitoids were also more abundant on farms with low insecticide usage, which is not surprising given the susceptibility of these parasitoids to pesticides (Flint & Dreistadt 1998). In general, practices used more often on organic farms, such as cover cropping and low intensity pesticide treatments, were associated with increases in parasitic wasps (primary source of variability among farms) and more predators. A different factor, crop phenology, was associated with the abundance of pest thrips, a pteromalid parasitoid of boring dipterans Halticoptera sp. 37, and a web spider. Abundance among farms for these species was associated with transplant date, a neutral practice not associated with either organic or conventional management. A landscape factor, the prominence of natural lands within 1 km of the field, may have strongly affected aphid densities by reducing crop source pools of aphids. A reduction of aphid pools in natural lands compared with surrounding crop lands is reasonable because most of the natural lands were sparse oak woodland, which does not support the aphids that feed on tomato, and agricultural lands were kept lush with irrigation. In contrast to the pest aphids, Empoasca leafhoppers and cereal thrips probably had important source pools early in the season in natural habitats with grasses, so may have colonized nearby farms in large numbers as the surrounding grasses dried in the mediterranean summer conditions. There also tended to be a higher percentage of parasitized aphids and a greater abundance of mirid and berytid predators when farms were near extensive natural habitats.

© 2001 British Ecological Society, Journal of Applied Ecology, **38**, 557–570

The dramatic, though not surprising, result of this extensive study of arthropod community profiles, then,

is that integrated management practices categorized broadly as 'conventional' and 'organic' explained community-level parameters such as species diversity and abundance of functional groups (herbivores, natural enemies, other), whereas specific management practices and landscape characteristics of farms within those categories were associated with abundance patterns of specific pests and natural enemies. Community-level parameters may be suitable indicators of vertebrate conservation value for such farms, if, for example, arthropod diversity (some combination of abundance and richness) predicts food availability for certain birds, reptiles and mammals. However, conservation goals for non-arthropod species will need policy based on more thorough studies of arthropod communities present throughout the year in different cropping systems and farm management schemes (McCracken & Bignal 1998).

Several explanations are possible for comparably effective pest regulation on organic farms despite their mandated reliance on natural or naturally derived pest controls. First, organic practices may have promoted the richness of herbivores such that the community was less dominated by severe pest species than were farms employing conventional methods of soil, weed, crop and insect pest management. This 'complementarity' of herbivores, in which resources are shared among a greater number of species, could result in a 'dilution effect' of lower detectable damage levels by pest species despite a similar overall abundance of herbivores in general. Secondly, it is possible that biological controls of insect pests on organic farms were compensating for more chemically intensive pest control practices used by conventional growers. Both of these notions were supported by community-level parameters, which showed that organic farming methods significantly promoted the conservation of arthropod species in all functional groups, and enhanced the abundance of natural enemies, compared with conventional practices. Thus, the combined effects of organic agricultural practices in California tomato production were comparable insect damage levels to those under conventional management practices but higher levels of associated biodiversity (sensu Vandermeer & Perfecto 1995), which may have been a source of biological compensation for insecticide use. In addition, if organic practices in general promote an increased diversity of potential beneficial insects and alternative prey, they should also be more sustainable in terms of ecological resilience in the face of environmental changes in agricultural landscapes (Duelli, Obrist & Schmatz 1999).

Acknowledgements

This study was funded by USDA-LISA grant 88-COOP-1-3525, which funded the main study with C. Shennan, L. Drinkwater and A. van Bruggen. K. Hansen, T. Jackson, S. Nilsson, J. McKelvy, R. O'Malley, K. Osborne and D. Sikes provided excellent field

assistance. K. Osborne placed thousands of specimens into morphospecies categories. R. Bugg, R. Burks, K. Osborne, M. Schultz, S. Triapitsyn and D. Ubick identified important species not in the tomato IPM manual. We thank J. Deck of the University of California GIS/ISC Laboratory for technical assistance and L. Drinkwater and K. Osborne for helpful suggestions on data analyses and interpretation.

References

- Adams, N. (1990) The case against organic farming. New Scientist, 127, 68-68.
- Agricultural Issues Center (1988) Agricultural Chemicals in California Plant Production: Are There Alternatives? University of California, Davis, CA.
- Allen, W.W., Coville, P.L. & Osborne, K.H. (1988) Integrated control of insects and mites on strawberries. *Annual Report* of Strawberry Research, pp. 43–61. California Strawberry Advisory Board, Watsonville, CA.
- Altieri, M.A. (1999) The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment, 74, 19–31.
- Avery, D.T. (1995) Saving the Planet with Pesticides and Plastic: The Environmental Triumph of High-Yield Farming. Hudson Institute, Indianapolis, IN.
- Barbosa, P. (1998) Conservation Biological Control. Academic Press, San Diego, CA.
- Basedow, T. (1995) Insect pests, their antagonists and diversity of the arthropod fauna in fields of farms managed at different intensities over a long term – a comparative survey. *Mitteilungen der Deutschen Gesellschaft fur Allgemeine* und Angewandte Entomologie, **10**, 565–572.
- Basedow, T. (1998) The species composition and frequency of spiders (Araneae) in fields of winter wheat grown under different conditions in Germany. *Journal of Applied Entomology*, **122**, 585–590.
- Berry, N.A., Wratten, S.D., McErlich, A. & Frampton, C. (1996) Abundance and diversity of beneficial arthropods in conventional and organic carrot crops in New Zealand. *New Zealand Journal of Crop and Horticultural Science*, 24, 307–313.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 1–19.
- Chamberlain, D.E., Wilson, J.D. & Fuller, R.J. (1999) A comparison of bird populations on organic and conventional farm systems in southern Britain. *Biological Conservation*, 88, 307–320.
- Drinkwater, L.E., Letourneau, D.K., Workneh, F., van Bruggen, A.H.C. & Shennan, C. (1995) Fundamental differences between conventional and organic tomato agroecosystems in California. *Ecological Applications*, **5**, 1098–1112.
- Duelli, P., Obrist, M.K. & Schmatz, D.R. (1999) Biodiversity evaluation in agricultural landscapes: above-ground insects. Agriculture, Ecosystems and Environment, 74, 33–64.
- Feber, R.E., Firbank, L.G., Johnson, P.J. & Macdonald, D.W. (1997) The effects of organic farming on pest and non-pest butterfly abundance. *Agriculture, Ecosystems and Environment*, 64, 133–139.
- Flint, M.L. (1985) Integrated Pest Management for Tomatoes, 2nd edn. University of California IPM Program, Publication 3274. University of California, Division of Agriculture and Natural Resources, Oakland, CA.

Ecological Society, *Journal of Applied Ecology*, **38**, 557–570

© 2001 British

Flint, M.L. & Dreistadt, S.H. (1998) Natural Enemies Handbook. University of California Statewide Integrated Pest Management Project, Publication 3386. University of California, Oakland, CA.

- Hald, A.B. (1999) Weed vegetation (wild flora) of long established organic versus conventional cereal fields in Denmark. *Annals of Applied Biology*, **134**, 307–314.
- Holland, J. & Fahrig, L. (2000) Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agriculture, Ecosystems, and Environment, 78, 115.
- Honek, A. (1997) The effect of plant cover and weather on the activity density of ground surface arthropods in a fallow field. *Entomological Research in Organic Agriculture*, **15**, 203–210.
- Jones, F.G.W. (1976) Pests, resistance and fertilizers. *Fertilizer* Use and Plant Health (ed. V. Taysi), pp. 233–258. Proceedings of the 12th International Potash Institute. Worblaufen-Bern, Switzerland.
- Kromp, B. & Meindl, P. (1997) Entomological research in organic agriculture: summary and recommendations. *Entomological Research in Organic Agriculture*, 15, 373–382.
- Lampkin, N. (1990) Organic Farming. Farming Press, Ipswich, NY. Distributed in North America by Diamond Farm Enterprises.
- Letourneau, D.K. (1997) Plant-arthropod interactions in agroecosystems. *Ecology and Agriculture* (ed. L.E. Jackson), pp. 239–290. Academic Press, New York, NY.
- Letourneau, D.K., Drinkwater, L.E. & Shennan, C. (1996) Effects of soil management on crop nitrogen and insect damage in organic vs. conventional tomato fields. *Agriculture, Ecosystems and Environment*, 57, 179–187.
- McCann, E., Sullivan, S., Ericson, D. & DeYoung, R. (1997) Environmental awareness, economic orientation, and farming practices: comparison of organic and conventional farmers. *Environmental Management*, 21, 747–758.
- McCracken, D.I. & Bignal, E.M. (1998) Applying the results of ecological studies to land-use policies and practices. *Journal of Applied Ecology*, **35**, 961–967.
- Moreby, S.J., Aebischer, N.J., Southway, S.E. & Sotherton, N.W. (1994) A comparison of the flora and arthropod fauna of organically and conventionally grown winter wheat in southern England. *Annals of Applied Biology*, **12**, 13–27.
- National Research Council (1989) *Alternative Agriculture*. National Academy Press, Washington, DC.
- Omerod, S.J. & Watkinson, A.R. (2000) Editors' introduction: birds and agriculture. *Journal of Applied Ecology*, 37, 699-705.
- Osborne, K.H. & Allen, W.W. (1999) Allen-vac: an internal collection bag retainer allows for snag-free arthropod sampling in woody scrub. *Environmental Entomology*, 28, 594–596.
- Pfiffner, L. & Niggli, U. (1996) Effects of bio-dynamic, organic and conventional farming on ground beetles (Col. Carabidae) and other epigaeic arthropods in winter wheat. *Biological Agriculture and Horticulture*, **12**, 353-364.
- Pickett, C.H. & Bugg, R.L. (1998) Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pests. University of California Press, Berkeley, CA.
- Pimentel, D., Krummel, J., Gallahan, D., Hough, J., Merrill, A., Schreiner, I., Vittum, P., Koziol, F., Back, E., Yen, D. & Fiance, S. (1981) A cost-benefit analysis of pesticide use in US food production. *CRC Handbook of Pest Management in Agriculture*, Vol. II. (ed. D. Pimentel), pp. 27–54. CRC Press Inc., Boca Raton, FL.
- Pimentel, D., McLaughlin, L., Zepp, A. & Lakitan, B. (1991) Environmental and economic effects of reducing pesticide use. A substantial reduction in pesticides might increase food costs only slightly. *Bioscience*, **41**, 402–409.
- Reddersen, J. (1997) The arthropod fauna of organic versus conventional cereal fields in Denmark. *Biological Agriculture and Horticulture*, **15**, 61–71.
- Reganold, J. (1989) Farming's organic future. *New Scientist*, **122**, 49–52.
- Roth, D.S., Perfecto, I. & Rathcke, B. (1996) The effects of management systems on ground-foraging ant diversity in

Costa Rica. *Ecosystem Management: Selected Readings* (eds F.B. Samson & F.L. Knopf), pp. 313–330. Springer-Verlag, New York, NY.

- Ryan, M. (1999) Is an enhanced soil biological community, relative to conventional neighbors, a consistent feature of alternative (organic and biodynamic) agricultural systems? *Biological Agriculture and Horticulture*, **17**, 131–144.
- Ryszkowski, L., Karg, J., Margarit, G., Paoletti, M.G. & Zlotin, R. (1993) Above ground insect biomass in agricultural landscapes of Europe. *Landscape Ecology and Agroecosystems* (eds R.G.H. Bunce, L. Ryszkowski & M.G. Paoletti), pp. 71–82. CRC Press/Lewis, Boca Raton, FL.
- SAS Institute Inc. (1993) SAS Companion for the Microsoft Windows Environment, Version 6, 1st edn. SAS Institute Inc., Cary, NC.
- Scriber, J.M. (1984) Nitrogen nutrition of plants and insect invasion. *Nitrogen in Crop Production* (ed. R.D. Hauck), pp. 441–460. American Society of Agronomy, Madison, Wisconsin.
- Shennan, C., Drinkwater, L.E., van Bruggen, A.H.C., Letourneau, D.K. & Workneh, F. (1991) Comparative study

of organic and conventional tomato production systems: an approach to on-farm systems studies. *Sustainable Agriculture Research and Education in the Field: A Proceedings*, pp. 109–132. National Academy Press, Washington, DC.

- Slansky, F. Jr & Rodriguez, J.G. (1987) Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. Wiley, New York, NY.
- Strand, L.L. (1998) Integrated Pest Management for Tomatoes, 4th edn. University of California IPM Program, Publication 3274. University of California, Division of Agriculture and Natural Resources, Oakland, CA.
- Ulen, B. (1999) Simulation of nitrate leaching before and after conversion to ecological farming. *Biological Agriculture* and Horticulture, 17, 59–75.
- Vandermeer, J.H. (1972) Niche theory. Annual Review of Ecology and Systematics, 3, 107–132.
- Vandermeer, J.H. & Perfecto, I. (1995) Breakfast of Biodiversity: The Truth About Rain Forest Destruction. Institute for Food and Development Policy, Oakland, CA.

Received 2 November 1999; revision received 22 November 2000