*Chapter 5*

# SOIL FERTILITY, BIODIVERSITY AND PEST MANAGEMENT

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## INTRODUCTION

Optimisation of agroecosystem health is based on two pillars: habitat manipulation and soil fertility enhancement. The latter is achieved through management of organic matter and conservation of below-ground biodiversity, and is the focus of this chapter. The chapter first looks at ways in which soil fertility management can reduce plant susceptibility to pests, both directly by mediating plant health and indirectly via interactions between above-ground and below-ground biodiversity. Appropriate management of organic soil fertility may reduce crop damage by increasing plant resistance through improving the foliage's nutritional balance, or by reducing pest populations via enhancement of natural enemies. In organically fertilised systems, several insect herbivores consistently show lower abundance due to emerging synergies between plant diversity, natural enemies and soil fertility. Healthy soil is probably more important than is currently acknowledged in determining individual plant response to stresses such as pest pressure. Combining crop diversification and organic soil enhancement is a key strategy to sustainable agroecosystem management.

Traditionally entomologists have explained pest outbreaks in cropping systems as a consequence of the absence of natural enemies or the effects of insecticides, such as the development of pesticide resistance by insect pests or secondary pest outbreaks due to disruptions of biological control. Entomologists have, however, been unaware of the theory of trophobiosis offered by French scientist Francis Chaboussou (Chaboussou, 2004 (English translation of 1985 French edition)). As early as 1967, Chaboussou contended that pest problems were also linked to disturbances in the nutritional balances of crop plants and destruction of life in the soil. He explained that heavy applications of soluble nitrogen (N) fertilisers (and also certain pesticides) increase the cellular amounts of N, ammonia and amino acids, faster than the rate at which plants synthesise them for proteins. These reductions in the rate of protein synthesis result in the temporary accumulation of free N, sugars and soluble amino acids in the foliage: substances needed for growth and reproduction by insect herbivores and also plant pathogens. Chaboussou's empirical evidence led him to postulate that insect pests and diseases grow and multiply faster when plants contain more soluble free nutrients, due to the inhibition of protein synthesis. He also believed that a healthy soil life is fundamental for a balanced uptake of mineral nutrients by the plant, especially micronutrients. A lack of micronutrients also causes inhibition in protein synthesis and therefore leads to a build-up in nutrients needed by pests and pathogens.

In the last 20 years a number of research studies have corroborated Chaboussou's assertions, showing 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 (Magdoff and van Es, 2000). Recent evidence suggests that the lower pest pressure observed in many organic systems, although associated with a greater use of practices that preserve beneficial insects, is also linked to enhanced soil biology and fertility (Zehnder *et al.*, 2007). Several studies also document that farming practices which cause nutrition imbalances can lower pest resistance (Magdoff and van Es, 2000). Evidence is mounting that synthetic fertilisers can reduce plant resistance to insect pests, tend to enhance insect pest populations, and can increase the need for insecticide application (Yardlm and Edwards, 2003). Furthermore, recent research shows how biotic interactions in soil can regulate the structure and functioning of above-ground communities (Harman *et al.*, 2004; Wardle *et al.*, 2004), suggesting that the below-ground component of an agroecosystem can be managed through a set of agroecological practices that can exert a substantial influence on pest dynamics (Altieri and Nicholls, 2003).

Slowly agroecologists are recognising that above-ground and below-ground biodiversity components of agroecosystems cannot continue to be viewed in isolation from each other (van der Putten *et al.*, 2009). In fact, the otherwise largely separate above-ground and below-ground components of agroecosystems are connected by the plant (Wardle *et al.*, 2004). This recognition of the biological linkages between above-ground and below-ground biota constitutes a key step on which a truly innovative ecologically based pest management strategy can be built.

Ecologically based pest management (EBPM) considers below-ground and above-ground habitat management as equally important, because enhancing positive ecological interactions between soils and pests can provide a robust and sustainable way of optimising total agroecosystem function (Figure 5.1). The integrity of the agroecosystem relies on synergies of plant
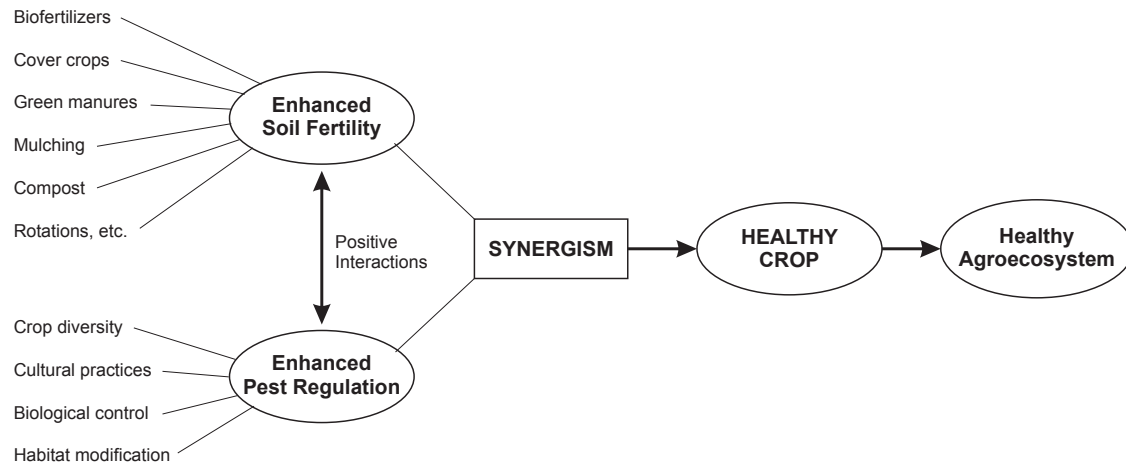
**Figure 5.1** The potential synergism between soil fertility management and IPM.

diversity and the continuing function of the soil microbial community supported by a soil rich in organic matter (Altieri and Nicholls, 1990). Despite the potential links between soil fertility and crop protection, the evolution of integrated pest management (IPM) and integrated soil fertility management (ISFM) have proceeded separately (Altieri and Nicholls, 2003). Since many soil management practices are already known to influence pest management interactions, it does not make ecological sense to continue with such an atomistic approach.

The overall goal of EBPM is to create soil and above-ground conditions that promote the growth of healthy plants, while stressing pests and promoting beneficial organisms. This approach constitutes the basis of a habitat management strategy aimed at enhancing above- and below-ground biological diversity which in turn creates the conditions that are hospitable to plant roots, allowing the development of strong and healthy crops while promoting the presence of naturally occurring biological control organisms (Magdoff, 2007).

## HEALTHY SOILS, HEALTHY PLANTS

One way soil fertility management can directly reduce plant susceptibility to pests is by mediating plant health (Phelan *et al.*, 1995). Many researchers and also practising farmers have observed that fertility practices that replenish and maintain high soil organic matter and that enhance the level and diversity of soil macro- and

microbiota provide an environment that through various processes enhances plant health (McGuiness, 1993). The following are a few of the suggested pest suppressive mechanisms linked to healthy soils:

• Competition: high levels and diversity of soil microbes diminish the populations or infectivity of soil-borne pathogens; this occurs because the soil microbes compete with the pathogens for food and space. Biodiverse soils also contain fungi and bacteria that consume, parasitise or are otherwise antagonistic to many soil-borne crop pathogens. Plant pathologists have known for years that a soil rich in microbiota lessens the danger of epidemic outbreaks caused by soil-borne pathogens (Campbell, 1994).

• Induced resistance: exposure to compost, compost extracts or certain microbes (both pathogenic and non-pathogenic) can induce plants to develop resistance to a broad range of soil-borne and airborne pathogens. Induced resistance is described as a broad-spectrum, long-lasting resistance and appears to be most effective against fungal pathogens (Kuć, 2001).

• Natural enemies: enriching the soil stimulates the proliferation of soil mesofauna which may serve as alternative prey for natural enemies such as carabid beetles and spiders, allowing them to develop high populations that can then respond quickly to pest outbreaks (Purvis and Curry, 1984). This effect is particularly important for generalist predators, as explored by Welch *et al.* in chapter 3 of this volume.

• Buffering of nutrient supply: humus and microbial biomass provide a more gradual and balanced release

of nutrients than is possible with synthetic fertilisers. Many insect pests and fungal pathogens are stimulated by lush growth and/or high N level in plants. As Chaboussou (2004) suggested, more balanced mineral nutrition makes crops more resistant to pests and diseases.

• Reduced stress: soils with high humus and biodiversity have improved capacity to take up and store water and thus reduce water stress. Water and other types of stress increase pest problems, possibly by restricting protein synthesis, which in turn increases soluble N in foliage making tissues more nutritious to many pests (Waring and Cobb, 1991).

Soil fertility practices can directly affect the physiological susceptibility of crop plants to insect pests by either affecting the resistance of individual plants to attack or altering plant acceptability to certain herbivores (Barker, 1975; Scriber, 1984). But the mechanisms can be more complex and include genetic and biochemical dimensions as suggested by the finding of scientists of the USDA Beltsville Agricultural Research Center in Maryland, which contributes to building a scientific basis to better understand the relationships between plant health and soil fertility (Kumar *et al.*, 2004). These researchers showed a molecular basis for delayed leaf senescence and tolerance to diseases in tomato plants cultivated in a legume (hairy vetch) mulch-based alternative agricultural system, compared to the same crop grown on a conventional black polyethylene mulch along with chemical fertiliser. Probably due to regulated release of C and N metabolites from hairy vetch decomposition, the cover-cropped tomato plants showed a distinct expression of selected genes, which ultimately led to a more efficient utilisation and mobilisation of C and N, promoting defence against disease and enhanced crop longevity. These results confirm that in intensive conventional tomato production, the use of legume cover crops offers advantages as a biological alternative to commercial fertilisers leading to disease suppression, in addition to other benefits such as minimising soil erosion and loss of nutrients, enhancing water infiltration, reducing runoff and more balanced natural control.

## INTERACTIONS BETWEEN ABOVE-GROUND AND BELOW-GROUND BIODIVERSITY

Plants function in a complex multitrophic environment. However, as pointed out by van der Putten *et al.*
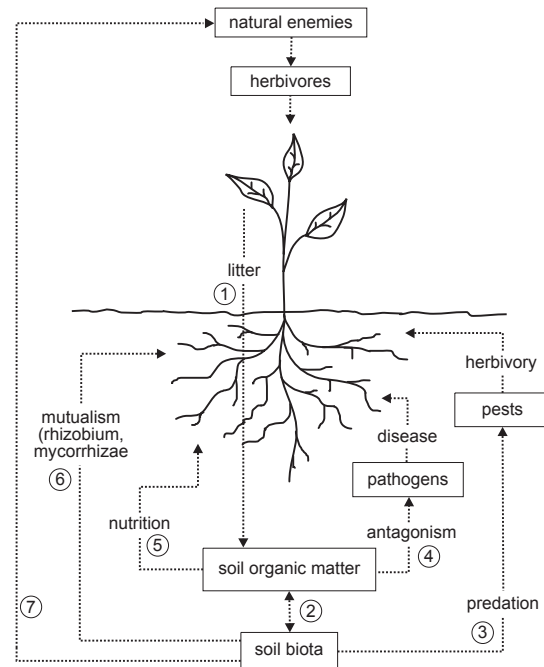


**Figure 5.2** Complex ways in which above- and below-ground biodiversity interact in agroecosystems: 1) crop residues enhance soil organic matter (SOM); 2) SOM provides substratum for micro, meso, and macro soil biota; 3) soil predators reduce soil pests; 4) SOM enhances antagonists which suppress soil-borne pathogens; 5) slow mineralisation of C and N activates genes which promote disease tolerance and crop longevity as well as low free N content in foliage; 6) mutualists enhance N fixation, P uptake, water use efficiency, etc.; 7) certain invertebrates (e.g. Collembola and detritivores) serve as alternative food to natural enemies in times of pest scarcity.

(2001), most multitrophic studies have focused almost exclusively on above-ground interactions, generally neglecting the fact that above- and below-ground organisms interact in complex ways (Figure 5.2). Several studies point to the interdependence of the population dynamics of above- and below-ground herbivores and associated natural enemies as mediated through defence responses by different plant compartments (above and below ground). Because plant chemical defence pathways against herbivores and pathogens can interact, root herbivory could affect the induction of plant defence compounds in leaves. But, as argued by van der Putten *et al.* (2001), the

interactions between the below- and above-ground compartments are even more complex, because the underlying mechanisms (nutrition and plant defence) are typically interlinked. In fact, the production of both direct and indirect plant defences is dependent on nutrient uptake by the roots. And the evidence in favour of such beneficial interactions is growing (Bezemer and van Dam, 2005; Erb *et al.*, 2008; Kempel *et al.*, 2010; Pineda *et al.*, 2010; Wurst, 2010; van Dam and Heil, 2011).

Below-ground organism activity can affect plant above-ground phenotype, inducing plant tolerance to herbivores and pathogens (Blouin *et al.*, 2005). In that study, an 82% decrease in nematode-infested plants was achieved when earthworms were present. Although earthworms had no direct effect on nematode population size, in their presence root biomass was not affected by nematodes and the expected inhibition of photosynthesis was suppressed. This is the first time earthworms have been shown to reduce nematode effects in infested plants. Apparently, the presence of earthworms in the rhizosphere induced systemic changes in plant gene expression, leading to increased photosynthetic activity and chlorophyll concentration in the leaves (Blouin *et al.*, 2005). Such findings indicate that soil fauna activities are probably more important than currently acknowledged in determining individual plant response to stress.

Above-ground communities are affected by both direct and indirect interactions with soil food web organisms (Wardle *et al.*, 2004). Feeding activities in the detritus food web stimulate nutrient turnover, plant nutrient acquisition and plant performance, and thereby indirectly influence above-ground herbivores. Studies in traditional Asian irrigated-rice agroecosystems showed that by increasing soil organic matter in test plots, researchers could boost populations of detritivores and plankton-feeders, which in turn significantly boosted abundance of above-ground generalist predators (Settle *et al.*, 1996). This system is explored in detail in chapter 13 of this volume. In addition, soil Collembola are regarded as important sources of alternative prey for predators such as carabid beetles when pests are scarce (Bilde *et al.*, 2000).

On the other hand, soil biota exerts direct effects on plants by feeding on roots and forming antagonistic or mutualistic relationships with their host plants (e.g. mycorrhizae). Such direct interactions with plants influence not just the performance of the host plants themselves, but also that of the herbivores and potentially their predators. Vestergard *et al.* (2004) found that interactions between aphids and rhizosphere organisms were influenced by plant development and by soil nutrient status. This is one of the first agricultural reports confirming that above- and below-ground biota are able to influence each other with the plant as a mediator. In a long-term agricultural experiment, Birkhofer *et al.* (2008) found that the use of synthetic fertilisers negatively affected interactions within and between below- and above-ground agroecosystem components, with consequent reduction of internal biological cycles and pest control.

## SOIL FERTILITY AND PLANT RESISTANCE TO INSECT PESTS

Plant resistance to insect pests varies with the age or growth stage of the plant (Slansky, 1990), suggesting that resistance is linked directly to the physiology of the plant. Thus any factor which affects the physiology of the plant (e.g. fertilisation) is potentially linked to changes in resistance to insect pests. In fact, fertilisation has been shown to affect all three categories of resistance proposed by Painter (1951): preference, antibiosis and tolerance. Furthermore, obvious morphological responses of crops to fertilisers, such as changes in growth rates, accelerated or delayed maturity, size of plant parts, and thickness and hardness of cuticle, can also indirectly influence the success of many pest species in utilising their host plant. For example, Adkisson (1958) reported nearly three times as many boll weevil larvae (*Anthonomus grandis* (Boheman)) from cotton receiving heavy applications of fertilisers compared to unfertilised control plants, probably due to the prolonged growing season for cotton resulting from the fertiliser amendment. Klostermeyer (1950) observed that N fertiliser increased husk extension and tightness of husks on sweet corn, which reduced corn earworm (*Heliothis zea* (Boddie)) infestation levels. Hagen and Anderson (1967) observed that zinc deficiency reduced the pubescence on corn leaves, which allowed a subsequent increase in feeding by adult western corn rootworm (*Diabrotica virgifera* (LeConte)).

Effects of soil fertility practices on pest resistance can be mediated through changes in the nutritional content of crops. At equivalent amounts of applied N (100 and 200 mg/pot), Barker (1975) found that nitrate-N concentrations in spinach leaves were higher

when receiving ammonium nitrate than in plants treated with five organic fertilisers. In a comparative study of Midwestern conventional and organic farmers, Lockeretz *et al.* (1981) reported organically grown (OG) corn to have lower levels of all amino acids (except methionine) than conventionally grown (CG) corn. Eggert and Kahrmann (1984) also showed CG dry beans to have more protein than OG beans. Consistently higher N levels in the petiole tissue were also found in the CG beans. Potassium and phosphorus levels, however, were higher in the OG bean petioles than in the CG beans. In a long-term comparative study of organic and synthetic fertiliser effects on the nutritional content of four vegetables (spinach, savoy, potatoes and carrots), Schuphan (1974) reported that the OG vegetables consistently contained lower levels of nitrate and higher levels of potassium, phosphorus and iron than CG vegetables.

Fertilisation with N may decrease plant resistance to insect pests by improving the nutritional quality of host plants and reducing secondary metabolite concentrations. Jansson and Smilowitz (1986) reported that N applications increased the rate of population growth of green peach aphid on potatoes and that the growth was positively correlated with the concentrations of free amino acids in leaves. High levels of N reduced glycoalkaloid synthesis, which has an inhibitory effect on insect pests of potatoes (Fragoyiannis *et al.*, 2001). Barbour *et al.* (1991), investigating interactions between fertiliser regimes and host-plant resistance in tomatoes, showed that the survival of Colorado potato beetles to adult emergence increased with larger amounts of fertiliser, and was related to decreases in trichome- and lamellar-based beetle resistance, in response to the improved nutritional quality of the host plant. In addition to increases in the survival rates of Colorado potato beetles from the first instar to adults, larger amounts of N in tomatoes could also cause significantly faster insect development and increased pupal biomass. More recently, Hsu *et al.* (2009) found that *Pieris rapae* (L.) butterflies laid more eggs on CG than on OG cabbage, and that caterpillars then grew faster on CG cabbage due to a diet with more nutrients (N and sugar) and less allelochemicals (sinigrin, the most important and abundant glucosinolate known for its feeding deterrent and antimicrobial properties). Their findings suggest that higher biomass (dry weight) and lower pest incidence may be jointly achieved in organically vs. synthetically fertilised cropping systems.

Meyer (2000) suggests that soil nutrient availability not only affects the amount of damage that plants sustain from herbivores, but also the ability of plants to recover from herbivory. Meyer's study reported the effects of soil fertility on both the degree of defoliation and compensation for herbivory by *Brassica nigra* (L.) plants damaged by *P. rapae* caterpillars. In this study, the percentage defoliation was more than twice as great at low fertility compared to high fertility, even though plants grown at high soil fertility lost a greater absolute amount of leaf area. At both low and high soil fertility, total seed number and mean mass per seed of damaged plants were equivalent to those of undamaged plants. Apparently, soil fertility did not influence plant compensation in terms of maternal fitness.

## INDIRECT EFFECTS OF SOIL NITROGEN ON CROP DAMAGE BY ARTHROPODS

Increases in N levels in plants can enhance populations of invertebrate herbivores living on them (Patriquin *et al.*, 1995). Such increases in populations of insect pests on their host plants in response to higher nitrogen levels can result from various mechanisms, depending on the insect species and host plant. Total N has been considered a critical nutritional factor mediating herbivore abundance and fitness (Mattson, 1980; Scriber, 1984; Slansky and Rodriguez, 1987; Wermelinger, 1989). Many studies report dramatic increases in aphid and mite numbers in response to increased N fertilisation rates. According to van Emden (1966), increases in fecundity and developmental rates of the green peach aphid, *Myzus persicae* (Sulzer), were highly correlated to increased levels of soluble N in leaf tissue. Changes in N content in poinsettias grown with ammonium nitrate stimulated the fecundity of the whitefly *Bemisia tabaci* (Gennadius) and attracted more individuals to oviposit on them (Bentz *et al.*, 1995).

Several other authors have also indicated increased aphid and mite populations from N fertilisation (Luna, 1988). Herbivorous insect populations associated with *Brassica* crop plants have also been reported to increase in response to increased soil N levels (Letourneau, 1988). In a two-year study, Brodbeck *et al.* (2001) found that populations of the thrips *Frankliniella occidentalis* (Pergande) were significantly higher on tomatoes that received higher rates of N fertilisation.

Other insect populations found to increase following N fertilisation include fall armyworm in maize, corn earworm on cotton, pear psylla on pear, Comstock mealybug (*Pseudococcus comstocki* (Kuwana)) on apple, and European corn borer (*Ostrinia nubilalis* (Hubner)) on field corn (Luna, 1988).

Because plants are the source of nutrients for 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 behaviour of the herbivores themselves (Pimentel and Warneke, 1989). For example, with increasing N concentrations in creosote bush (*Larrea tridentata* (Coville)) plants, populations of sucking insects were found to increase, but the number of chewing insects declined. It is plausible that with higher N fertilisation, the amount of nutrients in the plant increases, as well as the amount of secondary compounds that may selectively affect herbivore feeding patterns. In particular, 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). However this differential response does not seem to change the overall trend when one looks at studies on crop nutrition and pest attack (Altieri and Nicholls, 2003).

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-fertilised crops, versus fewer than 50 studies in which herbivore damage was reduced. In aggregate, these results suggest a hypothesis with implications for fertiliser use patterns in agriculture, namely that high N inputs can result in 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, as these generally result in lower N concentrations in the plant tissue. However, Letourneau (1988) questions if such a 'nitrogen-damage' hypothesis, based on Scriber's review, can be extrapolated to a general warning about fertiliser inputs associated with insect pest attack in agroecosystems. Letourneau reviewed 100 studies and found that two-thirds (67) of the insect and mite studies showed an increase in growth, survival, reproductive rate, population densities or plant damage levels in response to increased N fertiliser. The remaining third of the arthropods studied showed either a decrease in damage with fertiliser N or no significant change. The author also noted that experimental design can affect the types of responses observed.

The majority of Cakchiquel farmers responding to a survey conducted in Patzun, Guatemala, did not recognise herbivorous insects as a problem in their milpas (corn (*Zea mays*) intercropped with beans (*Phaseolus vulgaris*), fava (*Vicia faba*), and/or squash (*Cucurbita maxima*, *C. pepo*) (Morales *et al.*, 2001). The farmers attributed this lack of pests to preventative measures incorporated into their agricultural practices, including soil management techniques. Patzun farmers traditionally mixed ashes, kitchen scraps, crop residues, weeds, leaf litter and manure to produce compost. However, from about 1960 onward, synthetic fertilisers were introduced to the region and were rapidly adopted in the area. Today, the majority of farmers have replaced organic fertilisers with urea ($CO(NH_2)_2$), although some recognise the negative consequences of the change and complain that pest populations have increased in their milpas since the introduction of the synthetic fertilisers.

In their survey in the Guatemalan highlands, Morales *et al.* (2001) also found that corn fields treated with organic fertiliser (applied for two years) hosted fewer aphids (*Rhopalosiphum maidis* (Fitch)) than corn treated with synthetic fertiliser. This difference was attributed to a higher concentration of foliar N in corn in the synthetic fertiliser plots, although numbers of *Spodoptera frugiperda* (Smith) showed a weak negative correlation with increased N levels.

## DYNAMICS OF INSECT HERBIVORES IN ORGANICALLY FERTILISED SYSTEMS

Lower abundance of several insect herbivores in low-input systems has been partly attributed to a lower N content in organically farmed crops (Lampkin, 1990). Furthermore, farming methods utilising organic soil amendments significantly promote the conservation of arthropod species in all functional groups, and enhance the abundance of natural enemies compared with conventional practices (Moreby *et al.*, 1994; Basedow, 1995; Drinkwater *et al.*, 1995; Berry *et al.*, 1996; Pfiffner and Niggli, 1996; Letourneau and Goldstein, 2001; Mäder *et al.*, 2002; Hole *et al.*, 2005). This suggests that reduced pest populations in organic systems are a consequence of both nutritional changes induced in the crop by organic fertilisation and increased

natural pest control. Whatever the cause, there are many examples in which lower insect herbivore populations have been documented in low-input systems, with a variety of possible mechanisms proposed.

In Japan, the density of immigrants of the planthopper species *Sogatella furcifera* (Horváth) was significantly lower and the settling rate of female adults and survival rate of immature stages of ensuing generations were generally lower in organic than in conventional rice fields. Consequently, the density of planthopper nymphs and adults in the ensuing generations was found to decrease in organically farmed fields (Kajimura, 1995). In England, conventional winter wheat fields exhibited a larger infestation of the aphid *Metopolophium dirhodum* (Walker) than their organic counterparts. The conventionally fertilised wheat crop also had higher levels of free protein amino acids in its leaves during June, which were attributed to an N top dressing applied early in April. However, the difference in 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 (Kowalski and Visser, 1979). The authors concluded that chemically fertilised winter wheat was more palatable than its organically grown counterpart, hence the higher level of infestation.

Interesting results were found also in greenhouse experiments comparing maize grown on organic versus chemically fertilised soils collected from nearby farms (Phelan *et al.*, 1995). The researchers observed that European corn borer (*Ostrinia nubilalis* (Hübner)) females, when given a choice, laid significantly more eggs in the chemically fertilised plants versus the organically fertilised ones. But this significant variation in egg-laying between chemical and organic fertiliser treatments was present only when maize was grown on soil collected from conventionally managed farms. In contrast, egg laying was uniformly low in plants grown on soil collected from organically managed farms. 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 regimen. The authors suggested that this difference is evidence for a form of biological buffering characteristically found more commonly in organically managed soils.

Yardlm and Edwards (2003) conducted a two-year study comparing the effects of organic (composted cow manure) and synthetic (NPK) fertilisers on pests (aphids and flea beetles) and predatory arthropods (anthocorids, coccinellids and chrysopids) associated with tomatoes. In the second year aphids exhibited significantly lower numbers on plants that received organic fertiliser than on those treated with synthetic fertilisers, suggesting that the effects of organic fertilisers in reducing pest populations may be expressed more fully in the long term. The reductions in aphid populations could not be attributed to the increases in predator populations on tomatoes in the organic fertiliser-treated plots, because the predator populations did not differ significantly between the full-rate synthetic fertiliser-treated and the organic fertiliser-treated plots. However, it seems that both synthetic and organic fertiliser inputs were able to increase flea beetle populations significantly, even when the synthetic fertiliser application rate was reduced to half. Flea beetle populations were significantly higher on plants that received the full rates of synthetic and organic fertilisers during the two years of the study, despite the significant differences between years with respect to flea beetle and other pest numbers.

Altieri *et al.* (1998) conducted a series of comparative experiments in various growing seasons between 1989 and 1996, in which broccoli was subjected to varying fertilisation regimes (conventional vs. organic). The goal was to test the effects of different N sources on the abundance of the key insect pests: cabbage aphid (*Brevicoryne brassicae* (L.)) and flea beetle (*Phyllotreta cruciferae* (Goeze)). Conventionally fertilised monocultures consistently developed a larger infestation of flea beetles and in some cases of the cabbage aphid, than the organically fertilised broccoli systems. The reduction in aphid and flea beetle infestations in the organically fertilised plots was attributed to lower levels of free N in the foliage of plants. Applications of synthetic N fertilisation to individual broccoli plants within an organic field triggered aphid densities on the treated plants but not on the surrounding organic plants (Figure 5.3). These results further support the view that insect pest preference can be moderated by alterations in the type and amount of fertiliser used.

By contrast, a study comparing the population responses of *Brassica* pests to organic versus synthetic fertilisers measured higher *Phyllotreta* flea beetle populations on sludge-amended collard (*Brassica oleracea* (L.)) plots early in the season compared to mineral fertiliser-amended and unfertilised plots (Culliney and Pimentel, 1986). However, later in the season, in these
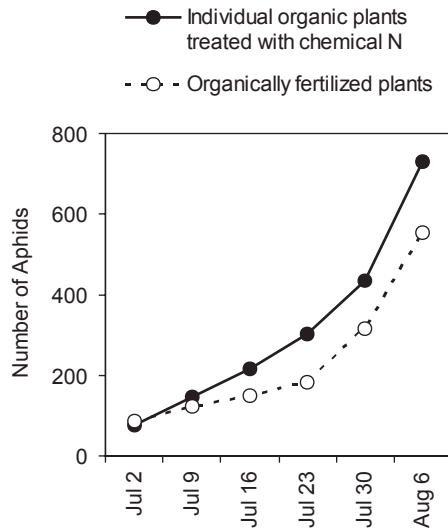
**Figure 5.3** Aphid population response (cumulative numbers) to treatment of individual organic broccoli plants with chemical N fertiliser within an organically managed field in Albany, California (Altieri, unpublished data).

same plots population levels of beetle, aphid and lepidopteran pests were lowest in organic plots. This suggests that the effects of fertiliser type vary with plant growth stage and that organic fertilisers do not necessarily diminish pest populations throughout the whole season. 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 at harvest time.

## SYNERGIES BETWEEN PLANT DIVERSITY, NATURAL ENEMIES AND SOIL FERTILITY

When examining weedy faba beans fields in Tunwath, Canada, Patriquin *et al.* (1988) found higher numbers of aphid enemies in the diverse systems but they also discovered that the reproductive rate of aphids is proportional to the supply of amino acids in the phloem. Legumes nodulate and fix gaseous N from air when the supply of mineral N in the soil is deficient; when it is

not, they preferentially take up soil N. Weeds among the faba beans take up and thereby reduce soil mineral N to a level below that which suppresses nodulation (about 5 ppm nitrate-N for faba beans at Tunwath). This causes the faba beans to nodulate more and to obtain more N from N fixation. Under those conditions, there is closer coupling of N uptake and assimilation than when mineral N predominates, and consequently accumulation of amino acids in the phloem is reduced. The reproductive rate of the aphids is restricted accordingly. When the weeds are removed, the soil N supply increases, phloem N increases, and the plants are more attractive and more nutritious to the aphids. Weedy plants also had higher yields than the plants in the weed-free plots because the benefits of increased nodulation outweighed any losses due to weeds. This beneficial interaction between weeds and the crop works only if levels of soil nitrate are relatively low (e.g. 10 ppm) to begin with. When plots were fertilised with urea, weeds overgrew the crop and greatly reduced yields. On another organic farm where soil nitrate levels were five to ten times higher than at Tunwath, weeds overgrew the faba bean crop. In spite of an abundance of natural enemies, large aphid infestations caused massive yield loss. Managing the soil N to keep it low under faba beans was thus critical for favourable crop–weed and crop–aphid interactions. At Tunwath, faba beans followed winter wheat in the rotation. The highly 'immobilising' (N robbing) wheat residues were worked into the soil following harvest. This was a deliberate strategy to lower soil nitrate levels under the faba beans and thereby stimulate nodulation and N fixation. Patriquin's data indicated that seed yield of aphid-infested plants at Tunwath Farm was not reduced and was even slightly higher than those of non-infested plants (Patriquin *et al.*, 1988).

In California, Ponti *et al.* (2007) reported that intercropping of broccoli with mustard and buckwheat significantly reduced aphid populations especially in the summer (Figure 5.4), when the proximity of flowers (i.e. polyculture with competition) significantly enhanced aphid parasitisation rates on nearby broccoli plants. Monoculture and polyculture broccoli consistently had lower aphid densities and higher parasitisation rates when fertilised with compost. In this study, synthetically fertilised broccoli produced more biomass (fresh weight), but also recruited higher pest numbers. Nevertheless, parasitism by *Diaeretiella rapae* (McIntosh) was higher in compost-fertilised plots. Intercropping and composting decreased pest abundance in
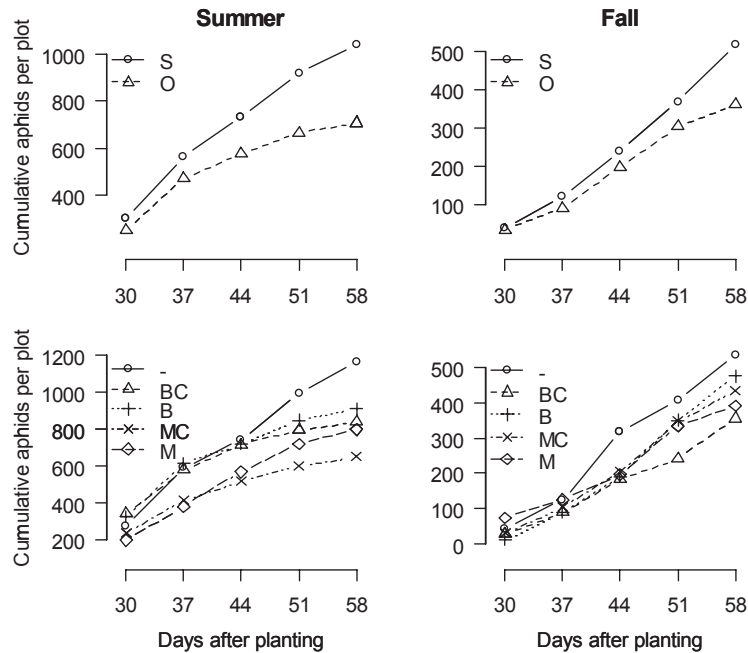
**Figure 5.4** Cumulative counts of aphids on five broccoli plants per plot at the different sampling dates as influenced by cropping system levels (-, monoculture; B, buckwheat polyculture without competition; BC, buckwheat polyculture with competition; M, mustard polyculture without competition; MC, mustard polyculture with competition) and by fertiliser levels (S, synthetic fertiliser; O, organic fertiliser-compost) in two (summer and fall) experiments at Albany, California, in 2004.

broccoli cropping systems with or without interspecific competition, suggesting a synergistic relationship between plant diversity and soil organic management. In addition, depending on the intercropped plant and the growing season (summer vs. autumn), intercropping enhanced parasitism of cabbage aphid. The seasonal effectiveness of *D. rapae* was increased by composting despite lower aphid abundance in compost-fertilised broccoli.

## CONCLUSIONS

Soil fertility management can have several effects on plant quality, which in turn can affect insect abundance and subsequent levels of herbivore damage. The reallocation of mineral amendments in crop plants can influence oviposition, growth rates, survival and reproduction in the insects that use these hosts (Jones, 1976). Although more research is needed, preliminary evidence suggests that fertilisation practices can influ-

ence the relative resistance of agricultural crops to insect pests. Increased soluble N levels in plant tissue were found to decrease pest resistance, although this is not a universal phenomenon (Phelan *et al.*, 1995; Staley *et al.*, 2010).

Chemical fertilisers can dramatically influence the balance of nutritional elements in plants, and it is likely that their excessive use will create nutrient imbalances, which in turn reduce resistance to insect pests. In contrast, organic farming practices promote an increase of soil organic matter and microbial activity and a gradual release of plant nutrients and should, in theory, allow plants to derive a more balanced nutrition. Thus, while the amount of N immediately available to the crop may be lower when organic fertilisers are applied, the overall nutritional status of the crop appears to be improved. Organic soil fertility practices can also provide supplies of secondary and trace elements, occasionally lacking in conventional farming systems that rely primarily on artificial sources of N, P and K. Besides nutrient concentrations, optimum

fertilisation, which provides a proper balance of elements, can stimulate resistance to insect attack (Luna, 1988). Organic N sources may allow greater tolerance of vegetative damage because they release N more slowly, over the course of several years.

Phelan *et al.* (1995) stressed the need to consider other mechanisms when examining the link between fertility management and crop susceptibility to insects. Their study demonstrated that the ovipositional preference of a foliar pest can be mediated by differences in soil fertility management. Thus, the lower pest levels widely reported in organic farming systems may, in part, arise from plant–insect resistances mediated by biochemical or mineral nutrient differences in crops under such management practices. In fact, we feel such results provide interesting evidence to support the view that the long-term management of soil organic matter can lead to better plant resistance against insect pests (Birkhofer *et al.*, 2008). This view is corroborated by recent research on the relationships between above-ground and below-ground components of ecosystems, which suggests that soil biological activity is probably more important than currently acknowledged in determining individual plant response to stresses such as pest pressure (Blouin *et al.*, 2005), and that this stress response is mediated by a series of interactions outlined in Figure 5.2. These findings are enhancing our understanding of the role of biodiversity in agriculture, and the close ecological linkages between above-ground and below-ground biota. Such understanding constitutes a key step towards building a truly innovative, ecologically based pest management strategy which combines crop diversification and organic soil enhancement.

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