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Chapter 9

Insect, Weed, and Plant Disease Management in Multiple Cropping Systems

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Multiple cropping systems constitute agricultural systems diversified in time and space. Much evidence suggests that this vegetational diversity often results in significant reduction of insect pest problems (Altieri and Letourneau, 1982; Cromartie, 1981; Perrin, 1980). A large body of literature cites specific crop mixtures that affect particular insect pests (Andow, 1983; Litsinger and Moody, 1976; Perrin, 1977; Perrin and Phillips, 1978), while other papers explore the ecological mechanisms involved in pest regulation (Root, 1973; Bach, 1980; Risch, 1981). Clearly, much knowledge has accumulated, and this acquired information is slowly providing a basis for designing crop systems so that pest problems and the need for active control measures are minimized (Murdoch, 1975).

Research on the effects of multiple cropping on weeds, pathogens, and nematodes has started to emerge, and studies indicate that their populations change in response to diversification of cropping systems (Bantilan et al., 1974; Sumner et al., 1981; Egunjobi, 1984). The effects of intensive systems on pests and weeds can neither be generalized nor predicted because of the enormous

variety of systems utilized throughout the world. As the temporal and spatial dimensions of vegetational diversity change, so does the magnitude of the effects on pest populations (Perrin, 1980). For example, strip cropping systems can preferentially act as trap crops or as sources of natural enemies which move from one strip to another. In intercropping systems where crops are more closely intermingled, other mechanisms (i.e., repellency, masking, natural enemy enhancement, physical barriers) may affect insect pests. Moreover, a particular crop mix might be of value in controlling one pest in one area [i.e., *Heliothis virescens* in corn (*Zea mays*)/cotton (*Gossypium* sp.) strip cropping in Peru], while increasing the same pest in other areas (i.e., *H. virescens* in Tanzania) (Smith and Reynolds, 1972).

Insect herbivore species were found to be less abundant in multiple crops than in monocultures (Risch et al., 1983). Predictive trends for weed populations are harder to establish because of the relative lack of quantitative studies. Plant pathogens, in turn, seem to be buffered in multispecies crop associations, especially in systems of high genetic diversity and with high populations of antagonists in the soil (Browning, 1975).

There are many reviews examining the effects of diversifying agroecosystems on insect pest abundance; therefore we emphasize recent findings and questions that are central to crop manipulation and agroecosystem design. Our review concentrates on the dynamics of insect, pathogen, and weed communities in intercropping systems. For discussion of pest relations in other systems (i.e., cover cropping in orchards and vineyards, agroforestry, living mulches, strip cropping) there are several available literature sources (see Cromartie, 1981; Altieri and D. K. Letourneau, 1982; Altieri and D. L. Letourneau, 1984; and references cited therein). The scarce information on the effects of multiple cropping on weed abundance and disease incidence is also assembled; however, it seems that much work is needed before a general theory of the effects of these patterns on weeds and diseases can be developed.

PATTERNS OF INSECT ABUNDANCE

In recent years, ecologists have conducted experiments in multiple cropping systems to test the theory that increased plant diversity fosters stability of insect populations (Pimentel, 1961; Root, 1973; van Emden and Williams, 1974). A recent examination of all available studies on the effects of these patterns on insect pest populations tends to support the theory, although confusion may arise depending on how diversity and stability are defined (Risch et al., 1983). In multiple cropping, structural and species vegetational diversity (a measure of the biotic, structural, and microclimatic complexity arising from the mixing of different plants) results from the addition of crop plants in time and space. Stability can refer to low pest population densities over time. Of 198 herbivore species examined, 53 percent exhibited lower abundance in multicrops than in monocultures, 18 percent were more abundant in multicrops, 9 percent showed

no difference, and 20 percent showed a variable response (Andow, 1983; Risch et al., 1983).

Examples of specific crop mixtures that result in reduced pest incidence can be found in Litsinger and Moody (1976), Altieri and D. K. Letourneau (1982), and Andow (1983). Results where no differences were observed or where higher pest incidence occurred in multicrops usually are not found. In Nigeria, populations of flower thrips (*Megalurothrips sjostedti*) were reduced by 42 percent on cowpea (*Vigna unguiculata*)/maize polycultures. However, cropping pattern had no effect on infestations of *Maruca testulalis*, pod-sucking bugs, and meloid beetles (Matteson et al., 1984).

In Nigeria, early infestations of *Maruca* were no different in monocrops and polycultures of maize and cowpea, but 12 weeks after planting infestations were significantly higher in the monocrops. Similar shifts were observed with *Laspeyresia* and thrips (Matteson et al., 198-). In India, larval populations of *Heliothis armigera* were higher in sorghum (*Sorghum bicolor*)/pigeon pea (*Cajanus cajan*) intercropping systems than in sole pigeon pea plots, which led to high grain losses in polycrops (Bhatnagar and Davies, 1981). In home garden plots of beans (*Phaseolus vulgaris*) bordered by marigolds (*Tagetes* spp.), Latheef and Irwin (1980) reported that their designs did not favor control of *Heliothis zea* and *Epilachna varivestris*. In Georgia, Nordlund et al. (1984) did not find significant reductions of *Heliothis zea* damage in maize ears, bean pods, or tomato (*Lycopersicon esculentum*) fruits in polycultures of maize, bean, and tomato. In the Philippines, Hasse and Litsinger (1981) found that intercropping maize with legumes did not reduce the numbers of egg masses laid by corn borers (*Ostrinia furnacalis*).

Ecological Hypotheses to Explain Insect Trends

A reduced insect pest incidence in multicrops may be the result of increased parasitoid and predator populations, availability of alternate food for natural enemies, decreased colonization and reproduction of pests, chemical repellency, masking and/or feeding inhibition from nonhost plants, prevention of pest movement and/or emigration and optimum synchrony between pests and natural enemies (Matteson et al., 1984). Perrin and Phillips (1978) described the stages in pest population development and dynamics that may be affected by mixed cropping. At the crop colonization stage they postulate that disruption of olfactory and visual responses, physical barriers, and diversion to other hosts are important mechanisms regulating herbivores in multiple cropping systems. Once the pests become established in the field, their populations may be regulated by limitation of dispersal, feeding disruption, reproduction inhibition, and mortality imposed by biotic agents.

Hasse and Litsinger (1981) described several mechanisms that have been put forward to explain pest reduction in intercropping systems. A list of the proposed mechanisms is given in Table 9.1. All available evidence suggests that the biotic, structural, and microclimatic complexity of multicrop systems work

Table 9.1 Possible Effects of Intercropping on Insect Pest Populations

Factor	Explanation	Example
Interference with host-seeking behavior		
Camouflage	A host plant may be protected from insect pests by the physical presence of other overlapping plants	Camouflage of bean seedlings by standing rice stubble for beanfly
Crop background	Certain pests prefer a crop background of a particular color and/or texture	Aphids, flea beetle, and *Pieris rapae* are more attracted to cole crops with a background of bare soil than to ones with a weedy background
Masking or dilution of attractant stimuli	Presence of nonhost plants can mask or dilute the attractant stimuli of host plants leading to a breakdown of orientation, feeding, and reproduction processes	*Phyllotreta cruciferae* in collards
Repellent chemical stimuli	Aromatic odors of certain plants can disrupt host finding behavior	Grass borders repel leafhoppers in beans, populations of *Plutella xylostella* are repelled from cabbage/tomato intercrops).
Interference with population development and survival		
Mechanical barriers	All companion crops may block the dispersal of herbivores across the polyculture. Restricted dispersal may also result from mixing resistant and susceptible cultivars of one crop by settling on nonhost components.	
Lack of arrestant stimuli	The presence of different host and nonhost plants in a field may affect colonization of herbivores. If a herbivore descends on a nonhost it may leave the plot quicker than if it descends on a host plant.	
Microclimatic influences	In an intercropping system favorable aspects of microclimate conditions are highly fractioned, therefore insects may experience difficulty in locating and remaining in suitable microhabitats. Shade derived from denser canopies may affect feeding of certain insects and/or increase relative humidity which may favor entomophagous fungi.	
Biotic influences	Crop mixtures may enhance natural enemy complexes. (See natural enemy hypothesis in text.)	

Source: Data from Hasse and Litsinger, 1981.

synergistically to produce an "associational resistance" (Tahvanainen and Root, 1972). Root (1973) hypothesized two ways that associational resistance may be achieved: (1) natural enemy and (2) resource concentration.

Natural Enemy Hypothesis This proposition predicts that there will be a greater abundance and diversity of natural enemies of pest insects in polycultures than in monocultures. Predators tend to be polyphagous and have broad habitat requirements, so they would be expected to encounter a greater array of alternative prey and microhabitats in complex environments. As a result, relatively stable populations of generalized predators can persist in these habitats because they can exploit the wide variety of herbivores that become available at different times or in different microhabitats. Specialized predator populations are less likely to fluctuate widely because the refuge provided by a complex environment enables their prey to escape widespread annihilation (Root, 1973). Moreover, diverse habitats offer many important requisites for adult predators and parasites, such as nectar and pollen sources, which are not available in a monoculture, reducing the probability that they will leave or become locally extinct (Risch, 1981).

Resource Concentration Hypothesis Insect herbivore populations can be influenced directly by the concentration or spatial dispersion of their food plants. Many herbivores, particularly chrysomelid beetles, are more likely to find and remain on hosts that are growing in dense or nearly pure stands (Root, 1973), and which are thus providing concentrated resources and homogeneous physical conditions. Bach (1980) found that diobroticite beetles spent a longer time on host rather than on nonhost plants. Thus, in habitats with higher concentrations of host plants, the beetles were more numerous on a per-plant basis.

In diverse systems, the visual and chemical stimuli from host and nonhost plants affect both the rate of colonization of herbivores and their behavior. A herbivorous insect approaching a habitat usually will have greater difficulty in locating a host plant when the relative resource concentration is lower. Theoretical questions relating to this hypothesis have been discussed in detail by Bach (1980) and Risch (1981).

Experimental Case Studies to Test the Hypotheses

Andow et al. (1983) contend that herbivore movement patterns are more important than the activities of natural enemies in explaining the reduction of monophagous pest populations in diverse annual crop systems. There are two classic studies that support this view. The first study (Risch, 1981) looked at the population dynamics of six chrysomelid beetles in monocultures and polycultures of maize/bean/squash (*Cucurbita pepo*). In polycultures containing at least one nonhost plant (maize), the number of beetles per unit was significantly lower relative to the numbers of beetles on host plants in monocultures. Measurement of beetle movements in the field showed that beetles tended to emigrate more from polycultures than from host monocultures. Apparently this was due

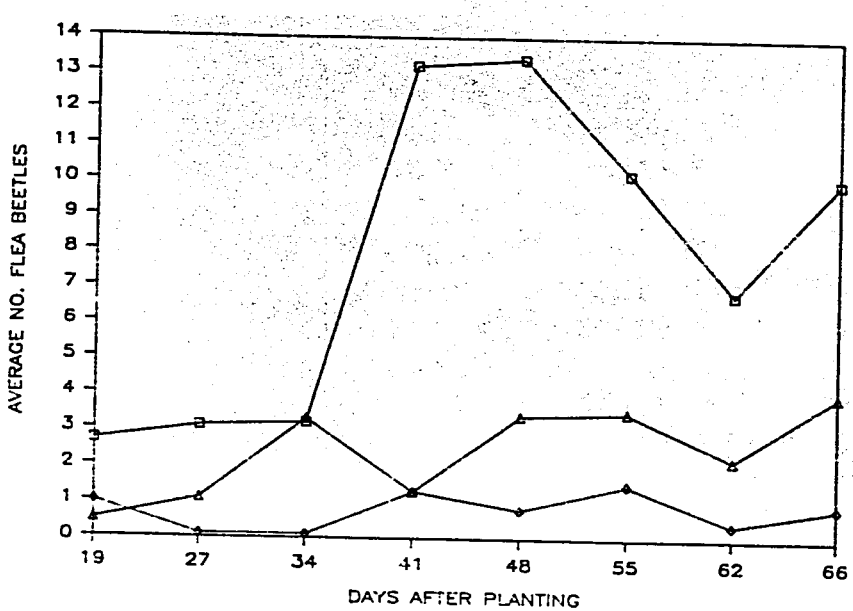

Figure 9.1 Population densities of flea beetles (*Phyllotetra cruciferae*) in collard monocultures (□), and collards associated with a nonhost crop, barley (△), and a host crop, wild mustard (◇), in Albany, California.

to several factors: (1) beetles avoided host plants shaded by maize, (2) maize stalks interfered with flight movements of beetles, and (3) as beetles moved through polycultures they remained on nonhost plants for a significantly shorter time than on host plants. There were no differences in rates of parasitism or predation of beetles between systems.

The second study examined the effects of plant diversity on the cucumber beetle, *Acalymma vittatum* (Bach, 1980). Population densities were significantly greater in cucumber (*Cucumis sativus*) monocultures than in polycultures containing cucumber and two nonhost species. Bach also found greater tenure time of beetles in monocultures than in polycultures. She also determined that these differences were caused by plant diversity *per se*, and not by differences in host plant density or host plant size. Many studies do not control differences in host plant density or size, thus they do not reveal if differences in numbers of herbivores between monocultures and polycultures are due to diversity or rather to the interrelated and confounding effects of plant diversity, plant density, and host plant patch size.

In northern California, densities of cabbage aphids (*Brevicoryne brassicae*) and flea beetles (*Phyllotreta cruciferae*) were significantly lower on cauliflower (*Brassica oleracea botrytis* var. Early Snowball) plants grown in association with weeds or vetch (*Vicia* sp.) than in clean cultivated monocultures (Altieri, unpublished data). The depression of crop growth and biomass in the diverse plots added a confounding effect in that it was not clear if herbivore reduction

Table 9.2 Effect of Flower Removal on the Abundance of Flea Beetles, *Phyllotreta cruciferae*, in Collard/Wild Mustard Intercrops

System	Flea beetle densities per collard plant[a]	
	Early July	Late July
Collard monoculture	3.0	5.0
Collard/wild mustard polyculture with flowers	0.5	1.5
Collard/wild mustard without flowers	0.7[b]	8.0

[a]Means derived from 10 plants per plot (6 × 6 m, each replicated 3 times).
[b]Before flowers were removed.
Source: Altieri, unpublished data.

resulted from poorer plant quality, which made cauliflowers less attractive to the herbivores.

In another study, flea beetle numbers were significantly lower in weedy collards (*Brassica oleracea acephala* var. Georgia), dominated by wild mustard (*Brassica campestris*), than in weed-free monocultures (Altieri and Gliessman, 1983). Flea beetles preferred this plant over collards, thus flea beetles were diverted from collards resulting in diluted feeding on the collards. The authors argue that wild mustards have higher concentrations of allylisothiocyanate (a powerful attractant to adults of *P. cruciferae*) than collards, and therefore the preference of flea beetles for wild mustard simply reflected different degrees of attraction to the foliage levels of this particular glucosinolate in the weeds and collards. Figure 9.1 illustrates this preference in the field by showing that population densities of flea beetles on collard plants grown as monocultures are greater than on collards intercropped with wild mustards and with nonhost barley (*Hordeum vulgare*) (Altieri and Schmidt, unpublished data). Although the barley effect might support the resource concentration hypothesis, the trap cropping effect of wild mustards exerts a stronger influence on beetle abundance in this case. A recent study also showed that removal of flowers of wild mustards results in a substantial reduction of the attractant effect (Table 9.2). Consequently collard plants in flowerless intercrops experienced greater flea beetle loads than the intercrop with flowers and even monocultures.

Risch et al. (1983) collected additional data that does not support the enemies hypothesis. They found that predation rates on egg masses of the European corn borer (*Ostrinia nubilalis*) by a predaceous beetle (*Coleomegilla maculata*) was significantly higher in maize monocultures than in the more densely planted maize/bean/squash polyculture. They argue that in polycultures, the beetles apparently spent more time foraging on plants (beans and squash) that contained no food, thus decreasing their foraging effectiveness. Even if prey densities per maize plant were the same in the two culture types, beetles might forage less efficiently in the polyculture due to unrewarded time spent foraging on bean and

squash plants. This lower reward rate leads to faster emigration of beetles from polycultures (Wetzler and Risch, 1984).

Wrubel (1984) contends that visual camouflage from nonhost plants may have resulted in more Mexican bean beetles colonizing soybean (*Glycine max*) monoculture than maize/soybean intercropped plots. Conversely, the higher concentration of food resources in clover/soybean (two legumes) than soybean monoculture plots may explain the slightly higher abundances of polyphagous acridids that Wrubel found in the clover/soybean plots. Differences in the structure of the crop canopy in tall maize/soybean and short maize/soybean plots appeared to affect the behavior of several groups of herbivores, with lower abundance of Japanese beetles due to shading of the soybean canopy by the taller maize plants.

There are studies that support the enemies hypothesis. In tropical corn/bean/squash systems, Letourneau (1983) studied the importance of parasitic wasps in mediating the difference in pest abundance between simple and complex crop arrangements. A squash-feeding caterpillar, *Diaphania hyalinata* (Lepidoptera: Pyralidae), occurred at low densities on intercropped squash in tropical Mexico. Part of the effect of the associated maize and bean plants may have been to render the squash plants less apparent to ovipositing moths. Polyculture fields also harbored greater numbers of parasitic wasps than did squash monocultures. Malaise trap captures of parasitic wasps in monoculture consisted of one-half the number of individuals caught in mixed culture. The parasitoids of the target caterpillars were also represented by higher numbers in polycultures throughout the season. Not only were parasitoids more common in the vegetationally diverse, traditional system, but the parasitization rates of *D. hyalinata* eggs and larvae on squash were higher in polycultures. Approximately 33 percent of the eggs in polyculture samples over the season were parasitized and only 11 percent of eggs in monocultures. Larval samples from polycultures showed an incidence of 59 percent parasitization for *D. hyalinata* larvae whereas samples from monoculture larval specimens were 29 percent parasitized.

Another study conducted in Davis, California, tested whether predator colonization rates can be manipulated through vegetational diversity (Letourneau and Altieri, 1983). We compared the densities of *Orius tristicolor* and its preferred prey, *Frankliniella occidentalis*, between squash monocultures and polycultures of squash, corn, and cowpea. The patterns of predator colonization rates and pest densities in these two cropping systems paralleled those documented for predator/prey interactions in the mite grapevine systems of Flaherty (1969). In both studies, the colonization rate of predators was increased in diverse habitats, and the prey (pest) populations in each case reached lower maximum levels. In Flaherty's study, the causative factor was the close proximity of the source of colonizing predators. The great variation between levels of Willamette mite (*Eotetranychus willamettei*) infestation on individual grape vines was caused by their variable proximity to clumps of Johnson grass (*Sorghum halepense*). The grass supported an alternate host for a predatory mite, *Metaseiulus occidentalis*. The predators then colonized contiguous vines sufficiently early to suppress the pest mite populations. In our study, the sources of colonizers were presumably at similar distances to randomly assigned plots of monoculture and

polyculture. We suggest that the determining factor for differential colonization by *Orius* sp. in monocultures and polycultures of squash was attraction to the early season crop habitat during the host location process.

Our results showed that mean density of thrips on squash leaves was initially much greater in monoculture than in polyculture and remained at significantly higher levels until 65 days after sowing. The *Orius* sp. density, however, was significantly higher on squash early in the season (days 30 and 42) in polyculture. A decrease in prey density accompanied an increase in adult *Orius* sp. colonization in both treatments until thrips were at low densities.

Predator manipulation experiments conducted in field cages, in which *Orius* sp. populations were either included or excluded, showed that the density of thrips was influenced by predation by *Orius* sp. (Letourneau and Altieri, 1983). On uncaged control plants, the mean density of thrips per leaf declined steadily from day 50, as it had in the general field samples. Inside the exclusion-inclusion cages, thrips density more than tripled the first week after *Orius* and *Erigone* spp. spiders were eliminated. When predators, equal in number to those that were eliminated, were added to cage 1, the thrips density fell in this cage.

Altieri (1984) recently found that brussel sprouts (*Brassica oleracea gemmifera* var. Jade Cross) grown in polycultures with fava beans or wild mustard supported more species of natural enemies (six species of predators, and eight species of parasites) than monocultures (three species of predators and three species of parasites). Apparently, the presence of flowers, extrafloral nectaries, and alternate prey/hosts associated with the companion plants allowed this enhancement.

Another aspect that has barely been considered in the enemies hypotheses is direct plant/natural enemy interactions. Price et al. (1980) have argued that the third trophic level is especially relevant in multispecies crop associations, not only because the herbivore/enemy interaction on one plant species can be influenced by the presence of associated plants, but also because the herbivore/enemy interactions on one plant species can be influenced by the presence of herbivores on associated plant species.

To our knowledge there are a few studies that have documented direct relations between plants and natural enemies. These studies show that some entomophagous insects are attracted to particular plants, even in the absence of host or prey, or by chemicals released by the herbivore's host plant or other associated plants. A few of these studies tested the attractance of plants to parasitoids and showed that certain parasitoids prefer particular plants over others. Others showed that parasitization of a pest was higher on a certain crop than on others. Of significant practical interest are the findings of Altieri et al. (1981), which showed that parasitization rates of *H. zea* eggs by *Trichogramma* sp. were greater when the eggs were placed on soybeans next to corn, *Desmodium* sp., *Cassia* sp., or *Croton* sp., than on soybeans grown alone. Although the same numbers of eggs were placed on the associated plants, few of these eggs were parasitized; results suggested that these plants were not actively searched by *Trichogramma* sp., but in some way the plants enhanced the efficiency of parasitization on the associated soybean plants. A possibility is that they emited

volatiles with kairomonal action. Further tests showed that application of water extracts of some of these associated plants to soybeans enhanced parasitization of *H. zea* eggs by *Trichogramma* spp. wasps. The authors stated that a better attraction and retention in the extract-treated plots may have caused the higher parasitization levels. The possibility that vegetationally complex plots are more chemically diverse than monocultures and therefore more acceptable and arousing to parasitic wasps opens many new dimensions for biological control through habitat management and behavior modification.

Entomological Studies Conducted in Traditional Farmers' Fields

For centuries small farmers have developed and/or inherited complex cropping systems. These systems are based on countless distinct crop varieties and crop mixtures that were selected by farmers over thousands of years for resistance to pests and for other characteristics. These varieties and mixtures are grown using agricultural practices that usually enhance cultural and biological pest control. Thus, many traditional cropping systems have built-in pest-control mechanisms (Matteson et al., 1984). Unfortunately, there are few references on pest dynamics in these systems, and on the control methods commonly used in traditional agriculture. The scattered information is of an anthropological nature, collected by nonentomologists, so that the identities of pests are only conjecture. Brown and Marten (1984) recently reviewed the literature on traditional pest management practices with the intention of providing information on which elements to retain in the course of agricultural modernization. Pest-control features of some traditional systems are described in Matteson et al. (1984) and descriptions of pest-control practices utilized by Southeast Asian peasants can be found in Litsinger and Moody (1976).

During 1982 and 1983, studies were conducted in Tlaxcala, Mexico, on the dynamics of insect communities associated with maize managed with traditional technologies (Trujillo and Altieri, unpublished data). In this state, maize is grown in a variety of situations: as monoculture, intercropped with fava beans (*Vicia faba*), strip-cropped with alfalfa (*Medicago sativa*), weedy, and in association with apple (*Malus pumila*) trees and forest trees. The results indicate that populations of the pestiferous scarab beetle, *Macrodactylus* sp., and a number of predaceous species (e.g., Coccinellidae, *Collops* sp., *Orius* sp.) vary significantly, depending on the location and size of the field, the associated plants, the surrounding vegetation and the type of cultural management. For example, in some areas, predaceous beetles (e.g., Coccinellidae and *Collops* sp.) were more abundant in maize rows adjacent to well-established alfalfa strips than in the center rows of the same maize field. In other areas, where the alfalfa was recently cut, this gradient was no longer apparent. In the area of Coaximulco, *collops* beetles were more abundant in maize fields intercropped with apples than in corresponding monocultures. Coccinellid beetles, however, exhibited the opposite trends.

A survey of insect communities associated with maize was conducted near Lembang, Indonesia. Two types of cropping systems are common in the area: (1) *Kebun*, a mixture of annual crops (e.g., maize/cauliflower, maize/sweet potatoes (*Ipomoea batatas*), maize/bean), and (2) *Kebun-campuran*, a mixture of annuals and perennial shrubs and trees [e.g., maize, cauliflower, and cassava (*Manihot esculenta*) grown under a canopy of citrus (*Citrus* sp.), coffee (*Coffea arabica*), banana (*Musa paradisiaca*), and clove (*Syzgium aromaticum*)]. Four agroecosystems in which maize was a dominant crop were surveyed in August 1983 (Altieri and Marten, unpublished data). Each system was mapped and measurements were taken on weed diversity and percentage of cover, insect abundance, species diversity, and level of pest damage. Observations were complemented by interviews with farmers about crop management practices and socioeconomic aspects. Table 9.3 summarizes the profile of predator abundance and pest damage in the four cropping systems. Although our survey revealed variations in insect pest incidence and natural enemy abundance between fields, it is not clear whether these differences were related to the vegetational structure of the systems, or were merely a consequence of differential management, location, or chance. It would seem worthwhile to examine the elements of natural pest control built in these cropping systems, so that these elements can be retained in the course of agricultural modernization.

Methodologies in the Study of Insect Dynamics

Many approaches have been tried in plots of monocultures and polycultures to explain the ecological mechanisms underlying the effects of diversity. Risch

Table 9.3 Profile of Pest Damage and Relative Abundance of Predators in Maize Agroecosystems in Lembang, West Java[a]

Parameter	Results[b]			
	System 1	System 2	System 3	System 4
Maize plants infested with aphids (%)[c]	38	52	56	100
Maize plants with *Heliothis* damage (%)[c]	0	10	2	13
Maize plants with *Spodoptera* damage (%)	63	46	18	68
No. of coccinellid adults per 50 maize plants	37	4	19	8
No. of coccinellid larvae per 50 maize plants	24	11	47	62
No. of syrphid larvae per 50 maize plants	7	4	13	18
No. of spiders per 50 maize plants	93	130	78	187

[a]Means derived from 50 surveyed maize plants in each system, 70 days after planting.
[b]System 1: Maize field surrounded by a belt of cassava, banana, citrus, coffee, and other trees.
System 2: Maize sweet potato intercropping system.
System 3: Terraced cauliflower field with maize rows in the edge of the terrace.
System 4: Maize cauliflower intercropping system.
[c]Mostly small aphid colonies and light leaf damage, respectively.

(1981) studied beetle movement behavior to see if this could account for lower numbers of beetles in maize/bean intercrops. He placed directional Malaise insect traps on each side of every plot. When beetles flew out of the plot, some of them landed on the vertical trap walls and were caught in the collecting jars. By counting these trapped beetles and estimating the total number of beetles in the plot at that time from direct counts, he calculated a ratio of the two groups and called the ratio "tendency to emigrate," which measures the beetle's relative tendency to leave a plot once it has arrived. After 60 to 65 days, there was a much greater tendency to emigrate from the maize monoculture and the polycultures than from the bean monoculture. This corresponds with the observation that there were far fewer beetles on beans planted with maize in the polycultures than in the bean monocultures, and that this large difference became apparent approximately 65 days after planting. Maize has some kind of inhibitory effect on the presence of this insect species.

How does maize exert its inhibitory effect? Beans grown with maize are shaded more than beans in monocultures. One possibility is that the beetles avoid feeding in shaded areas, preferring to feed on plants that are not shaded. This was tested directly by constructing two large shade screens and suspending them 80 cm above the ground. One screen provided little shade, allowing 65 percent light transmission, and the other provided much more shade, allowing only 25 percent light transmission. Squash and bean plants were grown in the greenhouse and placed under these screens. Then the numbers of beetles on the plants were counted over a series of days. The results showed that there were always significantly more beetles under the light shade screen than the dark.

Yet shade might not be the only way that the presence of maize interferes with beetle flight behavior. To determine if a vertical obstruction, like a maize stalk, could discourage beetle colonization in other ways, dry maize stalks were staked among potted bean plants and a light screen was erected over the plants. Potted beans without maize stalks were also placed in a nearby area with a darker screen over them, so that the total amount of light reaching the plants in both areas was identical. Risch consistently found many more beetles in the beans without maize stalks, indicating that maize physically inhibited beetle colonization in ways other than by just increasing the overall shade of a microhabitat.

Although the above experiments provided an indication of the underlying causes of the reduction in beetle numbers in maize/bean polycultures, they did not help in predicting numbers of beetles in different variations of the entire maize/bean/squash system. Risch and Andow (unpublished data) also studied the influence of size of the plot and relative proportions of maize, beans, and squash on the number of beetles in the field. They observed and modeled the movement of one beetle, *Acalymma vittatum*, a squash specialist that is much more abundant in monocultures of squash than in maize/bean/squash polycultures in Ithaca, New York. The variables Risch and Andow thought might be important in ultimately determining the rate at which a beetle leaves a maize/bean/squash polyculture versus a squash monoculture are the following: the time a beetle spends on a maize, bean, or squash plant; the probability of moving to a maize, bean, or squash plant; the distance a beetle flies when it leaves a maize, bean, or squash plant and flies over an intercrop or monoculture; and its orientation behavior at the edge of a plot.

Wetzler and Risch (1984) examined the behavior of a coccinellid beetle in the field in four diffusion experiments. Each involved the release of beetle populations in a matched pair of agricultural plots (10 × 10 m each) planted to various combinations of maize, beans, and squash. The day preceding each release, all *Coleomegilla* individuals were aspirated from every plant, ensuring "clean" fields for each experiment.

In the first experiment 314 beetles were released in a high-density maize monoculture and an equal number in a maize/bean/squash polyculture 34 days after planting. Maize density was 3 times higher in the monoculture than polyculture. Releases in the two fields were completed within 20 minutes of each other by gently pouring dormant (chilled) beetles onto basal leaves. All beetles were marked in the first release with Testor's model paint applied to an eletryum. Sight-counting census was done at 1, 3, 6, 12, and 24 hours after release along the east-west, northeast-southwest, and northwest-southeast radii. This sampling arrangement established concentric annuli spaced 0.5 m apart.

In the second experiment, 175 beetles were released in each of the same two plots at 40 days after planting. In the third experiment, 65 days after planting, maize plants were selectively removed from the dense maize monoculture so that the total maize density was the same in the maize monoculture and maize/bean/squash polyculture. Thus, total plant density was 3 times higher in the polyculture. In the last experiment, the fourth release, 71 days after planting, was preceded by removal of all squash and bean plants from the polyculture to yield two sparse maize monocultures. The influence of food resources on mobility was tested by pruning all anthers, which contained the bulk of aphids and pollen fed upon by *Coleomegilla*, from each maize plant in one field and intertwining them among the intact anthers of the other monoculture.

Wetzler and Risch (1984) conducted another experiment to determine whether differences in diffusion rates from monocultures and polycultures might be caused in part by differences in the average time a beetle spent on maize, bean, and squash plants (i.e., tenure time per plant). Maize, squash, and bean plants were first grown in pots until all the plants were in flower. Approximately half the maize plants had large numbers of the corn aphid *Rhopalosiphum maidis*. In the first trial, 50 *C. maculata* were placed on five aphid-infested maize plants, 50 beetles were placed on five bean plants, and 50 beetles were placed on five squash plants (10 beetles per plant). The beetles were cooled to approximately 6°C before being placed on plants. The number of beetles remaining on the plants was counted approximately every 10 minutes for a period of 100 minutes.

Sight counting is an effective means of population censusing since the beetles are highly visible, thus avoiding problems associated with trapping. Careful collection of individuals for release enabled uniform, almost equivalent releases of adults. Since each experiment was run for only 24 hours and was preceded by a minimum of handling of beetles, mortality was extremely low

(0.5 percent) and complications due to beetle reproduction were nonexistent. The timing of the 1-, 3-, and 6-hour censuses was arranged to correspond with maximum periods of diurnal activity to ensure that the most conservative diffusion estimates would arise during the final censuses. Since all experiments were conducted within a 5-week interval, seasonal variability (i.e., migratory movements) of *Coleomegilla* activity was restricted.

Bach (1980) focused on the response of one specialist herbivore, the striped cucumber beetle (*Acalymma vittata*) to cucumber monocultures versus cucumber/broccoli/maize polycultures. By controlling total plant density, host-plant density, and plant diversity, Bach was able to distinguish the effects of these three confounding variables. Applying a three-way analysis of variance to censuses of beetles per cucumber plant, Bach reported a significant effect of both plant density and diversity on *Acalymma* abundance, but the results only partially support the resource-concentration hypothesis. Although an increase in stand purity yielded the expected increase in beetles per cucumber plant, an increase in cucumber density reduced the number of beetles per plant (Bach, 1980). Bach also found that cucumber plants were on average smaller in polycultures than in monocultures and that beetle density was positively correlated with plant size. There were two polyculture plots with cucumbers equal in size to monoculture cucumbers; in these two thriving polycultures, beetles were still significantly fewer per plant than in monocultures. Thus, it is clear that the reduced beetle numbers in polycultures cannot simply be attributed to smaller cucumber plants. In a later study with *Acalymma vittata*, Bach (1980) provided evidence for a surprising reduction in foliage palatability associated with cucumber/tomato polycultures. Beetles given a laboratory choice between cucumber leaves grown in monoculture and cucumber leaves grown in a tomato/cucumber mixture significantly preferred monoculture leaves. This illustrates the subtle links that are possible between plant diversity and plant quality, quite apart from the conventional ideas concerning the influence of resource concentration on herbivores (Kareiva, 1983).

In their studies of corn/cowpea/squash polycultures, Letourneau and Altieri (1983) found visual inspection sampling of thrips and *Orius* to produce a more representative measure of density than did sticky traps, pan traps, or Malaise traps, each of which showed very low catches. Ten hills of squash (each hill consisting of two plants) were randomly selected, and the plant most southwest in the hill was sampled by gently turning each leaf and recording the numbers of *Orius* adults and nymphs (as well as any other common arthropods). Thrips were counted on one medium-sized leaf of each plant. During the season, *Orius* densities increased and plants grew so large that the number of leaves sampled was reduced to five per plant: the growing shoot, two young, and two old leaves. Biomass estimates were made at 2-week intervals by measuring leaf widths on all the leaves of 10 plants per plot. The leaf width of squash plants was highly correlated with leaf biomass, determined as dry weight of the leaf blade ($r = 0.93$). To standardize for possible leaf size differences between treatments (and thus, searching-area differences), predator numbers per plant were converted to numbers per 5 g of leaf biomass. Individual leaves sampled for thrips were also measured to allow for conversion of thrips per leaf to thrips per 5 g of leaf biomass.

To determine whether predators were concentrated within treatments on plants with higher thrips densities, an index of aggregation was calculated on day 30. Ratios of mean thrips density on plants with *Orius* to those without *Orius* present would be significantly greater than 1 if *Orius* were showing such a preference within a treatment. These examples illustrate the range of methodologies that have been employed.

Management Considerations

Multiple crop management is basically the design of spatial and temporal combinations of crops in an area. There are many possible crop arrangements and each can have different effects on insect populations. For insects, the attractiveness of crop habitats in terms of size of field, nature of surrounding vegetation, plant densities, height, background color and texture, crop diversity, and weediness is subject to manipulation.

In intercrop systems, the choice of a tall or short, early- or late-maturing, flowering or nonflowering companion crop can magnify or decrease the effects on particular pests (Altieri and Letourneau, 1982). The inclusion of a crop that bears flowers during most of the growing season can condition the buildup of parasitoids, thus improving biological control. Similarly, the inclusion of legumes or other plants supporting populations of aphids and other soft-bodied insects that serve as alternate prey/hosts can improve survival and reproduction of beneficial insects in agroecosystems. The presence of a tall associated crop such as maize or sorghum may serve as a physical barrier or trap to pests invading from outside the field. The inclusion of strongly aromatic plants such as onion (*Allium cepa*), garlic (*Allium sativum*), or tomato (*Lycopersicon esculentum*) can disturb mechanisms of orienation to host plants by several pests.

The date of planting of component crops in relation to each other can also affect insect interactions in these systems. An associated crop can be planted so that it is at its most attractive growth stage at the time of pest immigration or dispersal, diverting pests from other more susceptible or valuable crops in the mixture. Planting of okra (*Hibiscus esculentus*) to divert flea beetles (*Podagria* spp.) from cotton in Nigeria is a good example (Perrin, 1980). Maize planted 30 and 20 days earlier than beans reduced leafhopper population on beans by 66 percent compared with simultaneous planting. Fall armyworm damage on maize was reduced by 88 percent when beans were planted 20 to 40 days earlier than maize when compared to simultaneous planting (Altieri et al., 1978).

We still understand little of how spatial arrangements (e.g., row spacings) of crops affect pest abundance in intercrops. For example, there is greater reduction in damage to cowpea flowers by *Maruca testulalis* in intrarow rather than interrow mixtures of maize and cowpea. Selection of proper crop varieties can also magnify insect suppression effects. In Colombia, lower whorl damage by *Spodoptera frugiperda* was observed in maize associated with bush beans

than in maize mixed with climbing beans. In the same trials, maize hybrid H-207 seemed to exhibit lower *Spodoptera* damage than hybrid H-210, when intercropped with beans (Altieri et al., 1978). Clearly, much further work is needed before appropriate crop mixtures and row spacings are to be achieved.

The manipulation of weed abundance and composition in intercrops can also have major implications on insect dynamics (Altieri et al., 1977). When weed and crop species grow together, each plant species hosts an assemblage of herbivores and their natural enemies; thus trophic interactions become very complex. Many weeds offer important requisites for natural enemies such as alternate prey/hosts, pollen, or nectar as well as microhabitats that are not available in weed-free monocultures (van Emden, 1965). The beneficial insects associated with many weed species have been surveyed (Altieri and Whitcomb, 1979). Relevant weeds that support rich natural enemy faunas include the perennial stinging nettle (*Urtica dioica*), Mexican tea (*Chenopodium ambrosioides*), camphorweed (*Heterotheca subaxillaris*), and goldenrod (*Solidago altissima*). In the last 20 years, research has shown that outbreaks of certain types of crop pests are more likely to occur in weed-free fields than in weed-diversified crop systems (Altieri et al., 1977). Crop fields with a dense weed cover and high diversity usually have more predaceous arthropods than in weed-free fields. Ground beetles, syrphids, and lady beetles (Coccinellidae) are abundant in weed-diversified systems. Relevant examples of cropping systems in which the presence of specific weeds has enhanced the biological control of particular pests can be found in Altieri and Whitcomb (1974) and Altieri and D. K. Letourneau (1982). These observations suggest that selective weed control may change the mortality of insect pests caused by natural enemies. The ecological basis for obtaining crop/weed mixtures that enhance insect biological suppression awaits further development.

EFFECTS OF MULTIPLE CROPPING ON PLANT DISEASES

In the wild, the dispersion of host plants among other plant species restricts the spread of pathogens (Browning, 1975). The situation is little different in traditional agroecosystems in which many crop species are grown in species-rich or genetically diverse mixtures (Thresh, 1982). Such diversity gives a measure of stability in that the failure of some species or genotypes due to diseases may be compensated by the improved performance of others if adequate time is available for compensatory growth. The presence of immune or resistant plants in the mixtures impedes pathogen spread and increases the separation between susceptible plants. Based on this rationale, Larios and Moreno (1977) have convincingly argued that the most suitable agroecosystems to avoid disease damage in tropical areas are multiple cropping systems that resemble the local natural system.

Larios and Moreno (1977) documented evidence of disease buffering in various tropical intercropping systems. For example, *Ascochyta phaseolerum* was less prevalent in cowpea interplanted with maize than in cowpeas growing alone. The total number of diseased plants as well as the speed of dissemination

of the pathogen was less in the polyculture. The maize plants apparently act as a natural barrier to the free spread of the fungus propagules. In this same crop association, cowpea virus diseases were less prevalent. The total number of infected plants with cowpea mosaic virus (CPMV) and chlorotic cowpea mosaic virus (CCMV) was less in polycultures than in monocultures, apparently because fewer numbers of vector chrysomelid beetles (e.g., *Diabrotica cerotoma*) were present in the mixed stands. A similar situation occurred in Malawi, where beans trapped aphids, thus decreasing the spread of rosette disease of groundnut in mixed stands (Thresh, 1982). Radish mosaic in Japan decreased when radishes (*Raphanus sativus*) were sown between rows of rice (*Oryza sativa*) or trefoil, and pigeon pea in Haiti was completely protected from virus diseases when grown between rows of tall sorghum (Palti, 1981).

These data indicate that the use of nonhost crops in interplantings can significantly reduce the rate of virus spread in the field. A buffer crop such as maize, when grown between the source of peanut mottle and a susceptible soybean crop, can reduce the amount of separation required to prevent disease spread (Zitter and Simons, 1980). Mosaic virus of alfalfa is more prevalent in monocultures than in mixtures with cocksfoot grass (Thresh, 1982). The only example in which multiple crops have been adopted is for protecting sugar beet (*Beta saccharifera*) seed crops from aphid-borne viruses by intersowing with barley or other crops. Growing of mustard or barley which grows to heights of 66 and 41 cm, respectively, together with sugar beet stecklings lowers the incidence of beet mild yellowing virus in the stecklings (Palti, 1981).

Another example of disease reduction occurs when maize is grown in association with cassava. Cassava scab (*Sphaceloma sp.*) is notably reduced in cassava/maize polycultures. By doubling over the maize stalks before harvesting, there is an increase in the disease, thus showing the protective effect of the maize (Larios and Moreno, 1977). Similarly, dieback in cassava caused by *Glomerella cingulata* was more intense in the monocultures. On the other hand, the severity of angular leaf spot of beans caused by *Isariopsis griseola* was highest in bean polycultures that included maize and lowest in systems where beans were intercropped with sweet potato or cassava (Moreno, 1977).

Some crop associations, due to the microclimate modifications imposed by the dominant crop, result in increases in relative humidity and shade which may favor the incidence of diseases, such as angular leaf spot and wilt (*Thanatephorus cucumeris*) of the common bean. In such cases it is necessary to modify the spatial arrangement of the associations to alter the microclimate and thus minimize the negative impact of these diseases. In general, the shielding effect of the companion crops against airborne pathogens should more than offset the microclimatic advantage pathogens may derive from the dense foliage of mixed crops (Palti, 1981).

In summary, mixtures of different crop species buffer against disease losses by delaying the onset of the disease, reducing spore dissemination, or modifying microenvironmental conditions such as humidity, light, temperature, and air movement. Certain associated plants can function as repellants, antifeedants,

growth disrupters, or toxicants. In the case of soilborne pathogens, some plant combinations may enhance soil fungistasis and antibiosis through indirect effects on soil organic matter content; however, research in this area is largely lacking (Sumner et al., 1981). Provided the pathogen/host/environment relationship is understood in a particular cropping system, the use of mixed cropping and therefore a diversity of genotypes shows great possibilities for disease reduction. A parallel approach involves the use of multilines in cereal crops to achieve high genetic diversity (Browning, 1975).

IMPACT OF MULTIPLE CROPPING SYSTEMS ON NEMATODE POPULATIONS

The concept of crop diversification for the management of nematode populations has been applied mainly in the form of decoy and trap crops. Decoy crops are nonhost crops which are planted to make nematodes waste their infection potential. This is effected by activating larvae of nematodes in the absence of hosts that would enable them to continue their development. A list of nematodes that can be decoyed in this way is presented in Table 9.4.

Trap crops are host crops sown to attract nematodes but destined to be harvested or destroyed before the nematodes manage to hatch. This has been advocated for cyst nematodes, sowing crucifers to be plowed in before the nematodes of beets can develop fully. The same objective is achieved in pineapple (*Ananas comosus*) plantations by planting tomatoes and destroying them before root-knot nematodes can produce eggs (Palti, 1981).

There is also evidence that some plants adversely affect nematode populations through toxic action. Oostenbrink et al. (1957) showed that several varieties of *Tagetes erecta* and *T. patula* reduced the population of certain root-infecting nematode species such as *Pratylenchus*, *Tylenchorchynchus*, *Paratylenchus*, and *Rotylenchus*. The effect of marigolds on *Pratylenchus* eelworms appears to be due to the nematicidal action of the growing plant roots which exude alpha-terthienyl. In subsequent studies, Visser and Vythilingum (1959) also reported that these two marigold species considerably decreased *Pratylenchus coffeae* and *Meloidogyne javanica* populations in tea (*Camellia sinensis*) soil. The cultivation of marigolds reduced nematodes more quickly and more effectively than keeping the tea soil fallow. There are other plants whose root extracts show nematicidal action. For example, *Ambrosia* spp. and *Iva xanthiifolia* reduce populations of *Pratylenchus penetrans* (Hijink and Suatmadji, 1967).

Table 9.4 Decoy Crops Used for the Reduction of Nematode Populations

Crop	Nematode species	Decoy crops
Eggplant	*Meloidogyne incognita, M. javanica*	*Tagetes patula, Sesamum orientale*
Tomato	*M. incognita, Pratylenchus alleni*	*T. patula*, castor bean, chrysanthemum
Tomato	*M. incognita*	*T. patula*, groundnuts
Narcissus, tomato, okra	*Meloidogyne* sp.	*T. patula*
Soybean	*Rotylenchulus* sp., *Pratylenchus* sp.	*T. minuta, Crotalaria spectabilis*
Various	*Pratylenchus penetrans*	*T. patula*, hybrids of *Gaillardia* and *Hellenium*
Various	*Pratylenchus neglectus*	Oil-radish (*Raphanus cleiferus*)
Oats	*Heterodera avenae*	Maize
Various	*Trichodorus* sp.	Asparagus

Source: Data from Palti, 1981.

Little work has been conducted on nematode suppression in intercropping systems. The nematode *Anguina tritici*, which enters wheat seedlings from the soil and infests the ears, has been partially controlled in India by growing *Polygonum hydropiper* with wheat (*Triticum* sp.). Also in India, the plant *Sesamum orientale* has been found to produce root exudates that are nematicidal to root-knot nematodes and to decrease root-knot infestation in *Abelmoschus esculentus* growing alongside (Atwal and Mangar, 1969).

Egunjobi (1984) recently studied the ecology of *Pratylenchus brachyurus* in traditional maize cropping systems of Nigeria. Nitrogen/phosphorus/potassium fertilizer applications increased the numbers of the nematode more in soil under monoculture maize than in plots with maize intercropped with cowpea, groundnut, or green gram.

ECOLOGY AND MANAGEMENT OF WEEDS IN INTERCROP SYSTEMS

Weed management in intercrops has been the subject of very little research but is an important topic for four reasons. First, intercropping is a cultural method used by the majority of farmers in Latin America (Pinchinat et al., 1976; Francis et al., 1976), Africa (Okigbo and Greenland, 1976), and Asia (Harwood and Price, 1976). While intercropping is commonly practiced on small farms where capital inputs are limited, intercropping yield advantages are by no means restricted to such situations (Osiru and Willey, 1972; Bantilan et al., 1974; Andrews and Kassam, 1976; Sanchez, 1976). Second, in spite of their many beneficial uses (Van de Goor, 1954; Mishra, 1969; Kapoor and Ramakrishnan, 1975; Altieri et al., 1977; Bye, 1981; Chacon and Gliessman, 1982; Weil, 1982), weeds can seriously limit food production in both monoculture and intercropping systems (Muzik, 1970; Holm, 1971; Moody, 1977). Weed control is often the operation with the highest labor demand during the cropping cycle (Moody, 1977; Compton, 1982). Third, weed management is a central point of coordination for many farm operations. Effective weed management involves integration of soil fertility and water management, tillage practices, choice of crop sequences, crop density, crop species and cultivars, insect management, labor, available traction power, and cash inputs (Bantilan et al., 1974). Finally, interactions between three or more plant species can be complex and might not be predictable from knowledge of monoculture and binary mixture results (Haizel and Harper, 1973). Crop cultivars, proportions, densities, spatial arrangements, and management practices

that give high intercrop yields under weed-free conditions may not give acceptable yield and weed suppression under weedy conditions (Plucknett et al., 1977). Solutions to this problem will require detailed studies of weeds in intercrop systems, although knowledge about how crops and weeds grow alone and in binary mixtures will be very useful.

Weed management for any cropping system can involve the use of many kinds of biological, physical, and chemical techniques to promote crop dominance over weeds. There is no question that herbicides, tillage, and water management can be important components of weed management programs for intercrop systems (Bantilan et al., 1974; Plucknett et al., 1977; Akobundu, 1980a; Moody and Shetty, 1981). However, this review concentrates on biological factors affecting intercrop/weed balance. There are several reasons for this.

There is growing recognition among weed scientists that farmers in both industrialized and developing nations cannot rely entirely on herbicides for weed control (Akobundu, 1980a; Walker and Buchanan, 1982). Many weed species are evolving herbicide resistance, making chemical control less effective and more costly (Plucknett et al., 1977; Lebaron and Gressel, 1982). Many farmers lack the cash or credit necessary for the purchase of herbicides and the appropriate application devices, and in many areas extension education is inadequate for selection of appropriate chemicals for specific weed problems (Akobundu, 1980a). If they are affordable, available herbicides may be undesirable because of safety and environmental considerations (Pimentel et al., 1980; Revkin, 1983). Because herbicides are often crop specific it has been difficult to find compounds that will control a broad spectrum of weeds without causing damage to the component crops of the intercrop (Moody and Shetty, 1981).

Physical manipulations of the intercrop environment for weed control very closely resemble those used for sole crops. Technical problems of tillage operations for intercrops remain to be worked out for many crop combinations, but solutions appear possible with adaptations of existing technologies (Anderson, 1981).

In contrast to chemical and physical means of weed control in intercrop systems, the biological factors that promote intercrop dominance over weeds are complex and poorly understood. These factors are a farmer's first line of defense in preventing crop losses to weed interference and have critical importance in the design of effective weed management strategies for intercrop systems.

Intercrop weed management combines two qualitatively different aspects of plant/plant interactions. To increase intercrop yields, complementarity in patterns of resource use by the component crops must be emphasized. The goal is to minimize the degree of overlap in resource use by intersown crop species such that more resources are exploited and more yield can be harvested per unit of ground area. In contrast, to achieve weed control, the similarity of requirements of crop and weed species, the consequent competition for limited resources, and the suppression of growth and yield of the associated species are emphasized. Weed scientists and farmers work to create an environment that is detrimental to weeds and favorable to crops. Intercropping has potential as a

means of weed control because it offers the possibility of a mixture of crops capturing a greater share of available resources than in monocropping, preempting their use by weeds.

Intercropping can be practiced in two distinct ways. A farmer can desire a certain amount of yield from each component of an intercrop and use a cropping system that balances interference between crops to give a desirable result. Alternatively, a farmer can be primarily interested only in the yield of one main crop and intersow other species for insurance against crop failure, minor economic uses, erosion control, soil fertility maintenance, and/or weed control. In the first case it is the summed yield of the two or more components viewed on some sort of relative basis (e.g., land equivalent ratio, LER) that is important. In the latter case, the intercrop is meant to give full yield of the main crop, with the intersown minor species providing some additional benefit.

Provided that interference between crop components is weaker than that between crops and weeds, both types of intercropping can suppress the growth of weeds more than sole cropping (Yih, 1982). It should also be noted that intercropping may suppress weeds no more than sole-cropping but still provide more yield because of exploitation of otherwise unoccupied niches by one or more of the added crop components. This is shown (Table 9.5) by the results of two experiments conducted with barley and pea (*Pisum sativum*) (Liebman, unpublished data). Weed growth was similar in the intercrop and monoculture

Table 9.5 Barley, Pea, and Weed Yields from Two Experiments Conducted near Ithaca, New York[a]

Experiment	Yield (g/m²)	
	Warren Farm, 1982	Turkey Farm, 1983
Total seed crop:		
Weedy monoculture—barley	175.0 ± 4.1	153.3 ± 10.6
Weedy intercrop—barley	154.4 ± 13.6	139.9 ± 15.1
(Partial LER)	(0.88)	(0.92)
Weedy monoculture—pea	214.7 ± 8.1	63.4 ± 8.5
Weedy intercrop—pea	207.3 ± 13.1	62.6 ± 10.7
(Partial LER)	(0.96)	(0.99)
(Total LER)	(1.84)	(1.91)
Total aboveground weed biomass:		
"Weeds alone" control	523.9 ± 9.9	302.5 ± 24.3
Weedy pea monocultures	446.7 ± 50.6	266.6 ± 26.2
Weedy barley monocultures	183.2 ± 12.6	165.4 ± 11.4
Weedy intercrop	174.2 ± 5.6	166.1 ± 15.3

[a]Intercrops were additive mixtures of the two component monocultures. Weeds (mostly *Brassica* spp.) were intentionally sown at high densities, and no weed control was practiced during the course of the experiments. Means and their standard errors are shown.

Source: Liebman, unpublished data.

barley, however intercrop yield advantages were substantial because of the added yield of pea.

Factors Affecting Intercrop/Weed Balance

Although intercropping appears to offer considerable potential as a means of increasing crop dominance over weeds, the effectiveness of weed control by intercrop systems differs not only among intercrop combinations but also among replicated trials of a single combination (Moody, 1980). In a review of the intercrop/weed literature, Moody and Shetty (1981) noted that the growth of weeds in an intercrop may be either severely depressed or hardly affected, relative to crop-free control treatments. Moreover, weed growth in intercrops may be lower than in all component monocultures, lower than in one of the monocultures, or equal in the intercrop and monocultures. Intercrop yield data are similarly variable. Much research remains to be done before the reasons for these different results become clear, but the following factors have been suggested to influence intercrop/weed relationships. Their effects are reviewed by Moody (1980) and Moody and Shetty (1981). Zimdahl (1980) and Walker and Buchanan (1982) provide relevant reviews of the role of these factors for weed control in monocultures.

Crop Density Crop density is one of the most easily manipulated factors affecting crop production, and it is well known that increased seeding rates can promote crop dominance over weeds in monoculture cropping systems (Godel, 1935; Staniforth and Weber, 1956). Highest yields for many intercrop combinations grown under weed-free conditions are obtained with increased crop population densities (Osiru and Willey, 1972; Willey and Osiru, 1972; Willey, 1979). Similarly, maximum intercrop yields and weed suppression are obtained under weedy conditions with total crop densities significantly higher than those used for monocultures (i.e., the superposition of normal or even higher density monocultures of the components to form "additive" crop mixtures) (Moody and Shetty, 1981). Data from Shetty and Rao (1981) illustrate this principle very clearly (Table 9.6). Highest combined crop yields and the greatest degree of weed suppression were obtained from a sorghum/pigeon pea mixture with a normal density of pigeon pea sown with a twice normal population of sorghum.

Amy et al. (1929) found that weed growth in a flax/wheat intercrop was inversely proportional to crop density. As the seeding rate for either or both components of the mixture increased, weed weights decreased. Weeds were particularly sensitive to the presence of wheat, and the authors concluded that intercropping the two species made it possible to grow flax on land that was too weedy for flax alone. Economic returns from the intercrop were generally as good or better than those from the highest earning sole crop.

"Smother" intercrops and "live mulch" intercrops are high-density, additive crop mixtures that appear to offer great promise as means of weed control. In these situations low-growing weed-suppressive species are sown between rows

Table 9.6 Influence of Crop Density of Sorghum/Pigeon Pea Intercrops on Crop Yields and Weed Growth[a]

Treatment[b]	Yield (kg/ha)		LER	Weed count per meter of sorghum row	Weed dry matter at harvest (g/m²)	
	Sorghum	Pigeon pea			Sorghum	Pigeon pea
N-sorghum	4043	—	—	22	30	—
N-pigeon pea	—	1704	—	—	—	142
0.5N-sorghum + 0.5N pigeon pea	2108	809	1.0	21	36	118
0.5N-sorghum + N-pigeon pea	2438	970	1.2	15	32	95
0.5N-sorghum + 2N-pigeon pea	2540	1002	1.2	17	25	43
N-sorghum + 0.5N pigeon pea	2895	804	1.2	21	23	52
N-sorghum + N-pigeon pea	2615	1062	1.2	17	15	51
N-sorghum + 2N-pigeon pea	2913	1375	1.5	12	18	46
2N-sorghum + 0.5N pigeon pea	2675	661	1.0	15	10	45
2N-sorghum + N-pigeon pea	3168	1295	1.6	16	10	26
2N-sorghum + 2N-pigeon pea	3118	1071	1.4	12	9	31
LSD (0.05)[c]	902	517	—	—	39	15

[a]One initial hand weeding was given to all treatments 3 weeks after planting
[b]N-sorghum = "normal" sorghum population of 180,000 plants per hectare.
N-pigeon pea = "normal" pigeon pea population of 40,000 plants per hectare.
0.5N = one-half the normal; 2N = twice the normal.
[c]LSD, Least Significant Difference
Source: Data from Shetty and Rao, 1981.

of main crop species. Akobundu (1980a) reported that melon (*Citrullus lanatus*) and sweet potato could replace three hand weedings when intersown into sole-cropped yam or yam intercropped with maize and cassava. The vining smother crops not only served as a labor-saving means of weed control, but also provided erosion control through increased soil coverage. Two legume species, *Centrosema pubescens* and *Psophocarpus palustris*, gave excellent control of weeds when intersown between maize rows (Akobundu, 1980b). Maize yields were significantly higher in the live mulch plots that received no fertilizer than in unfertilized conventionally tilled and no-till plots. When fertilizer was applied to the treatments, maize yields in the live mulch plots were equal to or better than the conventionally tilled and no-tillage plots. Akobundu (1980b) concluded

that the intersown legume species contributed nitrogen to the maize and that this production system offers the opportunity for improving soil fertility, crop yield, and weed control on otherwise impoverished soils of the humid tropics.

The legume species, *Desmodium heterophyllum* and *Phaseolus vulgaris*, sown between rows of cassava, gave similar weed control to that achieved with continuous manual weeding (CIAT, 1980). The seed cost of the legumes was offset by the value of the bean crop and the long-lasting cover, erosion control, nitrogen fixation, and forage material from *D. heterophyllum*. Williams (1972) found that undersowing barley or fava bean with ryegrass (*Lolium* sp.) or red clover (*Trifolium pratense*) greatly decreased the growth and survivorship of weed seedlings. Although yields were not assessed, the barley crop appeared to be high yielding.

Shetty and Rao (1981) reported that interplanting cowpea and mung bean (*Vigna radiata*) into sorghum or pigeon pea minimized weed growth after one hand weeding. The weed suppression due to the smother crops was about the same as that obtained with two hand weedings. The smother crops had no significant effect on either sorghum or pigeon pea and provided additional grain yield themselves. However, the smother crops were ineffective for weed control in sorghum/pigeon pea intercrops and lowered yield of both intercrop components. Thus the results of the multicomponent mixture could not be predicted from knowledge of growth of the species in simpler combinations.

Robinson and Dunham (1954) found that soybean sown in narrow rows with winter wheat or winter rye as companion crops yielded as much or more than soybean without companion crops whether in noncultivated narrow rows or in cultivated wide rows. Weed control with companion crops was about equal to that achieved by cultivation. Intersowing wheat or rye into soybean was a relatively inexpensive method of weed control that could reduce soil erosion and organic matter losses associated with normal monoculture production methods.

It should be noted that intersown live mulch crops can greatly reduce the yields of main crop species if competition for water and/or nutrients is strong. Kurtz et al. (1952) reported that when maize was sown between strips of previously established legume and grass sods, maize yield was severely depressed. Decreases in maize yield from intercrop plots could be partially reversed with either added nitrogen or water and more fully reversed with both nitrogen and water, although maize yields from sole crop plots usually exceeded those from fertilized and irrigated intercrop plots by about 15 percent. The ability of live mulch crops to compete with main crop species may be limited by the use of growth retardants (Akobundu, 1980b) and low doses of herbicides (Vrabel et al., 1980b), use of less aggressive species and cultivars (Vrabel et al., 1980a; Nicholson, 1983), simultaneous planting dates for main crop and live mulch species (Robinson and Dunham, 1954; Vrabel et al., 1980a), and mowing the mulch species (Vrabel et al., 1980b).

Spatial Arrangement Crop and weed plants are sessile, and the capture of growth resources is a very local phenomenon. Because of this, the intensity of interference between neighboring plants tends to increase as the distance between them decreases (Harper, 1977). More equidistant spacing for a single crop species grown under weedy conditions should thus decrease the strength of interference between crop plants and increase interference between the crop and associated weeds. Walker and Buchanan (1982) note that at equal seeding rates sole crops are generally more weed-suppressive when planted in narrower (i.e., more equidistant) rather than wider (i.e., less equidistant) rows.

The effects of intercrop spatial arrangement on associated weeds have not yet received much attention from researchers. Because interference between crop components can have indirect effects on crop/weed relationships (Yih, 1982), the effects of intercrop spatial arrangement are more complex than for sole crops. Bantilan et al. (1974) found that with equal maize populations, mung bean reduced weed growth more when it was intercropped between wide maize rows than when it was sown between narrow maize rows. The researchers noted a similar but less pronounced effect for intercropped peanut.

Relative Proportions of Component Crops Shetty and Rao (1981) reported that sole-cropped pearl millet (*Pennisetum americanum*) suppressed the growth of weeds much more strongly than sole-cropped groundnut, and that weed growth in mixtures of the two crops closely reflected varying proportions of the components. Weed yields increased as the proportion of millet in the mixture decreased. A 1:3 pearl millet/groundnut row arrangement gave the highest combined crop yield (LER = 1.15), although it gave a small amount of weed suppression relative to that obtained from mixtures containing a higher proportion of millet.

Crop Species and Cultivar In intercrop/weed experiments in which crop components are varied, large differences in weed-suppression ability have been noted among species (Robinson and Dunham, 1954; Williams, 1972; Bantilan et al., 1974; Shetty and Rao, 1981). These reflect differences in the timing and nature of resource capture and are manifest in differences in growth form between species. For example, in maize-based intercrop systems, Bantilan et al. (1974) found that mung bean was more weed-suppressive than peanut and ascribed this to its more rapid early growth and more uniform canopy structure. Experiments with sole crops have shown that within species large differences in weed-suppression ability exist among genotypes (Kawano et al., 1974; McWhorter and Hartwig, 1972; Yip et al., 1974; Stilwell and Sweet, 1974). Few researchers have evaluated the effects of crop cultivars on weed suppression in intercrop systems. Bantilan et al. (1974) reported that when two cultivars of mung bean were intercropped with maize the more prostrate cultivar was more weed-suppressive. However, the cultivars were not compared in the same experiment. Rao and Shetty (1976) observed differences in weed suppression between two pigeon pea cultivars when they were sole cropped, but no such difference was apparent when they were intercropped with sorghum. Maize cultivars did show differences

in weed suppression when intercropped with sweet potato (Moody and Shetty 1981).

Fertility Differential response to applied fertilizer, especially nitrogen, can greatly alter the nature of interference between associated plant species (Blaser and Brady, 1950; Stern and Donald, 1962; de Wit et al., 1966; Appleby et al., 1976). The possibility of interactions between cropping systems and fertility levels must be considered carefully. Bantilan et al. (1974) reported that as the amount of applied nitrogen increased, maize/peanut (*Arachis hypogaea*) and maize/sweet potato intercrops were more weed-suppressive, whereas a maize/mung bean intercrop became less weed-suppressive. Crop yields (measured by LER) were thus determined by interactions between cropping systems, soil fertility level, and method of weed control.

Other Factors Other factors, such as soil moisture, weed density, weed community composition, herbivores, and pathogens undoubtedly have important influences on intercrop/weed relationships, but clarificiation of their roles awaits further investigation.

Shifts in Weed Species Composition in Intercrops

It has long been recognized that different species of weeds are commonly associated with different crops (Plucknett et al., 1977; Muenscher, 1980). This is the result not only of differences in weed control techniques normally associated with specific crops (e.g., tillage, herbicides), but also of differences in the nature of crop/weed interference (Buchanan et al., 1975). These species-specific types of interactions result in shifts in weed species dominance between crops (IRRI, 1975), and for this reason, crop rotation can be used as an effective means of preventing population increases of any single weed species (Walker and Buchanan, 1982).

In contrast to rotational sequences of crop monocultures which combine the weed-suppressive effects of different crops over an extended period of time, intercropping combines the weed-suppressive effects of different crops within a single season. It is therefore of interest to compare the composition of the weed flora associated with intercrops to the weed flora of each component monoculture.

Shetty and Rao (1981) found that the species composition of weeds associated with groundnut/pearl millet intercrops was greatly influenced by varying proportions of the intercrop components. In sole-cropped pearl millet, the weed flora was a mixture of many species, whereas in sole-cropped groundnut the predominant weeds (80 percent of total weed biomass) were species of only *Celosia*, *Digitaria*, and *Cyperus*. As more rows of groundnut were introduced in place of pearl millet rows, there was a striking increase in both numbers and biomass of the tall and competitive *Celosia*. The buildup of *Celosia* was found only in groundnut rows, for it occurred in negligible numbers in and around pearl millet rows. These results strongly suggest that with regard to weed community composition, crop/weed interactions are extremely localized and that shifts in weed floristics due to intercropping might be predicted from knowledge of weed community composition in sole crops of the components.

Mohler and Liebman (unpublished data) grew weedy barley and pea monocultures and intercrops and found that the influence of cropping treatment on the relative composition of the weeds paralleled effects on total weed productivity. As weed yields decreased due to increased interference from crops, the relative importance of the dominant weed species (*Amaranthus retroflexus* or *Brassica kaber*) decreased. These results are similar to those of Shetty and Rao (1981) who noted more mixed assemblages of weeds in more competitive crop systems. The extent that intercropping can increase interference from crops to weeds may thus be closely related to the usefulness of intercropping in preventing shifts in weed community composition toward dominance by a few, highly competitive species.

Mechanisms of Weed Suppression in Intercrops

Much of the recent research devoted to weed-free intercrop systems has stressed ecophysiological mechanisms by which overyielding takes place (Trenbath, 1975, 1981; Willey and Roberts, 1976; Wahua and Miller, 1978a, 1978b; Natarajan and Willey, 1981; Reddy and Willey, 1981; Martin and Snaydon, 1982). This research has placed crop growth and development in the context of resource capture and conversion and has shown very clearly how niche differences between crop species can lead to increased biological efficiency and yield advantages over sole cropping (Willey, 1979; Vandermeer, 1981). This situation is in marked contrast to that of intercrop/weed relationships, where hypotheses of niche preemption, competitive exclusion, and allelopathic interference cannot be adequately evaluated for lack of sufficient ecophysiological data. Collection of such data should prove exceptionally fruitful for the design and improvement of weed-suppressive intercrop systems.

Bantilan et al. (1974) provided evidence that light interception by maize/mung bean, maize/peanut, and maize/sweet potato intercrops was greater than that by the component monocultures. This effect was evident within 30 days after sowing the crops. The authors concluded that the intercrops were better at suppressing weeds because of increased preemptive use of light effected by earlier canopy closure.

The importance of belowground resource use in influencing intercrop/weed interactions should not be ignored. Mohler and Liebman (unpublished data) measured predawn water potential of the weed *Amaranthus retroflexus* growing in barley and pea monocultures, a replacement series barley/pea intercrop, and unplanted control plots. Large differences were detected among treatments (Table 9.7). In particular, water deficits for *Amaranthus* were greater in plots containing barley (i.e., the barley monoculture and the intercrop) than in plots without barley (i.e., the pea monoculture and the unplanted control). Growth of *Amaranthus* in association with pea was much depressed relative to the crop-free control treatment (Table 9.7), indicating that factors other than late-season soil moisture were also important in influencing crop/weed balance.

Table 9.7 Predawn Water Potentials and Final Aboveground Biomass of the Weed *Amaranthus retroflexus* Grown in Crop-free Control Plots, Barley and Pea Monocultures, and a Replacement Series Intercrop

Treatment	Predawn water potential (bars)[a]	Biomass at harvest (g/m²)
Crop-free control	−24.8 ± 2.7	516.7 ± 39.5
Pea monoculture	−23.2 ± 3.5	249.1 ± 53.3
Pea/barley intercrop	−33.9 ± 3.5	112.6 ± 44.6
Barley monoculture	−37.3 ± 3.5	73.7 ± 53.3

[a]Water potential (measured 58 days after planting) data reflect effects of long drought period. Results given as means and their standard errors.
Source: Mohler and Liebman, unpublished data.

The role of allelochemical interference between intercrop components and weeds has scarcely been explored, although this type of weed control has been shown to be potentially useful in monoculture cropping systems (Putnam and Duke, 1974; Fay and Duke, 1977; Lockerman and Putnam, 1979). The question of allelochemical control of weeds in intercrop systems is complicated by the possibility of interference between crop species. For allelopathy to be effective for weed control in intercrops there must be selectivity in the effects of toxins released by the crops: weed species must be more susceptible than crop components. Recent work by Gliessman (1983) shows that this selectivity may indeed be possible.

Gliessman (1983) evaluated the effect of squash leaf extract on radicle elongation of maize, cowpea, and cabbage (*Brassica oleracea capitata*). The extract was found to have a stronger inhibitory effect on cabbage than on the other two species. Gliessman suggested that the interplanting of squash into maize/cowpea intercrops by farmers in southeastern Mexico is an effective means of weed control (Gliessman et al., 1981; Letourneau, 1983) not only because of the shade cast by the squash leaves, but also because of selective allelochemical inhibition. Gliessman (1983) also found that extracts of certain "nonweed" species intentionally maintained by local farmers in maize/cowpea fields (Chacon and Gliessman, 1982) had only weak inhibitory effects against maize and cowpea, but strong inhibitory effects against cabbage. He proposed that noncrop species offer possibilities for selective allelochemical weed control.

Recommendations for Further Reseach

It is clear from the preceding discussion that manipulations of the biological characteristics of intercrop systems can strongly affect crop/weed relationships. However, understanding of the biology of intercrops and associated weeds has not yet developed to the point where meaningful predictions of crop and weed responses to altered environmental conditions can be made.

Knowledge of patterns of resource use by intercrops and weeds would clearly be helpful in generating general theories of intercrop/weed interactions. Such ecophysiological studies should provide invaluable information about the altered

environments that intercropping presents to weeds as well as the responses of intercrops and weeds to resource deficits resulting from biotic interactions. The role of allelopathy in intercrop/weed dynamics may be important and warrants investigation. In both resource preemption and allelochemical approaches to intercrop weed control emphasis should be placed on understanding and exploiting the differential response of crop and weed species to altered environmental conditions.

Current knowledge of genotype resource environment, and cropping system interactions is very poorly developed. Morphological and physiological characteristics of species and cultivars exhibiting different yield and interference abilities should be investigated in intercrop/weed communities. Better understanding of the ecophysiological factors responsible for shifts in weed species composition might allow manipulation of intercrop systems to prevent population increases of particularly noxious weeds.

CONCLUSIONS

A considerable amount of work has emerged in the last decade, showing that diversification of crop habitats frequently results in reduced pest incidence. The studies have disproportionately focused on insect dynamics, with little attention given to the effects of multiple cropping systems on disease epidemiology and especially weed ecology. Research projects that integrate the simultaneous effects of polycultures on all biotic components of the agroecosystems are sorely lacking. There is every reason to expect an increase of multitrophic level interactions as the crop systems become richer in plant, insect, and microorganism species diversity. Unraveling these complex relationships can lead to pest management systems that integrate cropping practices, weed control measures, and soil management to provide effective and harmonious means of disease, weed, and insect control.

It is clear that these complex systems affect insect populations by either interference with herbivore movement and colonization or by increased herbivore mortality caused by natural enemies. Whatever the underlying mechanisms accounting for pest reduction, data are of some predictive value. However, generalizations and recommendations are difficult for yet untried systems. It is here where studies of traditional polycultures may be of value in guiding the design of pest resistant cropping systems. Evidence suggests that in many areas, peasants have kept pest damage within acceptable bounds by employing a wide variety of traditional management practices centered around the use of polycultures. Some mixtures, like the maize/bean/squash of Central America and Mexico or the genetically rich potato fields of the Andes, have persisted for centuries, exhibiting an array of stabilizing properties (Wilken, 1977).

It has been suggested that multiple cropping potentials are restricted to less developed countries where low-input agriculture is practiced, because they are capital-restricted, labor demanding, and management-intensive production systems. It is also implied that these systems cannot be efficiently mechanized,

limiting their adoption in developed countries. One of the main reasons why the cotton/alfalfa strip cropping system, which efficiently reduced *Lygus* bugs in California, was not adopted was because of added costs in the alfalfa cutting operations and different water needs of both crops, thus upsetting irrigation schedules. Some agronomists argue that mixed agriculture cannot be implemented within the actual structure of U.S. agriculture (large farms with capital-intensive operations). In an era of increasing costs of chemical-based agriculture and accelerating concern about the contamination of an environment, these multiple species systems provide an alternative on farms of all sizes. Further research is needed to explore the applications of multiple cropping systems as one component of a management-intensive approach to insect, pathogen, and weed control.

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19