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Chapter 5

Plant Interactions in Multiple Cropping Systems

Stephen R. Gliessman

In much of conventional agriculture where optimal densities of single crop plantings are the rule, the strict management of the physical factors of the crop ecosystem usually suffices in order to obtain maximum yields. This includes optimum fertilizer levels, water availability, light capture, and other factors that can be manipulated to the benefit of crop output. With additional weed, insect, and disease control, the monoculture cropping system can lead to substantial harvests. But as the advantages of multiple cropping become more recognized (ASA, 1976; Kass, 1978; Harwood, 1979; Willey, 1979a, 1979b; ICRISAT, 1981; Gliessman et al., 1981; Vandermeer et al., 1983), and the move is made toward intercropping two or more different plant species on the same land at the same time, the need for a more in-depth understanding of the biotic components of plant interactions becomes very important. Such information is key to designing and managing complex multiple cropping systems capable of advantageous and consistent results.

Most of our knowledge about the ecological basis for plant interactions comes from the study of natural ecosystems and plant ecology (Daubenmire, 1974). A great variety of classification schemes has been presented in order to better understand the diversity of types of biotic interactions between species, and one I feel best represents the broadest range has been summarized by Odum

(1971, Chap. 7). As can be seen in Table 5.1, the type of interaction will determine the resulting shift in population levels of the species involved. This classification scheme is very broad, and covers plant/animal and animal/animal interactions as well. It focuses on the end result of the interactions as expressed by population growth and survival. The actual mechanisms of interaction are not emphasized. In the design and management of multiple cropping systems, a knowledge of these mechanisms can be very important.

Harper (1977, Chap. 11) most thoroughly examined the importance of understanding the mechanisms of plant interactions. When describing the nature of interactions, he focuses on the fact that a plant may influence its neighbors by changing their environment. These changes may be by means of an addition or removal reaction, and there has been much controversy recently as to which is most important. Many indirect effects on the environment can also affect neighboring species, not by addition or removal of some factor, but by affecting conditions such as temperature, soil insulation, or wind movement, and by altering the balance between beneficial and harmful insects. It can be extremely difficult to separate these factors, but it becomes very important to do so as our desire to intercrop different crops increases. Proper management of such systems

Table 5.1 Analysis of Two-species Population Interactions
(Effect on Population Growth and Survival of Two Populations, A and B)

Type of Interaction	When not Interacting		When Interacting		General result of Interaction
	A	B	A	B	
Neutralism (A and B independent)	0	0	0	0	Neither population affects the other
Competition (A and B competitors)	0	0	−	−	Population most affected eliminated from niche
Mutualism (A and B partners or symbionts)	−	−	+	+	Interaction obligatory for both
Protocooperation (A and B cooperators)	0	0	+	+	Interaction favorable to both, but not obligatory
Commensalism (A commensal; B host)	−	0	+	0	Obligatory for A; B not affected
Amensalism (A amensal; B inhibitor or antibiotic)	0	0	−	0	A inhibited; B not affected
Parasitism (A parasite; B host)	−	0	+	−	Obligatory for A; B inhibited
Predation (A predator; B prey)	−	0	+	−	Obligatory for A; B inhibited

Note: + Population growth increased (positive term added to growth equation).
− Population growth decreased (negative term added to growth equation).
0 Population growth not affected (no additional term in growth equation).
Source: Odum 1971, Chap. 7, by permission of Saunders Publ. Co.

can come only from detailed ecological research. As a guide for such studies, I propose the concept of interference interactions, permitting a mechanistic approach to understanding how the interactions function. For the purpose of this discussion, I break such interactions initially into the reactions the plant has on the environment. This then forms a basis on which to understand the responses observed in crop mixtures.

INTERFERENCE INTERACTIONS

Based on concepts developed by Harper (1961, 1964) and expanded by Muller (1969), interference can be divided into removal reactions of one plant on its environment, and additive reactions where something is added. When some factor is removed from the environment, the resulting response of neighboring species can be negative, positive, or neutral. Examples are competition or herbivory. Where some factor is added to the environment with the same range of responses, we get additive reactions such as allelopathy or symbiosis. Examination of both types of reactions should aid in illustrating such mechanisms.

Removal Interactions

It is reasonable to think that when the resources required for crop growth and yield maintenance are in limited supply, the crop yield will drop. If the resources are limited in an intercrop system, one species of the mixture may be able to remove the needed resource better or sooner than the other. The resulting depression of yield of the other species can be caused by competition. Examples of competition in plant mixtures have been reviewed by many authors, especially in crop mixtures (Trenbath, 1976; Harper, 1977) and weed/crop combinations (Zimdahl, 1980; Radosevich and Holt, 1984). Agronomic journals abound with cases where crop response is improved by the addition of some "limiting" resource, and after such a growth response, the prior limitation is most often ascribed to competition. When an investigation is carried out in order to understand the mechanisms of the competition, most often the result is to encounter a more complex interaction of factors.

The unequal capture of light by one crop over another seems to account for part of the dominance in mixtures. Competition for limited light under the canopy of a crop mixture seems to take place. Stern and Donald (1962) studied canopy development over time in a grass and clover mixture (Fig. 5.1) with four levels of nitrogen application. The effect of the nitrogen levels was to change the balance of species enough so that by the last sample date the mixture at low nitrogen levels was dominated by clover, but at high nitrogen levels the grass was dominant. Clover and grass react differentially to nitrogen supply. Although the application of nitrogen increases early leaf production by clover in the mixture it also increases the height of the grass canopy. The grass increases its advantage over clover when adequately supplied with nitrogen, finally reaching almost total suppression of the clover. An initial look at these results might imply that nitrogen competition was the principal problem. When no additional nitrogen was sup-

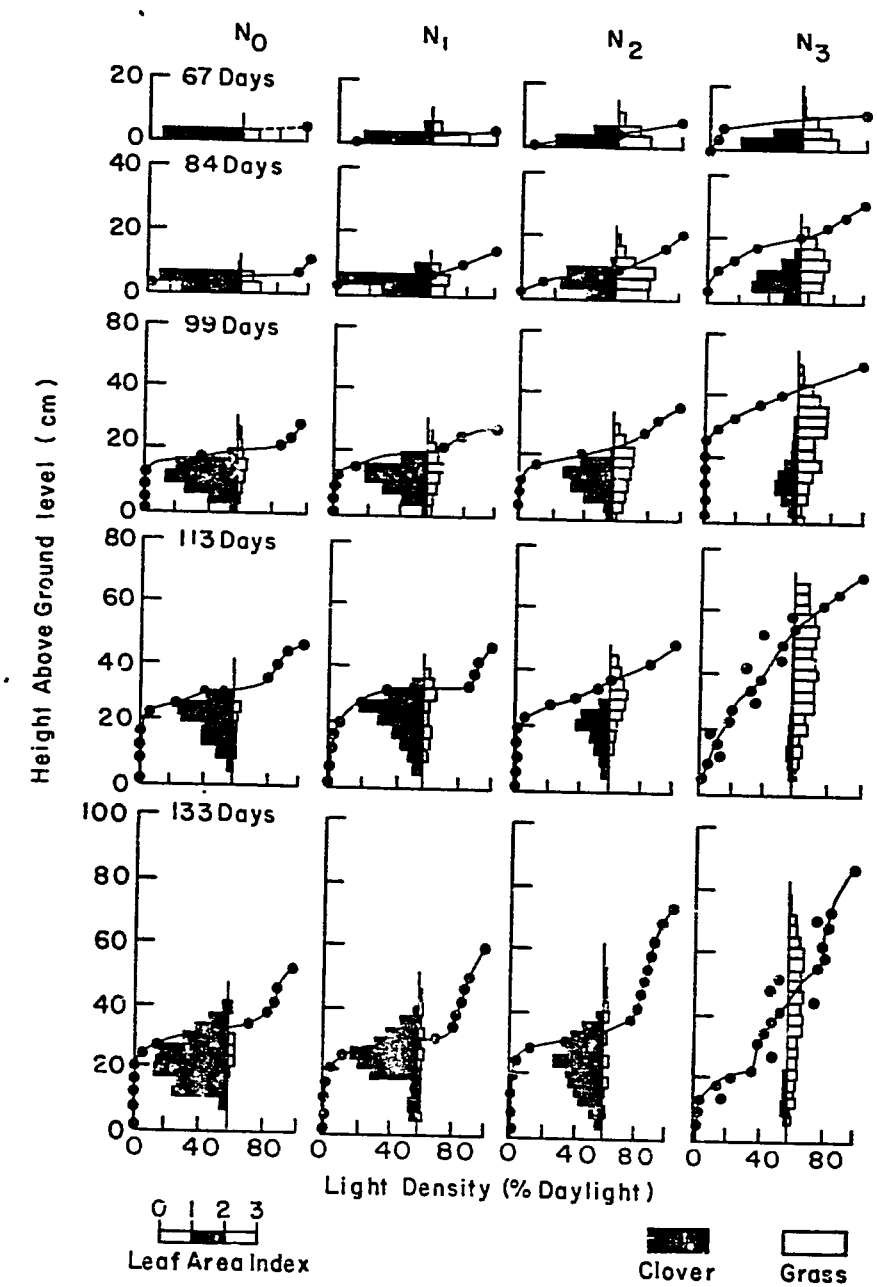

Figure 5.1 Vertical distribution of the leaf area index of grass and clover under four nitrogen treatments together with the profile of light density relative to daylight. (Adapted from Stern and Donald, 1961.)

plied, the nitrogen-fixing legume was at an advantage and able to avoid competition for a limited resource. But the addition of nitrogen shifted dominance to the grass. In the end result, it is impossible to separate nitrogen availability from variable light use. An experiment that started with the examination of a single factor resulted in a complex study of interaction between factors.

The use of water by a crop mixture provides a condition under which competition for a limited resource might come about. There are many reported examples in which one component of a mixture suffers yield depression when water is limiting (Trenbath, 1976; Harper, 1977). However, it is quite difficult to show that competition for water is the actual mechanism. Water as a resource interacts with many other resources. Lowered assimilation rates during water shortage may slow plant canopy development, thus making a crop susceptible to shading. Or, nitrate uptake during water shortage may manifest itself as a nutrient deficiency by the crop. A reduction in root extension during an earlier stage of development by a crop puts it at a distinct disadvantage during water stress, although the reduction initially may have had little to do with water supply. Factors such as interference zones between individual roots, depletion zones caused by root activity, root elongation rates, and root/shoot ratios are some of the characteristics that need to be examined in order to fully understand the nature of the interactions. This is true not only of water, but of the broad range of plant nutrients taken in through the soil solution.

A more specific example comes from a study of rooting depths of different cover-crop grasses sown in apple orchards (Milthorpe, 1961). By comparing moisture availability at different depths, it was found that under *Lolium perenne* moisture levels were reduced to a much greater depth than with two other species (*Poa annua* and *Phleum pratense*), and that subsequent yield reductions occurred in the apples undersown with *Lolium*. Without studies of simultaneous nutrient uptake rates, it would be risky indeed to say that "water competition" was the only factor.

There are enough cases to the contrary that show yield increases, or at least no significant yield reductions, in crop mixtures, despite the fact that removal of resources is occurring (Trenbath, 1974). Very few of these more positive mixtures have been studied experimentally. Yield advantages are most often attributed to complementary interactions between the component crops, with the result of more efficient use of environmental resources. One such study was done by Willey and Reddy (1981) on a pearl millet and groundnut mixture. Partitions in the ground were used to experimentally eliminate belowground interactions between the crops. By calculating LERs for final yields, it was found that the control and dug but nonpartitioned intercrops had a final LER of 1.22 (Table 5.2). The partitioned intercrop suffered a slight reduction in its LER, indicating the loss of some advantage gained from the mixture. The authors concluded that millet benefits from nitrogen available in the soil in groundnut rows; without it, the plants were reportedly pale from nitrogen stress. The belowground interaction could possibly be important for maintaining a competitive balance between the two crops. However, it was concluded that aboveground

Table 5.2 Land-equivalent Ratios of Total Dry Matter Yields throughout the Season and of Final Grain and Pod Yields[a]

	Intercrop control			Intercrop dug (no partitions)			Intercrop partitioned		
Days after sowing	Millet	Groundnut	Total	Millet	Groundnut	Total	Millet	Groundnut	Total
35	0.45	0.72	1.17	0.46	0.72	1.18	0.36	0.77	1.13
50	0.50	0.69	1.19	0.49	0.71	1.20	0.38	0.78	1.16
65	0.52	0.71	1.23	0.53	0.70	1.23	0.44	0.77	1.21
80	0.54	0.71	1.25	0.54	0.72	1.26	0.44	0.80	1.24
95	—	0.68	1.22	—	0.70	1.24	—	0.78	1.22
110	—	0.70	1.24	—	0.71	1.25	—	0.79	1.23
Grain and pod yields	0.50	0.72	1.22	0.52	0.70	1.22	0.43	0.76	1.19

[a]"Expected" LER (i.e., where the degree of competition in intercropping is the same as in sole cropping) is 0.25 for millet and 0.75 for groundnut.
Source: Willey and Reddy, 1981, by permission of Cambridge University Press.

canopy interactions were of greater overall importance, presumably through partitioning of available light (Willey and Reddy, 1981).

Broad application of agricultural inputs usually can overcome any deficiency and eliminate the result of the removal reaction. By being able to determine the specific resource that is limiting, as well as the ecological basis of the interaction, it might be possible to alter the timing, spacing, or even composition of the mixture so that the resource is no longer the limiting factor, avoiding competition and thus yield reduction. Mixtures can be designed more on the basis of the particular ecological requirements of the crop components and by striving for mixtures for which a particular limiting factor is not contested. Such an approach will become increasingly important, either as outside inputs to agriculture become more scarce and/or costly, or as the environmental effects of their more intensive use become better known. This is especially true for smaller-scale systems or those with limited economic resources.

Addition Reactions

From an ecological point of view it is an entirely different situation in a crop mixture when plants are adding to rather than removing materials from the environment. The production of secondary chemicals by plants, followed by their release into the environment and subsequent effects on associated plant species, a concept known as allelopathy, has been recently reviewed in great detail (Rice, 1984). Yet there are many difficulties involved when trying to separate allelopathy from other forms of interference, especially competition (Putnam and Duke, 1978). These include a general lack of nomenclature to describe adequately plant responses that occur in this way, a lack of techniques to separate allelopathy from competition, and the difficulty of proving the existence of direct versus indirect influences from other organisms or microenvironmental modification. Nevertheless, a considerable body of experimental information has been gathered that implicates allelopathy as an important form of interference. Crops that produce allelopathic compounds can have important effects when planted in mixtures, either on the other crops or on weeds. Allelopathy has been demonstrated to play an important role in reducing yields in crops that follow another in rotation, usually due to decomposition products of the residues of the previous crop, or a crop that is inhibited by its own toxins with continual sole cropping of the same soils (see Rice, 1984).

Yet very few studies have been performed in mixed crop systems with the specific intention of looking for the effects of compounds actively being added to the environment by the different members of the mixture. Reports from Russian scientists show both beneficial and detrimental effects from phytotoxins produced in mixtures. In one case, several varieties of legumes were interplanted with corn (*Zea mays*) (Lykhvar and Nazarova, 1970). Many varieties produced yield reductions for corn, and as a consequence, new varieties were selected specifically for use in the mixed cultures. Pronin and Yakovlev (1970) reported that yields of corn and fodder beans increased in mixed plantings, and imply that the influence was associated with a favorable increase of root excretions of each

Table 5.3 Allelopathic Potential of Water Extracts of Air-dried Squash Leaves (*Cucurbita pepo*) in Laboratory Bioassays, Tabasco, Mexico

Test plant	Germination	Radicle length
Corn (*Zea mays*)	100%	85.4%[a]
Beans (*Vigna sinensis*)	96	79.0[b]
Cabbage (*Brassica oleracea*)	92	43.0[b]
Control	100	100.00

[a]*T* test significant at 5 percent.
[b]*T* test significant at 1 percent.
Source: Gliessman, 1983, by permission of *J. Chem. Ecology*.

plant on the other, rather than merely an improvement of nitrogen nutrition by the legume. The interplanting of squash (*Cucurbita pepo*) in corn/bean (*Phaseolus vulgaris*) polycultures in southeastern Mexico aids in weed control (Chacon and Gliessman, 1982; Gliessman, 1983) and produces increases in corn yields and elevated LERs (Amador and Gliessman, 1982). Water extracts of air-dried squash leaves demonstrate a strong allelopathic potential (Table 5.3), especially against the test species that is a recent introduction to the New World. Local farmers describe the use of squash for weed control (Fig. 5.2); in fact, they claimed to plant it for that purpose, and any harvest of fruit was an added bonus (Chacon and Gliessman, 1982). The squash forms a continuous cover over the low-lying weedy species, combining shade with phytotoxins, as well as returning

Figure 5.2 Squash (*Cucurbita pepo*) cover crop dominance following harvest of maize (*Zea mays*); both crops planted simultaneously, near Cárdenas, Tabasco, Mexico. (Photo by Dr. Stephen Gliessman.)

large amounts of biomass to the soil (8 to 10 t dry matter per hectare) (Amador and Gliessman, 1982).

Mutualisms

In contrast to purely additive or removal interactions, mutualisms can often combine several components of interference. The benefits gained by each partner link them into mutual, physiological interdependence. When one component species is absent, the others suffer, and in some cases cannot even exist as free-living organisms. It is difficult to separate mutualisms from the benefits found in beneficial intercropping systems. Yield advantages often come about from the avoidance of direct interference through competition for limited resources or production of phytotoxins which eliminate other competitors. It is much more difficult to demonstrate that benefits are directly derived from the interference. Symbiosis is another term that refers to mutualistic interactions. Ecologically, symbiosis is defined as the permanent, intimate association of two or more dissimilar organisms (Whittaker, 1975). The two terms are frequently interchanged.

Symbiotic nitrogen fixation is the most commonly known mutualistic interaction. Legumes with their accompanying *Rhizobium* bacteria have played important roles in agriculture (Phillips, 1980). The benefits of the mixture of legumes with other crops stem from interactions such as the excretion of nitrogen by the legume for use by the nonlegume, stimulation of soil microorganisms, and the return of nitrogen to the soil (Wilson, 1940). Either through legume/nonlegume mixture or legume/nonlegume rotations, many intercropping systems with this mutualism are practiced today.

The much more widespread importance of mutualisms in ecology are currently being discussed (Boucher et al., 1982). In an evolutionary sense, the benefits gained from mutualisms may tend to be favored over competitive interactions. For example, success of a plant at low levels of available nutrients may come about more through a mutualistic relationship with other species requiring the nutrients, rather than by out-competing them. Resources can be partitioned rather than competed for. Mutual defense from predators, herbivores, or disease organisms can become possible. The long-term benefits to be gained from such an approach to multiple cropping becomes important, then, as we learn to exploit the positive interactions between crop species in mixtures, as well as try to overcome the negative ones.

INTERACTION OF MECHANISMS

In any agroecosystem, the component plant species and the factors of the environment are going to be in constant interaction. The resultant environmental complex changes both temporally and spatially as the crops develop. An excellent example of such a dynamic mixed crop system is the traditional corn/bean/squash polyculture used extensively by farmers throughout mesoamerica (Fig. 5.3). Studies in Tabasco, Mexico, have provided much ecological information on how

Figure 5.3 Interior view of a traditional maize (*Zea mays*), cowpea (*Vigna unguiculata*), and squash (*Cucurbita pepo*) intercrop, near Cárdenas, Tabasco, Mexico. (Photo by Dr. Stephen Gliessman.)

such a system functions (Amador, 1980; Vandermeer et al., 1983; Gliessman, 1984). Corn yields could be stimulated as much as 50 percent beyond monoculture yields when planted in the beans and squash (Table 5.4). Despite yield reductions for beans and squash, the LER of the system was very high. The mechanisms of the stimulation of corn yields have been the subject of further study. On the one hand, beans planted with corn nodulate more and potentially are more active in fixing nitrogen which could become directly available to the corn (Boucher and Espinosa, 1982). This led to observations of net gains of nitrogen in the agroecosystem biomass despite the removal of harvest yields (Gliessman, 1982). This helps ensure better sustainability of the system. Squash fruit yields were low, but foliar biomass was high, contributing to weed control through both removal (shade) and addition (allelopathy) reactions described previously. Noncrop weedy species can impact beneficially on soil resources and insect populations (Gliessman and Altieri, 1982; Altieri and Liebman, Chap 9). Damaging insects are at a disadvantage (Risch, 1980), and the presence of beneficial insects is promoted (Letourneau, 1983). Every component of the system plays an ecological role in maintaining productivity, the combined effects of which have been selected by local farmers for many generations. A cultural and ecological mutualism has been selected for by humans, and an understanding of the intricacies of the interactions teach us a great deal which can be of use for improving present-day cropping systems.

Table 5.4 Yields of Polyculture Corn/Bean/Squash Compared to Monocultures Planted at Four Different Densities, Cárdenas, Tabasco, Mexico

	Monoculture densities				
	Very low	Low	High	Very high	Polyculture
Densities of corn[a]	33,000	40,000	66,000	100,000	50,000
Yield (kg/ha)[b]	990	1,150	1,230	1,170	1,720
Densities of beans	56,800	64,000	100,000	133,200	40,000
Yield (kg/ha)	425	740	610	695	110
Densities of squash	1,200	1,875	7,500	30,000	3,330
Yield (kg/ha)	15	250	430	225	80

[a]Densities expressed as number of plants per hectare.
[b]Yields for corn and beans expressed as dried grain, squash as fresh fruits.
Source: Amador, 1980, by permission of the author.

CONCLUSIONS

Most plants occur in association with other species in natural ecosystems. Our understanding of the complexity of interactions involved in establishing and maintaining such associations has increased greatly (Harper, 1977). Tools exist, then, to better understand the manner in which individual plants in crop mixtures interact with their neighbors. The term interference is used to describe the effect that the presence of one plant has on the environment of another. Addition and removal reactions on the environment are the basis of interference interactions.

The most commonly invoked explanation for yield reduction in mixtures is the removal reaction through competition for a limited resource. Density, the number of plants per unit of area, is the primary component of competition, and agronomists have perfected knowledge of optimal density plantings for sole-crop plantings in order to maximize yields. Very little work has been done on optimizing densities for intercrop systems. In order to accomplish this, our understanding of species proportions and arrangements must be increased. Additive versus substitution arrangements need to be examined from the perspective of interference interactions and resource use in the agroecosystem. Complementary crop mixtures based on different resource needs, either physiologically or temporally, permit crop mixtures capable of over-yielding. Addition reactions, either through allelopathic interference or mutualisms, alter the crop environment and can be of benefit in crop mixtures. The potential role of such mixtures for weed or pest management needs considerably more research. Expanding our view of intercrop systems, then, to include such aspects as pest management, soil conservation, and optimal resource utilization on the one hand, and over-yielding, crop diversification, and multiple-use benefits on the other, can contribute to more resource-conserving and sustainable agroecosystems.

Figure 5.4 Complex, multistoried home garden agroforestry system combining annuals, shrubby perennials, and trees with different ecological requirements and cultural uses, near Cañas, Guanacaste, Costa Rica. (Photo by Dr. Stephen Gliessman.)

From an ecological perspective, all plants in the agroecosystem can be shown to play a role. This includes what are considered to be weeds, perennial shrub and tree components, and even more complex agroforestry combinations (Fig. 5.4). As the need for resource use efficiency combines with the demand for agricultural outputs, being able to employ multiple cropping techniques will become more essential. A theoretical basis for intercropping is being developed (Vandermeer, 1984; other chapters in this volume), and this must be supported by an understanding of the dynamics and complexity of plant interactions involved. This process can contribute greatly to successful multiple crop system design and management.

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