Agroecology: contributions towards a renewed ecological foundation for pest management

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14.1 Introduction

The integrated pest management concept (IPM) arose in the early 1970s in response to concerns about impacts of pesticides on the environment. By providing an alternative to the strategy of unilateral intervention with chemicals, it was hoped that IPM would change the philosophy of crop protection to one that entailed a deeper understanding of insect and crop ecology, thus resulting in a strategy which relied on the use of several complementary tactics. It was envisioned that ecological theory should provide a basis for predicting how specific changes in production practices and inputs might affect pest problems. It was also thought that ecology could aid in the design of agricultural systems less vulnerable to pest outbreaks. In such systems pesticides would be used as occasional supplements to natural regulatory mechanisms. In fact, many authors wrote papers and reviews depicting the ecological basis of pest management (Southwood and Way, 1976; Price and Waldbauer, 1975; Pimentel and Goodman, 1978; Levins and Wilson, 1979). But despite all this early work, which provided much of the needed ecological foundations, most IPM programs deviated to become schemes of "intelligent pesticide management" and failed in putting ecologically based theory into practice.

Lewis et al. (1997) argue that the main reason why IPM science has been slow to provide the productive understanding that will assist farmers to move beyond the current production methods is that IPM strategies have long been dominated by quests for "magic bullet" products to control pest outbreaks. IPM approaches have not addressed the ecological root causes of pest problems in modern agriculture. There still prevails a narrow view
that specific pests affect productivity, and overcoming such limiting factors via new technologies continues to be the main goal. Emphasis is now placed on purchased biological inputs such as microbial pesticides now widely applied in place of chemical insecticides. This type of technology pertains to a dominant technical approach called input substitution. The thrust is highly technological, characterized by a limiting-factor mentality that has driven conventional agricultural research in the past. Agronomists and other agricultural scientists have for generations been taught the "law of minimum" as a central dogma. According to this dogma, at any given moment there is a single factor limiting yield and the only way to overcome that factor is to use an appropriate external input. Once the hurdle of the first limiting factor has been surpassed (e.g., mites) with a specific insecticide as the correct input, then yields may rise until another factor (e.g., mites) becomes limiting, owing to the elimination of predaceous mites. The factor then requires another input, miticide in this case, and so on, perpetuating a process of treating symptoms rather than dealing with the real causes that evoked ecological imbalance (Altieri and Rosset, 1996). Thus, while understanding the insects' abilities and needs, which explains why pests quickly adapt and succeed in agroecosystems is important, it is more crucial to pinpoint what makes agroecosystems susceptible to pests. By designing agroecosystems that on the one side work against the pests' performance and on the other are less vulnerable to pest invasion, farmers can substantially reduce pest numbers.

It is herein argued that long-term solutions to pest problems can be achieved only by restructuring and managing agricultural systems in ways that maximize the array of "built-in" preventive strengths, with therapeutic tactics serving strictly as backups of natural regulator processes. Lewis et al. (1997) suggested three approaches to bringing pest populations within acceptable bounds by harnessing the inherent strengths within ecosystems: (1) ecosystem management; (2) crop attributes and multi-trophic level interactions; and (3) therapeutic treatments with minimal disruptions. These approaches suppose a deep knowledge of the underlying processes of the managed ecosystem, including the natural factors that suppress pest populations, with the final goal of designing agricultural practices that augment these pest natural regulatory processes. Borrowing concepts from landscape ecology, Thies and Tscherner (1999) argue that approaches to insect management should involve working at a regional scale, recognizing the spatial heterogeneity of the landscape. This strategy requires a cooperative areawide approach, because the sources of pests extend beyond field boundaries and include a variety of landscape elements.

14.2 Agroecology and pest management

One way of further advancing the ecosystem management approach in JPM is through the understanding that crop health and sustainable yields in the agroecosystem derives from the proper balance of crops, soils, nutrients, sunlight, moisture, and co-existing organisms. The agroecosystem is productive and healthy when this balance of rich growing conditions prevail, and when crop plants remain resilient to tolerate stress and adversity. Occasional disturbances can be overcome by vigorous agroecosystems, which are adaptable, and diverse enough to recover once the stress has passed (Altieri and Rosset, 1996). If the cause of disease, pest, soil degradation, etc. is understood as imbalance, then the goal of agroecological treatment is to recover the balance, setting in motion the agroecosystem's natural tendency toward repairing itself. This tendency is known in ecology as homeostasis, the maintenance of the system's internal functions and defense mechanisms to compensate for external stress factors. But achieving and maintaining homeostasis requires a deep understanding of the nature of the agroecosystems and the principles by which they function. Fortunately, there is a new integrative scientific approach which allows for such understanding. Agroecology provides basic ecological principles on how to study, design and manage agroecosystems that are productive, enduring, and natural resource conserving (Altieri, 1995). Agroecology goes beyond a one-dimensional view of agroecosystems, their genetics, agronomy, edaphology, etc. to embrace an understanding of ecological and social levels of co-evolution, structure, and function. Instead of focusing on one particular component of the agroecosystem, agroecology emphasizes the interrelatedness of all agroecosystem components and the complex dynamics of ecological processes such as nutrient cycling and pest regulation (Gliessman, 1999).

From a management perspective, the agroecological objective is to provide a balanced environment, sustainable yields, biologically mediated soil fertility, and natural pest regulation through the design of diversified agroecosystems and the use of low-input technologies (Altieri, 1994). The strategy is based on ecological principles that lead management to optimal recycling of nutrients and organic matter turnover, close energy flows, water and soil conservation, and balanced pest-natural enemy populations. The strategy exploits the complementation that results from the various combinations of crops, trees, and animals in spatial and temporal arrangements (Altieri and Nicholls, 1999). These combinations determine the establishment of a planned and associated functional biodiversity which,
when correctly assembled, delivers key ecological services which subsidize processes that underlie agroecosystem health.

In other words, ecological concepts are utilized to favor natural processes and biological interactions that optimize synergies, so that diversified farms are able to sponsor their own soil fertility, crop protection, and productivity through the activation of soil biology, the recycling of nutrients, the enhancement of beneficial arthropods and antagonists. Based on these principles, agroecologists involved in pest management have developed a framework to achieve crop health through agroecosystem diversification and soil quality enhancement, key pillars of agroecosystem health. The main goal is to enhance the immunity of the agroecosystem (i.e., natural pest control mechanisms) and regulatory processes (i.e., nutrient cycling and population regulation) through management practices and agroecological designs that enhance plant species and genetic diversity in time and space, and the enhancement of organic matter accumulation and biological activity of the soil (Altieri, 1999).

Agroecosystems can be manipulated to improve production and produce more sustainably, with fewer negative environmental and social impacts and fewer external inputs (Altieri, 1995). The design of such systems is based on the application of the following ecological principles (Reinhart et al., 1992).

1. Enhancing recycling of biomass and optimizing nutrient availability and balancing nutrient flow.
2. Securing favorable soil conditions for plant growth, particularly by managing organic matter and enhancing soil biotic activity.
3. Minimizing losses due to flows of solar radiation, air, and water by way of microclimate management, water harvesting, and soil management through increased soil cover.
4. Promoting species and genetic diversification of the agroecosystem in time and space.
5. Enhancing beneficial biological interactions and synergisms among agrobiodiversity components, thus resulting in the promotion of key ecological processes and services.

These principles can be applied by way of various techniques and strategies. Each of these will have different effects on productivity, stability, and resiliency within the farm system, depending on the local opportunities, resource constraints, and, in most cases, on the market. The ultimate goal of agroecological design is to integrate components so that overall biological efficiency is improved, biodiversity is preserved, and agroecosystem productivity and its self-sustaining capacity are maintained.

14.2.1 The ecology of modern mechanized agroecosystems: understanding pest vulnerability

Contemporary agriculture is highly mechanized and has implied the simplification of the structure of the environment over vast areas, replacing nature’s diversity with a small number of cultivated plants. In such systems, genetic manipulation replaces natural processes of plant evolution and selection. Throughout the crop domestication process, humans tended to select plants with fewer morphological and chemical defenses. Such intense human selection for fast growth and high reproductive output resulted in a general lowering of the plants’ allocation to defense. Of course, significant amounts of toxic secondary compounds remain in many edible crops, but the general trend has been the gradual reduction of those chemicals and morphological features that protected plants from arthropod herbivores. This often left crop plants more vulnerable than their wild relatives, and it largely explains the widespread belief that there are more outbreaks of insects in agroecosystems than in natural ecosystems (Feeny, 1976).

Even decomposition is altered since plant growth is harvested and soil fertility maintained, not through nutrient recycling but with fertilizers. It is well known that cultivated plants grown in genetically homogeneous monocultures do not possess the necessary ecological defense mechanisms to tolerate outbreaks of pest populations. Modern agriculturalists have selected crops for high yields and high profitability, making them more susceptible to pests by sacrificing natural resistance for productivity (Robinson, 1996). Due to the simplification of the environment and a reduction in trophic interactions, populations of crop plants in agroecosystems are rarely self-reproducing or self-regulating. Biological diversity is reduced, trophic structures tend to become simplified, and many niches are left unoccupied. The danger of increased invasions and catastrophic pest or disease outbreaks is high, despite the intensive human input in the form of agrochemicals. On the other hand, modern agricultural practices (principally pesticides) negatively affect natural enemies (predators and parasites), which do not thrive well in toxic environments, or do not find the necessary environmental resources and opportunities in monocultures to effectively suppress pests (Altieri, 1994). As long as monocultures are maintained as the structural base of modern agricultural systems, pest problems will continue to be the result of a negative treadmill that reinforces
itself, as vegetational simplification, pesticides residues, and nutrition imbalances caused by excess fertilizers compound pest invasions (Figure 14.1). Thus the major challenge for those advocating ecologically based pest management (EBPM) is to find strategies to overcome the ecological limits imposed by monocultures.

Human manipulation and alteration of ecosystems for the purpose of establishing agricultural production makes agroecosystems structurally and functionally very different from natural ecosystems (Table 14.1). Understanding such differences is instructive, according to several researchers who have postulated that agroecosystems should mimic the structure and function of natural communities (a practice followed by thousands of indigenous farmers for centuries), as these systems exhibit tight nutrient cycling, resistance to pest invasion, and vertical structure, and preserve

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>Agroecosystem</th>
<th>Natural ecosystem</th>
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<tbody>
<tr>
<td>Net productivity</td>
<td>High</td>
<td>Medium</td>
</tr>
<tr>
<td>Trophic chains</td>
<td>Simple, linear</td>
<td>Complex</td>
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<tr>
<td>Species diversity</td>
<td>Low</td>
<td>High</td>
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<tr>
<td>Genetic diversity</td>
<td>Low</td>
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<tr>
<td>Mineral cycles</td>
<td>Open</td>
<td>Closed</td>
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<tr>
<td>Stability (resilience)</td>
<td>Low</td>
<td>High</td>
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<tr>
<td>Entropy</td>
<td>High</td>
<td>Low</td>
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<tr>
<td>Human control</td>
<td>Definite</td>
<td>Not needed</td>
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<tr>
<td>Temporal permanence</td>
<td>Short</td>
<td>Long</td>
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<tr>
<td>Habitat heterogeneity</td>
<td>Simple</td>
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<tr>
<td>Phenology</td>
<td>Synchronized</td>
<td>Seasonal</td>
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<tr>
<td>Maturity</td>
<td>Immature, early successional</td>
<td>Mature, climax</td>
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biodiversity (Ewel, 1986; Soule and Piper, 1992). Browning and Frey (1969) suggested that the exclusive study of agricultural systems can lead to spurious or at least skewed conclusions about pest–crop interactions. He advised researchers to study a natural ecosystem from which knowledge can be gained that is readily applicable to agroecosystems. Most ecologists agree that any pest management approach should try to develop an agroecosystem that emulates later stages of succession (that is, mature communities) as much as possible, for this is how biological stability can be achieved (Root, 1973; van Emden and Williams, 1974; Price and Wadlauer, 1978). This is particularly true in the tropics, where the ecological futility of promoting mechanized monocultures in areas of overwhelming biotic intricacy and where pests flourish year-round, has been amply demonstrated. A more reasonable approach is to imitate natural cycles rather than struggle to impose horticultural simplicity in ecosystems that are inherently complex. Ewel (1986) argues that successional ecosystems can be particularly appropriate templates for the design of sustainable tropical agroecosystems.

14.2.2 Ecological features of modern agroecosystems

Agroecosystems are artificial ecosystems that are solar powered. As are natural ecosystems, but differ in that (1) the auxiliary energy sources that enhance productivity are processed fuels (along with animal and human labor) rather than natural energies; (2) diversity is greatly
reduced by human management in order to maximize yield of specific food and other products; (3) the dominant plants and animals are under artificial rather than natural selection; and (4) control is external and goal oriented rather than internal via subsystem feedback as in natural ecosystems. Some processes that occur in natural ecosystems can be observed, albeit in a much altered way in agroecosystems. Main features of modern agroecosystems relevant to pest management include (Gall and Atkins, 1974; Landis et al., 2000):

1. Landscape simplification: of major significance is the fact that, with agriculture, the original flora and fauna are completely replaced over a vast area. Where patches of natural vegetation persist they often occur on sites unsuitable for agriculture and contribute only minimally to the ecological stability of the area. Such agroecosystems are unfavorable environments for natural enemies; therefore their capacity to control invaders is lower than in more diverse agricultural landscapes. Due to their reduced structural and functional diversity in relation to natural ecosystems, agroecosystems have generally lower resiliency than natural ecosystems.

2. Continuity: one of the most obvious features of intensive agricultural systems is their well-defined spatial arrangement. Agroecosystems usually have clearly defined boundaries. The boundary between cultivated land and the natural ecosystems from which it was carved is also typically well delineated and ecotones are abrupt. Within the converted area there are plots clearly separated by fences, ditches, canals, windbreaks, and access roads. Sometimes a single crop extends over many square miles, but at times a large agricultural area is broken up into a mosaic of plots or a quilt of agroecosystems defining diverse landscapes.

3. Disruption of succession: intensive agriculture prevents normal succession from taking place. Agricultural fields usually represent the first stage of succession where an existing community is disrupted by deforestation and/or plowing, developing a new, simple, immature, human-made plant community at the site that is neither persistent nor steady-state. All tendencies towards complexity (i.e., insect and weed colonization) are suppressed with agrochemicals, keeping succession in check via maintenance of monocultures.

The objective of growing a crop is to obtain the greatest possible harvest. The best means for this is to establish a system for which the ratio between primary production and biomass is at its highest level; that is, one in which little primary production is required for maintenance. To maintain a system of this type, it is necessary for humans to assume responsibility for the costs of maintenance and regulation normally taken care of by the natural processes that lead to the establishment of a climax ecosystem.

4. Adaptability in natural ecosystems the assemblage of organisms is the result of natural selection and co-evolution. Agroecosystems consist of unnatural assemblages of human-selected domesticated species and an assortment of native or imported opportunistic species that manage to invade the site. These two groups have not been integrated into a steady-state system by the process of co-evolution, and the opportunistic species frequently constitute weed, insect, and disease pests that must be dealt with by the farmer.

14.3 Factors triggering insect pest outbreaks in agroecosystems

Given the major differences between mechanized agroecosystems and natural ecosystems, especially the prevalence of monocultures and the high levels of disturbance, modern agricultural systems lack a suitable ecological infrastructure to resist pest invasions and outbreaks (Altieri, 1994; Landis et al., 2000). Many factors underlie the vulnerability of monocultures to pest invasions, as outlined below.

14.3.1 Decreased landscape diversity

The spread of modern agriculture has resulted in tremendous changes in landscape diversity. There has been a consistent trend toward simplification that entails (a) the enlargement of fields; (b) the aggregation of fields; (c) an increase in the density of crop plants; (d) an increase in the uniformity of crop population age structure and physical quality; and (e) a decrease in inter- and intraspecific diversity within the planted field. Although these trends appear to exist worldwide, they are more apparent, and certainly best documented, in industrialized countries. Increasingly, evidence suggests that these changes in landscape diversity have led to more insect outbreaks due to the expansion of monocultures at the expense of natural vegetation, through decreasing habitat diversity. One of the main characteristics of the modern agricultural landscape is the large size and homogeneity of crop monocultures, which fragment the natural landscape. Massive expansion and increases in production of crops such as coffee, cocoa, rice, soybean, and oil palm in various regions of the developing world led
to major environmental degradation and loss of biodiversity, especially in bird populations (Donald, 2004). Such agricultural intensification can also directly affect the abundance and diversity of natural enemies, as the larger the area under monoculture the lower the viability of a given population of beneficial fauna. At hand is also the issue of colonization of crop "islands" by insects. In the case of annual crops, insects must colonize from the borders each season, and the larger the field, the greater is the distance that must be covered. Several studies suggest (not surprisingly) that natural enemies tend to colonize after their host/prey and that the lag time between the arrival of pest and natural enemy increases with distance from border (source pool). For instance, Price (1976) found that the first occurrence of an herbivore and that of a predatory mite in a soybean field were separated by one week on the edge versus a three week lag in the center. To the extent that this is a general phenomenon, increased field size should lead to more frequent insect outbreaks.

14.3.2 Decreased on-farm plant diversity

Many ecologists have conducted experiments testing the theory that decreased plant diversity in agroecosystems allows greater chance for invasive species to colonize, subsequently leading to enhanced herbivorous insect abundance. Many of these experiments have shown that mixing certain plant species with the primary host of a specialized herbivore gives a fairly consistent result: specialized species usually exhibit higher abundance in monocultures than in diversified crop systems (Andrews, 1983).

Several reviews have been published documenting the effects of within-habitat diversity on insects (Altieri and Letourneau, 1984; Risch et al., 1983). Two main ecological hypotheses (the natural enemy hypothesis and the resource concentration hypothesis), have been offered to explain why insect populations tend to explode in monocultures and how in agroecosystems insect populations can be stabilized by constructing vegetational architectures that support natural enemies and/or that directly exert inhibitory effects on pest attacks (Root, 1973). A recent study in Portugal illustrates the effects of decreased on-farm plant diversity on increased pest incidence. As new policy and market forces prompt the conversion of traditional complex agroforest vineyard systems to monocultures, Altieri and Nicholls (2002) found higher prevalence of grape herbivores and Bynyi cutworm. Although monocultures may be productive, such gains occurred at the expense of biodiversity and agricultural sustainability, reflected on higher pest vulnerability.

14.3.3 Pesticide-induced insect outbreaks

Many examples are reported in the literature of insect pest outbreaks and/or resurgence following insecticide applications (Pimentel and Peskin, 1980). Pesticides either fail to control the target pests or create new pest problems. Development of resistance in insect pest populations is the main way in which pesticide use can lead to pest control failure. More than 500 species of arthropods have become resistant to one or more insecticide or acaricide (Van Driesche and Bellows, 1996).

Another way in which pesticide use can foster outbreaks of pests is through the elimination of the target pest's natural enemies. Predators and parasitoids often experience higher mortality than herbivores following a given spray (Morse et al., 1987). This is due, in part, to the greater mobility of many natural enemies, which exposes them to more insecticide per unit time following a spray.

In addition, natural enemies appear to evolve resistance to insecticides much more slowly than herbivores. As a consequence there is a lower probability that some individuals in populations of natural enemies will have genes for insecticide resistance. This in turn is due to the much smaller size of the natural enemy population relative to the pest population and the different evolutionary history of natural enemies and herbivores. Pesticides also create new pest problems when natural enemies of ordinarily non-economic species are destroyed by chemicals. These "secondary pests" then reach higher density than normal and begin to cause economic damage (Pimentel and Lehman, 1993).

14.3.4 Fertilizer-induced pest outbreaks

Luna (1988) suggested that the physiological susceptibility of crops to insects might be affected by the form of fertilizer used (organic vs. chemical fertilizer). Studies documenting lower abundance of several insect herbivores in organic farming systems have partly attributed such reduction to low nitrogen content in the organically farmed crops. In comparative studies, conventional crops (treated with chemical fertilizer) tend to develop a larger infestation of insects (especially Homoptera) than organic counterparts. Interestingly, it has been found that certain pesticides can also alter the nutritional biochemistry of crop plants by changing the concentrations of nitrogen, phosphorus, and potassium, by influencing the production of sugars, free amino acids, and proteins, and by influencing the aging process which affects surface hardness, drying, and wax deposition (Oka and Pimentel, 1976; Rodriguez et al., 1957).
14.2.5 Weather-induced insect pest outbreaks

Some authors argue that weather can be the most important factor triggering insect outbreaks (Milne, 1957). For example, Miyasita (1963), in reviewing the dynamics of seven of the most serious insect pests in Japanese crops, concluded that weather was the principal cause of the outbreaks in each case. There are several ways in which weather can trigger insect outbreaks. Perhaps the most straightforward mechanism is direct stimulation of the insect and/or host plant physiology. The development and widespread use of degree-day models to predict outbreaks of particular pests and appropriate control strategies are an indication of the importance of the linkage between temperature and growth and the development of herbivorous insects and their host plants. Gutierrez et al. (1974) have shown that weather plays a key role in the development of cowpea aphid populations in southeast Australia. In this case, a series of climatic events favors complex changes in aphid physiological development, migration, and dispersal in such a way as to cause localized outbreaks.

14.2.6 Transgenic crops and insect pest outbreaks

In the last six years, transgenic crops have expanded in area, reaching today about 42 million hectares worldwide. Such areas are dominated by monocultures of few crop varieties, mainly herbicide-resistant soybeans and Bt corn, with a clear tendency toward increased agricultural habitat diversity (Marvier, 2001). Agroecologists have argued that such massive and rapid deployment of transgenic crops will exacerbate the problems of conventional modern agriculture (Rissler and Mellon, 1996; Altieri, 2000). At issue is the genetic homogeneity of fields with bioengineered crops which in turn can make such systems increasingly vulnerable to pest and disease problems (NAS, 1972). Transgenic crops affect natural enemies in several ways; the enemy species may feed directly on corn tissues (e.g. pollens) or on hosts that have fed on Bt corn, or host populations may be reduced. By keeping Lepidoptera pest populations at extremely low levels, Bt crops could potentially starve natural enemies, as predators and parasitic wasps that feed on pests need a small amount of prey to survive in the agroecosystem. Among the natural enemies that live exclusively on insects which the transgenic crops are designed to kill (Lepidoptera), egg and larval parasitoids would be most affected because they are totally dependent on live hosts for development and survival, whereas some predators could theoretically thrive on dead or dying prey (Schuler et al., 1999). In a two-year field study in Iowa, abundance of parasitoid species Macrocentrus vicarius, which is specific to corn borer larvae, was found to be lower in Bt cornfields than in non-Bt fields, as might be expected because of significant reductions in larval hosts in Bt corn (Groot and Dicke, 2002).

Natural enemies could also be affected directly through inter-trophic level effects of the toxin. The potential of Bt toxins moving through arthropod food chains poses serious implications for natural biocontrol in agricultural fields. Recent evidence shows that the Bt toxin can affect beneficial insect predators that feed on insect pests present in Bt crops. According to Groot and Dicke (2002) natural enemies may come in contact more often with Bt toxins via non-target organisms, because the toxins do not bind to receptors on the midgut membrane in the non-target herbivores. Studies in Switzerland showed that mean total mortality of predaceous lacewing larvae (Chrysopidae) raised on Bt-fed prey was 62% compared to 37% when raised on Bt-free prey. These Bt prey fed Chrysopidae also exhibited prolonged development time throughout their immature life stage (Hilbech et al., 1998). The observed sublethal effect shows scope for the fitness of natural enemies to be indirectly affected by Bt toxins expressed in transgenic crops via feeding on suboptimal food or because of host death and scarcity (Groot and Dicke, 2002). Moreover, the toxins produced in Bt plants may be passed on to predators and parasitoids in pollen or leaf tissue.

These findings are of concern to small and organic farmers who rely for insect pest control on the rich complex of predators and parasitoids associated with the mixed cropping systems (Altieri, 1994). Inter-trophic level effects of the Bt toxin raise serious concerns about the potential of the disruption of natural pest control. Polyphagous predators that move within and between mixed crop cultivars will encounter Bt-containing non-target prey throughout the crop season (Altieri, 2000). Disrupted biocontrol mechanisms may result in increased crop losses due to invasive pests or to the increased use of pesticides by farmers, with consequent health and environmental effects.

Despite all the pressures for US farmers to adopt this technology, benefits of using transgenic corn are not assured because population densities of the European corn borer (ECB) are not predictable. Due to this and other factors, the use of transgenic corn has not significantly reduced insecticide use in most of the corn-growing areas of the Midwest. Until 2001, the percentage of field corn treated with insecticides in the United States remained at approximately 30%, despite a significant increase in the hectares of Bt corn planted (Obycky et al., 2001). Moreover, the potential benefits of Bt crops are now in question given that the high-dose-refuge strategy for delaying pest resistance is threatened from the contamination of refuges by...
transgenic maize. Variable Bt toxin production in seeds of refuge plants undermines the refuge strategy and could accelerate pest resistance to Bt crops (Chilcutt and Tabashnik, 2004).

14.4 Reinstating ecological rationale in modern agriculture

The instability of agroecosystems, manifesting as the worsening of most insect pest problems (and therefore greater dependence on external inputs), is increasingly linked to the expansion of crop monocultures (Altieri, 1994). Plant communities that are modified to meet the special needs of humans become subject to heavy pest damage and generally the more intensely such communities are modified, the more abundant and serious the pests. The inherent self-regulation characteristics of natural communities are lost when humans modify such communities by promoting monocultures. Some agroecologists maintain that this breakdown can be repaired by the addition or enhancement of plant biodiversity at the field and landscape level (Gliessman, 1999; Altieri, 1999).

Emergent ecological properties develop in diversified agroecosystems allowing biodiversity to thrive and establish complex food webs and interactions. But biodiversity must be accompanied by improvement of soil quality, as the link between healthy soils and healthy plants is fundamental to truly ecologically based IPM. The lower pest levels widely reported in organic-farming systems may, in part, arise from plant–insect resistance mediated by biochemical or mineral–nutrient dynamics typical of crops under such management practices. Results from such studies provide interesting evidence to support the view that the long-term joint management of plant diversity and soil organic matter can lead to better plant resistance against insect pests (Retouneaud and Goldstein, 2001).

14.5 Harmonizing soil and plant health in agroecosystems

Although the integrity of the agroecosystem relies on synergies of plant diversity and the continuing function of the soil microbial community, and its relationship with organic matter (Altieri and Nicholls, 1999), the evolution of IPM and integrated soil fertility management (ISFM) have proceeded separately. This has prevented many scientists from realizing that most pest management methods used by farmers can also be considered soil fertility management strategies and vice versa. There are positive interactions between soils and pests that once identified can provide guidelines for optimizing total agroecosystem function (Figure 14.2). Increasingly, new research suggests that the ability of a crop plant to resist or tolerate insect pests and diseases is tied to optimal physical, chemical, and mainly biological properties of soils. Soils with high organic matter and active soil biological activity generally exhibit good soil fertility as well as complex food webs and beneficial organisms that prevent infection (Maggoff et al., 2000). Studies in tropical Asian irrigated rice agroecosystems by Settle et al. (1996) showed that, by increasing organic matter in test plots, researchers could boost populations of detritivores and plankton-feeders, and in turn significantly boost the abundance of generalist predators. Surprisingly, organic matter management proved to be a key mechanism in the support of high levels of natural biological control. Organically managed soils usually exhibit a richer community of natural enemies that feed on alternative prey found above or within the soil. Collembola have been shown to be an important prey group for generalist predators, such as the ground beetle limniontus laevis (Bilde et al., 2000) and lynx spider spiders in arable fields, helping to sustain and retain these predators as pest control agents within the crop (Bilde et al., 2000). Such relationships and mechanisms have been ignored by scientists as important elements in pest management.

Much of what we know today about the relationship between crop nutrition and pest incidence comes from studies comparing the effects of organic agricultural practices and modern conventional methods on specific pest populations. Soil fertility practices can impact the physiological susceptibility of crop plants to insect pests by either affecting the resistance of individual plants to attack or by altering plant acceptability.
to certain herbivores. Some studies have also documented how the shift from organic soil management to chemical fertilizers has increased the potential of certain insects and diseases to cause economic losses (Phelan et al., 1995).

14.5.1 The effects of nitrogen fertilization on insect pests

The indirect effects of fertilization practices acting through changes in the nutrient composition of the crop have been reported to influence plant resistance to many insect pests. Among the nutritional factors that influence the level of arthropod damage in a crop, total nitrogen (N) has been considered critical for both plants and their consumers (Matson, 1980; Scriber, 1984; Slansky and Rodriguez, 1987).

In most studies evaluating aphid and mite response to N fertilization, increases in nitrogen rates dramatically increased aphid and mite numbers. According to van Emden (1966), increases in fecundity and developmental rates of the green peach aphid, Myzus persicae, were highly correlated to increased levels of soluble nitrogen in leaf tissue. Several other authors have also indicated increased aphid and mite populations from nitrogen fertilization (Tables 14.2 and 14.3). Herbivorous insect populations associated with Brassica crop plants have also been reported to increase in response to increased soil nitrogen levels (Table 14.4).

In a two-year study, Brodeck et al. (2001) found that populations of the thrips Frankliniella occidentalis were significantly higher on tomatoes that received higher rates of nitrogen fertilization. Seasonal trends in F. occidentalis

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Mite species</th>
<th>Crop</th>
<th>Numerical response of insect</th>
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<tbody>
<tr>
<td>N</td>
<td>Panonychus ulmi</td>
<td>Apple</td>
<td>+</td>
</tr>
<tr>
<td>N</td>
<td>Tetramyces urticae</td>
<td>Apple</td>
<td>+</td>
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<tr>
<td>N</td>
<td>T. urticae</td>
<td>Beets</td>
<td>+</td>
</tr>
<tr>
<td>N, P, K</td>
<td>Tetranychidae spp.</td>
<td>Beets/peaches</td>
<td>+</td>
</tr>
<tr>
<td>N</td>
<td>T. urticae</td>
<td>Tomato</td>
<td>+</td>
</tr>
<tr>
<td>N, P, K</td>
<td>T. urticae</td>
<td>Apples</td>
<td>++/–</td>
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<tr>
<td>N</td>
<td>Brevicoryne brassicae</td>
<td>Beets</td>
<td>++/–</td>
</tr>
<tr>
<td>N, Ca</td>
<td>Iphisechinus kueneni</td>
<td>Beets</td>
<td>++/–</td>
</tr>
</tbody>
</table>

+ Indicates increase in density with increasing rates of fertilizer element.
- Indicates decrease in density with increasing rates of fertilizer element.

Table 14.3. Summary of effects of inorganic fertilizers on aphid abundance from selected studies (Luna, 1980)

<table>
<thead>
<tr>
<th>Nutrients</th>
<th>Insect</th>
<th>Crop</th>
<th>Numerical response of insect</th>
</tr>
</thead>
<tbody>
<tr>
<td>N, P</td>
<td>Myzus persicae</td>
<td>Tobacco</td>
<td>+/–</td>
</tr>
<tr>
<td>N</td>
<td>S. graminum (greenbug)</td>
<td>Oats</td>
<td>–</td>
</tr>
<tr>
<td>N, Lime</td>
<td>S. graminum</td>
<td>Oats</td>
<td>–</td>
</tr>
<tr>
<td>N</td>
<td>Rhopalosiphum maidis</td>
<td>Soybeans</td>
<td>+</td>
</tr>
<tr>
<td>N, K, Ca</td>
<td>Myzus persicae</td>
<td>Brussels sprouts</td>
<td>++/–</td>
</tr>
<tr>
<td>N, P</td>
<td>Tetranychidae plantarum</td>
<td>Aldilis</td>
<td>+/–</td>
</tr>
</tbody>
</table>

+ Indicates increase in density with increasing rates of fertilizer element.
- Indicates decrease in density with increasing rates of fertilizer element.

Table 14.4. Response of herbivores to increased soil nitrogen levels on Brassica host plant (Letourneau, 1988)

<table>
<thead>
<tr>
<th>Host plant</th>
<th>Herbivore species</th>
<th>Factor</th>
<th>Response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brussels sprouts</td>
<td>Myzus persicae</td>
<td>No. progeny</td>
<td>Increase</td>
</tr>
<tr>
<td>Brussels sprouts</td>
<td>Necrocerus tristis</td>
<td>No. progeny</td>
<td>Increase</td>
</tr>
<tr>
<td>Rape</td>
<td>Artiepis nigri</td>
<td>Occupation frequency</td>
<td>Increase</td>
</tr>
<tr>
<td>Kale and cabbage</td>
<td>A. rapax</td>
<td>Occupation frequency</td>
<td>Increase</td>
</tr>
<tr>
<td>Kale</td>
<td>A. rapax</td>
<td>Occupation frequency</td>
<td>Increase</td>
</tr>
<tr>
<td>Cabbage</td>
<td>A. rapax</td>
<td>Growth rate</td>
<td>Increase</td>
</tr>
<tr>
<td>Cabbage</td>
<td>A. rapax</td>
<td>Growth rate ultimate size</td>
<td>Increase</td>
</tr>
<tr>
<td>Cabbage</td>
<td>Plutella xylostella</td>
<td>Feeding preference</td>
<td>Increase</td>
</tr>
</tbody>
</table>

on tomato were found to be correlated to the number of flowers per host plant and changed with the nitrogen status of flowers. Plants subjected to higher fertilization rates produced flowers that had higher nitrogen content as well as variations in several amino-acid profiles that coincided with peak thrip population density. Abundance of F. occidentalis (particularly adult females) was most highly correlated to flower concentrations of phenylalanine during population peaks. Other insect populations found to increase
following N fertilization included fall armyworm in maize, corn earworm on cotton, pear psylla (Cacopsylla pricina) on pear, Comstock mealybug (Pseudococcus comstockii) on apple, and European corn borer (Ostrinia nubilalis) on field corn (Luna, 1988).

In contrast, because plants are a source of nutrients to herbivorous insects, an increase in the nutrient content of the plant may be argued to increase its acceptability as a food source to pest populations. Variations in herbivore response may be explained by differences in the feeding behavior of the herbivores themselves (Frentzen and Warnke, 1989). For example, with increasing nitrogen concentrations in creosote bush (Larrea tridentata) plants, populations of sucking insects were found to increase, but the number of chewing insects declined. With higher nitrogen fertilization, the amount of nutrients in the plant increases, as well as the amount of secondary compounds that may selectively affect herbivores feeding patterns. Thus protein digestion inhibitors that are found to accumulate in plant cell vacuoles are not consumed by sucking herbivores, but will harm chewing herbivores (Mattson, 1980).

In reviewing 50 years of research relating to crop nutrition and insect attack, Scriber (1984) found 135 studies showing increased damage and/or growth of leaf-chewing insects or mites in N-fertilized crops, vs. fewer than 50 studies in which herbivore damage was reduced by normal fertilization regimens. In aggregate, these results suggest a hypothesis with implications for fertilizer use patterns in agriculture, namely that high N inputs can precipitate high levels of herbivore damage in crops. As a corollary, crop plants would be expected to be less prone to insect pests and diseases if organic soil amendments are used, these generally resulting in lower N concentrations in the plant tissue.

Letourneau (1988), however, questioned if the “nitrogen-damage” hypothesis, based on Scriber’s review, could be extrapolated to a general warning about fertilizer inputs associated to insect pest attack in agroecosystems. Of 100 studies of insects and mites on plants treated experimentally with high and low N fertilizer levels, Letourneau found two-thirds (67–100) of the insect and mite studies to show an increase in growth, survival, reproductive rate, population densities or plant damage levels in response to increased N fertilizer. The remaining third of the arthropods studied showed either a decrease in damage with fertilizer N or no significant change. The author also noted that experimental design can affect the types of responses observed, suggesting that more reliable data emerged in experiments conducted in field plots, using damage level, population levels, and reproductive rate in individual insect species as best predictors of insect response to increase N.

14.5.2 The dynamics of insect herbivores in organically managed systems

Studies documenting lower abundance of several insect herbivores in low-input systems have partly attributed such reductions to the lower nitrogen content in organically farmed crops (Lampkin, 1990). In Japan, density of immigrants of the planthopper species Sogataeia foretula was significantly lower and the settling rate of female adults and survival rate of immature stages of ensuing generations were generally lower in organic, compared with conventional, rice fields. Consequently, the density of planthopper nymphs and adults in the ensuing generations was found to decrease in organically farmed fields (Kajimura, 1998). In India, the introduction of high-yielding Green Revolution rice varieties was accompanied by increased and more frequent inputs of fertilizers. In Tamil Nadu, the consumption of NPK (nitrate/phosphate/potassium) fertilizers increased from 296, 000 MT in 1970–1 to 791, 000 MT in 1996–7. Surprisingly, those changes unexpectedly influenced mosquito breeding and thereby affected the incidence of mosquito-borne disease. Victor and Reuben (2000) found that the application of urea in rice fields significantly increased the population densities of mosquito larvae and pupae (anophelines as well as culicines) in a dose-related manner. In contrast fields treated with organic fertilizers (farmyard manure or green manure from blue-green algae) exhibited significantly lower population densities of mosquito immatures.

In England, conventional winter wheat fields exhibited a larger infestation of the aphid Myzus persicae than their organic counterpart. The conventionally fertilized wheat crop also had higher levels of free protein amino acids in its leaves during June, which were attributed to a nitrogen top dressing applied early in April. However, the difference in the aphid infestations between crops was attributed to the aphid’s response to the relative proportions of certain non-protein to protein amino acids present in the leaves at the time of aphid settling on crops (Bowalski and Visser, 1979). The authors concluded that chemically fertilized winter wheat was more palatable than its organically grown counterpart; hence the higher level of infestation.

In greenhouse experiments, when given a choice of maize grown on organic versus chemically fertilized soils collected from three nearby farms, European corn borer (Ostrinia nubilalis) females laid significantly more eggs...
in the chemically fertilized plants (Phelean et al., 1995). Interestingly, there was significant variation in egg laying among chemical fertilizer treatments within the conventionally managed soil, but in plants under the organic soil management, egg laying was uniformly low. Pooling results across all three farms showed that variance in egg laying was approximately 18 times higher among plants in conventionally managed soil than among plants grown under an organic regime. The authors suggested that this difference is evidence for a form of biological buffering characteristically found more commonly in organically managed soils.

Altieri et al. (1998) conducted a series of comparative experiments on various growing seasons between 1989 and 1996 in which broccoli was subjected to varying fertilization regimes (conventional vs. organic). The goal was to test the effects of different nitrogen sources on the abundance of the key insect pests, cabbage aphid (Brevicoryne brassicae) and flea beetle (Phyllotreta cruciferae). Conventionally fertilized monoculture consistently developed a larger infestation of flea beetles and in some cases of the cabbage aphid, than the organically fertilized broccoli systems. The reduction in aphid and flea beetle infestations in the organically fertilized plots was attributed to lower levels of free nitrogen in the foliage of plants. This further supports the view that insect pest preference can be moderated by alterations to the type and amount of fertilizer used.

By contrast, a study comparing the population responses of Brassica pests to organic versus synthetic fertilizers, measured higher Phyllotreta flea beetle populations on sludge-amended collard (Brassica oleracea) plots early in the season compared with mineral-fertilizer-amended and unfertilized plots (Colliney and Pimentel, 1986). However, later in the season, in those same plots, insect population levels were lowest in organic plots for beetles, aphids and lepidopteran pests. This suggests that the effects of fertilizer type vary with plant growth stage and that organic fertilizers do not necessarily diminish pest populations but, at times, may increase them. For example, in a survey of California tomato producers, despite the pronounced differences in plant quality (N content of leaflets and shoots) both within and among tomato fields, Letourneau et al. (1996) found no indication that greater concentrations of tissue N in tomato plants were associated with higher levels of insect damage.

14.6 Conversion

In reality, the implementation of an IPM strategy usually occurs while an agroecosystem is undergoing a process of conversion from a high-input conventional management system to a low-external-input system. This conversion can be conceptualized as a transitional process with three marked phases (MacRae et al., 1990).

1. Increased efficiency of input use as emphasized by traditional integrated pest management.
2. Input substitution or substitution of environmentally benign inputs for agrochemical inputs as practiced by many organic farmers.
3. System redesign: diversification with an optimal crop/animal assemblage, which encourages synergism so that the agroecosystem may sponsor its own soil fertility, natural pest regulation, and crop productivity.

Many of the practices currently being promoted as components of IPM fall in categories 1 and 2. Both of these stages offer clear benefits in terms of lower environmental impacts as they decrease agrochemical input use and often can provide economic advantages compared to conventional systems. Incremental changes are likely to be more acceptable to farmers as drastic modifications that may be viewed as highly risky or requiring complicated management. But does the adoption of practices that increase the efficiency of input use or that substitute biologically based inputs for agrochemicals, which leaves the monoculture structure intact, really have the potential to lead to the productive redesign of agricultural systems?

In general, the fine-tuning of input use through IPM does little to move farmers toward an alternative to high input systems. In most cases IPM translates to “intelligent pesticide management” as it results in selective use of pesticides according to a pre-determined economic threshold, which pests often “surpass” in monoculture situations. On the other hand, input substitution follows the same paradigm of conventional farming: overcoming the limiting factor, but this time with biological or organic inputs. Many of these “alternative inputs” have become commodified, therefore farmers continue to be dependent on input suppliers, many of a corporate nature (Altieri and Rosset, 1996).

System redesign, on the contrary, arises from the transformation of agroecosystem function and structure by promoting management guided to ensure fundamental agroecosystem processes. Promotion of biodiversity within agricultural systems is the cornerstone strategy of system redesign, as research has demonstrated that higher diversity (genetic, taxonomic, structural, resource) within the cropping system leads to higher diversity in associated biota, usually leading to more effective pest control and...
tighter nutrient cycling. As more information about specific relationships between biodiversity, ecosystem processes, and productivity in a variety of agricultural systems is accumulated, design guidelines can be developed further and used to improve agroecosystem sustainability and resource conservation.

14.7 Syndromes of production

One of the frustrations of research in sustainable agriculture has been the inability of lowinput practices to outperform conventional practices in side-by-side experimental comparisons, despite the success of many extant commercial organic and low-input production systems (Vandermeer, 1997). A potential explanation for this paradox was offered by Andow and Hidas (1989) in their description of "syndromes of production". These researchers compared the traditional shizukuri system of rice (Oryza sativa) production with the contemporary Japanese high input system. Although rice yields were comparable in the two systems, management practices differed in almost every respect: irrigation practice, transplanting technique, plant density, fertility source and quantity, and management of insects, diseases, and weeds. Andow and Hidas (1989) argued that systems like shizukuri function in a qualitatively different way than conventional systems. This array of cultural technologies and pest management practices result in functional differences that cannot be accounted for by any single practice.

Thus a production syndrome is a set of management practices that are mutually adaptive and lead to high performance. However, subsets of this collection of practices may be substantially less adaptive; that is, the interaction among practices leads to improved system performance that cannot be explained by the additive effects of individual practices. In other words, each production system represents a distinct group of management techniques and, by implication, ecological relations. This re-emphasizes the fact that agroecological designs are site-specific and what may be applicable elsewhere are not the techniques but rather the ecological principles that underlie sustainability. It is of no use to transfer technologies from one site to another, if the set of ecological interactions associated with such techniques cannot be replicated.

14.8 Diversified agroecosystems and pest management

Diversified cropping systems, such as those based on intercropping and agroforestry or cover cropping of orchards, have been the target of much research recently. This interest is largely based on the emerging evidence that these systems are more stable and more resource conserving (Vandermeer, 1998). Much of these attributes are connected to the higher levels of functional biodiversity associated with complex farming systems. As diversity increases, so do opportunities for coexistence and beneficial interference between species that can enhance agroecosystem sustainability (van Emden and Williams, 1974). Diverse systems encourage complex food webs which entail more potential connections and interactions among members, and many alternative paths of energy and material flow through it. For this and other reasons a more complex community exhibits more stable production and less fluctuations in the numbers of undesirable organisms. Studies further suggest that the more diverse the agroecosystems and the longer this diversity remains undisturbed, the more internal links develop to promote greater insect stability. It is clear, however, that the stability of the insect community depends not only on its trophic diversity, but also on the actual density-dependence nature of the trophic levels (Southwood and Way, 1970). In other words, stability will depend on the precision of the response of any particular trophic link to an increase in the population at a lower level. Recent studies conducted in grassland systems suggest, however, that there are no simple links between species diversity and ecosystem stability, despite empirical evidence that increasing the richness of a particular guild of natural enemies can reduce the diversity of a widespread group of herbivorous pests (Cardinale et al., 2003). What is apparent is that functional characteristics of component species are as important as the total number of species in determining processes and services in ecosystems (Tilman et al., 1996). This latest finding has practical implications for agroecosystem management. If it is easier to mimic specific ecosystem processes rather than duplicate all the complexity of nature, then the focus should be placed on a specific biodiversity component that plays a specific role, such as a plant that fixes nitrogen, provides cover for soil protection or harbors resources for natural enemies. In the case of farmers without major economic and resource limits and who can withstand a certain risk of crop failure, a crop rotation or a simple polyculture may be all it takes to achieve a desired level of stability. But in the case of resource-poor farmers, who can not tolerate crop failure, highly diverse cropping systems would probably be the best choice. The obvious reason is that the benefit of complex agroecosystems is low risk; if a species falls to disease, pest attack or weather, another species is available to fill the void and maintain full use of resources. Thus there are potential ecological benefits to having several species
in an agroecosystem: compensatory growth, full use of resources and nutrients, and pest protection (Jewel, 1999).

14.8.1 Plant diversity and insect pest incidence

An increasing body of literature documents the effects that plant diversity has on the regulation of insect herbivore populations by favoring the abundance and efficacy of associated natural enemies (Altieri and Letourneau, 1984). Research has shown that mixing certain plant species usually leads to density reductions of specialized herbivore. In a review of 150 published investigations, Risch et al. (1983) found evidence to support the notion that specialized insect herbivores were less numerous in diverse systems (53% of 198 cases). In another comprehensive review 209 published studies that deal with the effects of vegetation diversity in agroecosystems on herbivore arthropod species. Andow (1991) found that 52% of the 287 total herbivore species examined in these studies were less abundant in polycultures than in monocultures, while only 13.5% (44 species) exhibited higher densities in polycultures. In a more recent review of 287 cases, Helenius (1998) found that the reduction of monophagous pests was greater in perennial systems, and that the reduction of polyphagous pest numbers was less in perennial than in annual systems. Helenius (1998) concluded that monophagous (specialists) insects are more susceptible to crop diversity than polyphagous insects. He cautioned about the increased risk of pest attack if the dominant herbivore fauna in a given agroecosystem is polyphagous.

The ecological theory relating to the benefits of mixed versus simple cropping systems involves around two possible explanations of how insect pest populations attain higher levels in monoculture systems compared with diverse ones. The two hypotheses proposed by Root (1973) are as follows.

1. The natural enemy hypothesis, which argues that pest numbers are reduced in more diverse systems because the activity of natural enemies is enhanced by environmental opportunities prevalent in complex systems.

2. The resource concentration hypothesis argues that the presence of a more diverse flora has direct negative effects on the ability of the insect pests to find and utilize its host plant and also to remain in the crop habitat.

The resource concentration hypothesis predicts lower pest abundance in diverse communities because a specialist feeder is less likely to find its host plant due to the presence of confusing masking chemical stimuli, physical barriers to movement or other environmental effects such as shading: it will tend to remain in the intercrop for a shorter period of time simply because the probability of landing on a non-host plant is increased; it may have a lower survivorship and/or fecundity (Bach, 1980). The extent to which these factors operate will depend on the number of host plant species present and the relative preference of the pest for each, the absolute density and spatial arrangement of each host species, and the interference effects from more host plants.

The natural enemy hypothesis attributes lower pest abundance in intercropped or more diverse systems to a higher density of predators and parasitoids (Bach, 1980). The greater density of natural enemies is caused by an improvement in conditions for their survival and reproduction, such as a greater temporal and spatial distribution of nectar and pollen sources, which can increase parasitoid reproductive potential and abundance of alternative host/prey when the pest species are scarce or at inappropriate stages (Risch, 1983). Diversification can increase the effectiveness of specialist parasitoids on a given target herbivore as a result of them spilling over from herbivores on one host plant species to herbivores on the crop (Fentling et al., 2003). These factors can, in theory, combine to provide more favorable conditions for natural enemies and thereby enhance their numbers and effectiveness as control agents.

Some researchers have been busy figuring out which of the two hypotheses is the most important for influencing the relative abundance of pest insects in diverse systems. The question has been approached in two ways: (a) reviews of the literature relating to crop diversity and pest abundance; and (b) by experimentation. Risch et al. (1983) concluded that the resource concentration hypothesis was the most likely explanation for reductions in pest abundance in diverse systems. However, 19 studies that tested the natural enemy hypothesis were reviewed by Russell (1989), who found that, of these 19 studies, mortality rates from predators and parasitoids in diverse systems were higher in nine, lower in two, unchanged in three and variable in five. Russell (1989) concluded that the natural enemy hypothesis is an operational mechanism, but he considered the two hypotheses complementary. In studies of crop/weed systems, Balidava (1985) found that 56% of pest reductions in weed diversified cropping systems were caused by natural enemies. A recent review by Sunderland and Sime (2000) showed that spider abundance was increased by diversification in 63% of studies. The literature supports that spiders tend to remain in diversified patches and that extending diversification throughout the whole crop offers the best prospects for improving pest control.
One of the major problems has been predicting which cropping systems will reduce pest abundance, since not all combinations of crops will produce the desired effect and blind adherence to the principle that a more diversified system will reduce pest infestation is clearly inadequate and often totally wrong (Gurr et al., 1998). To some researchers this indicates the need for caution and a greater understanding of the mechanisms involved to explain how, where, and when such exceptions are likely to occur. It will only be through more detailed ecological studies that such an understanding can be gained and an appropriate predictive theory developed. This means that a greater emphasis has to be placed on ecological experiments rather than on purely descriptive comparative studies.

14.8.2 Recent practical case studies

Despite some of the above mentioned knowledge gaps, many studies have transcended the research phase and have found applicability to regulate specific pests. Examples include:

1. Researchers working with farmers in ten townships in Yunnan, China, covering an area of 5350 hectares, encouraged farmers to switch from rice monocultures to planting variety mixtures of local rice with hybrids. Enhanced genetic diversity reduced blast incidence by 94% and increased total yields by 89%. By the end of two years, it was concluded that fungicides were no longer required (Zhu et al., 2000; Wolfe, 2000).

2. In Africa, scientists at ICIPE (International Center of Insect Physiology and Ecology) developed a habitat management system for stem borers control, which uses two kinds of crops planted together with maize: a plant that repels these borers (the push) and another that attracts (pulls) them (Khan et al., 1998). The push-pull system has been tested on over 450 farms in two districts of Kenya and has now been released for uptake by the national extension systems in East Africa. Participating farmers in the breadbasket of Trans-Nzoia are reporting a 15-20% increase in maize yield. In the semi-arid Suba district, plagued by both stemborers and the parasitic weed Striga, a substantial increase in millet yield has occurred in the last four years, with farmers now being able to support grade cows on the fodder produced. When farmers plant maize, napier, and Desmodium together, a return of US$2.30 for every dollar invested is made, as compared to only US$1.40 obtained by planting maize as a monocrop. Two of the most useful trap crops that pulls in the borers’ natural enemies are napier grass (Pennisetum purpureum) and Sudan grass (Sorghum vulgare sudanense), both important fodder plants; these are planted in a border around the maize. Two excellent borers-repelling crops which are planted between the rows of maize are molasses grass (Melinis minutiflora), which also repels ticks, and the leguminous silverleaf (Desmodium). This plant can also suppress Striga by a factor of 40 compared to maize monocrops, its N-fixing ability increases soil fertility, and it is an excellent forage. As an added bonus, sale of Desmodium seed is proving to be a new income-generating opportunity for women in the project areas.

3. Several researchers have introduced flowering plants in strips within crops as a way to enhance the availability of pollen and nectar, necessary for optimal reproduction, fecundity, and longevity of many natural enemies of pests. Phacelia tanacetifolia strips have been used in wheat, sugar beets, and cabbage leading to enhanced abundance of aphidophagous predators, especially syrphid flies, and reduced aphid populations. In England, in an attempt to provide suitable over-wintering habitat within fields for aphid predators, researchers created “beetle banks” sown with perennial grasses such as Dactylis glomerata and Holcus lanatus. When these banks run parallel with the crop rows, great enhancement of predators (up to 1500 beetles per square meter) can be achieved in only two years (Landsl et al., 2000).

4. In perennial cropping systems the presence of flowering undergrowth enhances the biological control of a series of insect pests. The beneficial insectary role of Phacelia in apple orchards was well demonstrated by Russian and Canadian researchers more than 30 years ago (Altieri, 1994). Maintenance of floral diversity by organic farmers throughout the growing season in California vineyards, in the form of summer cover crops of buckwheat (Fagopyrum esculentum) and sunflower (Helianthus annuus), had a substantial impact on the abundance of western grape leaffopper, Berytus ventralis (Hemiptera: Cicadellidae), and western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae), and associated natural enemies. During two consecutive years, vineyard systems with flowering cover crops were characterized by lower densities of leaffoppers and thrips, and larger populations and more species of general predators, including spiders. Although Anagyris foenea (Hymenoptera: Mymaridae), the most important parasitoid, achieved high numbers and inflicted noticeable mortality of grape leaffopper eggs, no differences in egg parasitism rates were observed between cover cropped and monoculture systems.
Mowing of cover crops forces movement of Anagrus and predators to adjacent vines resulting in the lowering of leafhopper densities in such vines. Results indicated that habitat diversification, using summer cover crops that bloom most of the growing season, supports large numbers of predators and parasites thereby favoring enhanced biological control of leafhoppers in vineyards (Nicholls et al., 2000).

5. In Washington state (USA), researchers reported that organic apple orchards that retained some level of plant diversity in the form of weeds mowed as needed, gave apple yields similar to those of conventional and integrated orchards. Their data showed that the low external-input organic system ranked first in environmental and economic sustainability as this system exhibited higher profitability, greater energy efficiency, and lower negative environmental impact (Reganold et al., 2001).

6. In Central America, Staver et al. (2001) designed pest-suppressive multispecies shade-grown coffee systems, selecting tree species and associations, density, and spatial arrangement, as well as shade management regimes, with the main goal of creating optimum shade conditions for pest suppression. For example, in low-elevation coffee zones, 35-65% shade promotes leaf retention in the dry season and reduces Ceroplastes cossmi, weeds and Plamocassus citri; at the same time, it enhances the effectiveness of microbial and parasitic organisms without contributing to increased Hemileia vastatrix levels or reducing yields.

7. Several entomologists have concluded that the abundance and diversity of predators and parasites within a field are closely related to the nature of the vegetation in the field margins. There is wide acceptance of the importance of field margins as reservoirs of the natural enemies of crop pests. Many studies have demonstrated increased abundance of natural enemies and more effective biological control where crops are bordered by wild vegetation from which natural enemies colonize. Parasitism of the armyworm, Spodoptera exigua, was significantly higher in maize fields embedded in a complex landscape than in maize fields surrounded by simpler habitats. In a two-year study researchers found higher parasitism of Osminia subulata larvae by the parasitoid Eriotypa servula in edges of maize fields adjacent to wooded areas than in field interiors (Landis et al., 2000). Similarly, in Germany, parasitism of rape pollen beetle was about 50% at the edge of the fields, while at the center of the fields parasitism dropped significantly to 20% (Thies and Techamthke, 1999).

8. One way to introduce the beneficial biodiversity from surrounding landscapes into large-scale monocultures is by establishing vegetationally diverse corridors that allow the movement and distribution of useful arthropod biodiversity into the center of monocultures. Nicholls et al. (2001) established a vegetation corridor which connected to a riparian forest and cut across a vineyard monoculture. The corridor allowed natural enemies emerging from the riparian forest to disperse over large areas of otherwise monoculture vineyard systems. The corridor provided a constant supply of alternative food for predators, effectively decoupling predators from a strict dependence on grape herbivores and avoiding a delayed colonization of the vineyard. This complex of predators continuously circulated into the vineyard interstices, establishing a set of trophic interactions leading to natural enemy enrichment, and consequently, lower numbers of leafhoppers and thrips on vines located up to 30-40 m from the corridor.

All of the above examples constitute forms of habitat diversification that provide resources and environmental conditions suitable for natural enemies. The challenge is to identify the type of biodiversity that is desirable to maintain and/or enhance to carry out ecological services of pest control, and then to determine the best practices that will encourage such desired biodiversity components.

14.9 Designing pest-stable agroecosystems

The key challenge for the 21st century pest managers is to translate ecological principles into practical alternative systems to suit the specific needs of farming communities in different agroecological regions of the world. A major strategy emphasized in this paper to design a more sustainable agriculture is to restore agricultural diversity in time and space by following key agroecological guidelines:

- Increase biodiversity in time and space through multiple cropping and agroforestry designs.
- Increase genetic diversity through variety mixtures, multilines, and use of local germplasm and varieties exhibiting horizontal resistance.
- Include and improve fallow through legume-based rotations, use of green manures, cover crops, and livestock integration.
Landis et al. (2000) recommended the following guidelines to be considered when implementing habitat management strategies:

- Selection of the most appropriate plant species.
- The spatial and temporal arrangement of such plants within and/or around the fields.
- The spatial scale over which the habitat enhancement operates, with implications at the field or landscape level.
- The predator-parasitoid behavioral mechanisms which are influenced by the habitat manipulation.
- Potential conflicts that may emerge when adding new plants to the agroecosystem (e.g., in California, Rubus blackberries around vineyards have increased populations of grape leafhopper parasitoids but can also enhance abundance of the sharpshooter which serves as a vector for Pierce’s disease).
- Develop ways in which added plants do not upset other agronomic management practices, and select plants that preferentially have multiple effects such as improving pest regulation but at the same time improve soil fertility, weed suppression, etc.

What is crucial is the identification of the type of biodiversity worthwhile maintaining or enhancing to carry out ecological services, and then determining those practices that will best encourage the desired biodiversity components. Figure 14.4 shows that there are many agricultural practices and designs with the potential for enhancing functional biodiversity and those having negative effect. The idea is to apply the best management practices for enhancing or regenerating the kind of biodiversity that not only subsidizes the sustainability of agroecosystems by providing ecological services such as biological control, but also enhances nutrient cycling, water and soil conservation, etc. (Nicholls et al., 2001).

If one or more alternative diversification schemes are used, the possibilities of complementary interactions between agroecosystem components are enhanced, resulting in one or more of the following effects:

- continuous vegetation cover for soil protection
- constant production of food, ensuring a varied diet and several marketing items
- closing nutrient cycles and effective use of local resources
- soil and water conservation through mulching and wind protection
- enhanced biological pest control by providing through diversification resources to beneficial biota
increased multiple use capacity of the landscape
- sustained crop production without relying on environmentally degrading chemical inputs.

In summary, key ecological principles for the design of diversified and sustainable agroecosystems include:

- Increasing species diversity as this promotes fuller use of resources (nutrient, radiation, water, etc.), pest protection, and compensatory growth. Researchers have highlighted the importance of various spatial and temporal plant combinations to facilitate complementary resource use or to provide intercrop advantage, such as in the case of legumes facilitating the growth of cereals by supplying extra nitrogen. Compensatory growth is another desirable trait as, if one species succumbs to pests, weather or harvest, another species fills the void maintaining full use of available resources.
- Enhancing longevity through the addition of perennials that contain a thick canopy, thus providing continual cover that can also protect the soil. Constant leaf fall builds organic matter and allows uninterrupted

References

Applications of molecular ecology to IPM: what impact?

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15.1 Introduction

The use of molecular markers in biology, phylogeny and ecology has a long and distinguished history. Variable heritable protein markers (mostly allozymes) formed the basis of numerous studies in population biology and genetics (see Loxdale and den Hollander, 1988; Symondson and Liddell, 1996 for reviews). They enabled boundaries between functionally independent populations to be identified and allowed estimation of gene flow (and inferred migration) between them. Their use has been largely replaced by the use of DNA-based techniques referred to as "molecular" techniques and it is here where we focus our discussion. We use "molecular ecology" to mean the application of molecular biology to population ecology (see reviews in Avise, 1994; Schierwater et al., 1994; Moritz and Lavery, 1996; Carvalho, 1998; Sunnucks, 2000; see Loxdale and Lushai, 1999; MacDonald and Loxdale, 2004 for reviews on entomological applications).

Reasons for the shift to DNA-based methods for studying pests include the following:

a. Technological factors, such as the fact that usable DNA can be obtained from very small specimens (e.g. tiny grape phylloxera Daktulosphaira vitifoliae, Downie, 2000; individual aphid eggs, Sloan et al., 2001) and preserved specimens such as pinned museum collections or ethanol-preserved suction-trapped insects.

b. Issues of resolution: DNA techniques often yield sufficient variation where allozymes and morphology cannot because invading populations have lost variability (e.g. Davies et al., 1999a; b), the taxa have low allozyme variation (e.g. aphids, De Barro et al., 1999a; b; c;