INTERFIELD AND INTERPLANT SPACING IN TROPICAL INSECT CONTROL

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We may assume that the degree of spatial and temporal heterogeneity of tropical crop plants will influence their harvest by insects and by man. The question then becomes one of recognizing those types of heterogeneity that will yield desired agricultural results given the unique environment and insect fauna of a particular area. There is further difficulty in recognizing those agricultural results which cannot be achieved even with optimal heterogeneity; such recognition is important if we are to consciously arrive at steady-state tropical agroecosystems rather than have them forced upon us through country-wide exploitationist experimentation. This brief essay is intended to draw attention to some general ecological guidelines in dealing with tropical crop heterogeneity and crop pests.

Philosophical Generalities

There are at least three general statements about tropical insect control that are in dire need of exposure and discussion by the scientific community. They are important background considerations in any discussion of crop heterogeneity and its impact on pest insects.

1) *Ecological generalizations must not be used as the rationale to rule out specific pragmatic trials in integrated control of tropical pests.* This is to say that an insect pest does not always behave as does the average insect. Further, while we are fond of calling tropical agricultural systems "ecosystems," in fact they differ very strongly from natural ecosystems in that they have a single herbivore (man) harvesting an abnormally high amount of the community productivity. It is clear that the optimal strategies of heterogeneity will depend not only on general principles of insect ecology, but also on the specific harvest rates, types of harvest and particular insect pests that happen to be in the area. These factors

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are not set by general ecological principles but by man's desires. It may well be that a particular steady-state tropical agroecosystem will violate many ecological generalizations.

2) *In steady-state tropical agroecosystems, purely natural communities are probably of trivial importance, both as models and useful entities except for their aesthetic value.* This is to emphasize that man's needs are very far from those of the average herbivore in the community. It should almost always be possible to replace major parts of the natural community with species complexes that do not reduce the overall stability yet increase the yield available to man (at the expense of other herbivores).

3) *On an aggregate world-wide basis, the theoretical and pragmatic knowledge of tropical crop/pest interactions has far surpassed its incorporation into the decision-making machinery from the farmer to the president.* This is to say that a major cause of the failures in tropical agroecosystems that we see around us is not because the human race as a whole lacks the knowledge needed to avoid those failures. Further, where the knowledge is in fact lacking, experimental work is usually not directed at remedying the lack but rather to alleviate pressure from the political-economic-demographic sector.

Pragmatic Generalities

A few generalities on tropical insect control may be offered here to illustrate the types of information that are relevant background for studies of intercrop and interplant spacing in tropical agriculture.

1) *Current agricultural practices do much to destroy one of the two major defenses of a tropical plant—its distance from conspecifics.* This problem is far more severe in the tropics than in temperate zones. In the lowland tropics, and especially the wet tropics, inter-plant spacing may be the only defense that a plant has against its host-specific herbivores (those that have breached its chemical-morphological defenses). In temperate zones, the plant also has the winter on its side; the northern winter may produce some of the same kinds of pest mortality as long distances between conspecific plants can in the tropics. The more severe the tropical dry season, the more we have a situation like the northern winter; this observation is underlined by the fact that much of the most productive lowland tropical agriculture is in areas with severe dry seasons but an adequate water supply part of the year. The spatial analog is a series of oases surrounded by desert.

2) *Agricultural evolution has led to partial destruction of the other*

major defense of a tropical plant—its internal chemical defenses. By selecting edible strains from their toxic wild relatives, tropical man has produced plants that are edible to a very wide variety of animals. By pesticide application, he is currently replacing the secondary compounds, rendering the pest community somewhat more host-specific (i.e., pesticide specific). However, temperate zone plants rely much more heavily on timing their growth with lows in herbivore populations than do tropical plants, and the selective breeding by man has not resulted in as gross a departure from normal as in the tropics. In short, pesticide application may get things back to natural in the tropics while in temperate zones it can also greatly augment the plant's defenses.

3) *Polyculture of tropical plants must be based on plant dissimilarity in the eyes of the insect, not dissimilarity in the eyes of the plant taxonomist.* For example, to the seed-eating weevil, five different species of beans may be the same plant since the toxic alkaloids and uncommon amino acids that cause wild seed weevils to be very host specific have been bred out of commercial beans. Again, the specifics of plant chemical defenses *vis à vis* the herbivores unique to a given habitat can only be worked out by experimentation at the site rather than through some set of predictive rules.

4) *Plants with natural protection may be grown much more readily in tropical permanent monocultures than highly edible plants.* Those tropical plants grown for their secondary compounds (e.g., rubber, coffee, tea, cacao) should be more successful in pure stands than those where man's crop is highly edible and of high energetic value. Plants with underground tubers and naturally toxic above-ground parts (e.g., manioc, taro) or with aquatic early stages should be much more readily grown in permanent fields than annual seed crops (the crops of most tropical shifting agriculture).

5) *The common contemporary practice of growing tropical crop plants on continents other than their homeland is a shorthand form of breeding for resistance—and probably doomed to the same failure.* The new plant in a foreign land may have sufficiently novel secondary compounds to be resistant to local insects, but it is only a matter of time before local strains are selected that can breach these chemical defenses (just as with resistance to pesticides). Further, the more the native strains of plants are removed, the larger will be the proportion of the herbivore population that has to survive on the introduced plant and the more rapidly will selection operate to produce resistant strains.

6) *Temperate zone entomophagous parasites and predators appear to have higher reproductive rates than their tropical counterparts, perhaps making them more effective in biological control programs.* This difference probably originates in temperate zone entomophagous animals having evolved in habitats where food (prey) is available in relative excess at some times and nearly absent at others. The crop ecosystem, temperate or tropical, is very much this type of system and it is doubtful if tropical entomophagous animals will be able to respond rapidly to the sudden increase in prey associated with annual crops.

Specific Examples

I have just finished a five-year study that compares the foliage-inhabiting insect community of a variety of tropical habitats in Costa Rica and on Caribbean Islands (Janzen 1972). In numerous ways the results appear of importance to tropical agricultural theory in the area of interfield spacing, though not always in a positive manner. A few examples are offered here in hopes of showing how complicated tropical ecological prediction can become.

IN AREAS WITH A MILD DRY SEASON

I found that there was less than 1 percent overlap between the species of insects in primary forest understory and the immediately adjacent secondary vegetation in an area where there is sufficient rain during the dry season for luxuriant plant growth in secondary vegetation. In contrast, the analogous situation in eastern Kansas showed 15 per cent in common between the fauna of secondary vegetation and adjacent forest understory.

It is hardly a new concept that tropical rainforest is not likely to be a major reservoir for the insect fauna of adjacent disturbed sites; this relationship is probably a major driving force in the evolution of shifting agriculture. What it leaves unanswered is where do the insects come from that invade a new field, and the answer is probably older fields. Such a discussion also leads one to the following question: Is overall crop production highest with a few high-yield acres scattered through generally unproductive acres of tropical forest, or with all the forest cut and the habitat converted to a low yield (per acre) system? The answer very clearly depends on whether the local species of pest treat rainforest as a barrier to dispersal or as a refuge when crops are unavailable. The same qualification applies to the entomophagous animals that feed on the pest species.

That there are active adult insects in reproductive diapause in moist refugia during the dry season has interesting implications for tropical agricultural ecology. This means that whenever a crop is planted, there are likely to be at least some adults ready to oviposit on it (in contrast to temperate zones where some weather cue may be required to bring the insect out of dormancy). When these insects are not reproducing, they require less specialized diets and more host plants are used (for water and perhaps carbohydrates for maintenance metabolism); this may mean that their effectiveness as plant disease carriers may increase during the dry season. Since they can go into reproductive diapause during the dry season, presumably in response to the absence of appropriate food, they may well be able to do the same when a crop is harvested even if it is the rainy season. Again, this contrasts with temperate zones where insects often use direct environmental cues to turn on and off and thus may not be so flexible in the face of crop manipulation. Further, different forests can have parasite and predator communities of very different sizes. At San Vito, an intermediate elevation forest site in Costa Rica, there were roughly 10 times as many species and individuals of parasitic Hymenoptera as in lowland rainforest on the Osa Peninsula (Costa Rica).

IN AREAS WITH A SEVERE DRY SEASON

I found a very striking migration of insects into riparian forest and other moist refugia during the dry season in tropical deciduous forest; they appear to pass the dry season as active adults in reproductive diapause. It is obvious that the effect of interfield spacing in the deciduous tropics depends largely on the type of vegetation between the fields, and the proximity of dry season refugia.

We may even argue that riparian forest should be destroyed. However, again it will depend on the local pests and their entomophagous associates. It is quite possible that the particular pest species of importance do not use the riparian forest to pass the dry season, while some important parasites and predators do. The advisability of irrigating croplands derived from deciduous forest may be subjected to the same analysis. It may produce an insect outbreak, but this is only of importance if it contains pest species, and further, that these pest species do more damage than the overall gain from year-round pasture growth and cropping.

ON ISLANDS

The Caribbean island insect samples, during both wet and dry season, had very greatly reduced numbers of species and individuals in them as compared with the mainland. We may safely predict that interfield and interplant spacing of crop plants would not be nearly as important as on the mainland with the same crops and weather regimes. This means that it will be difficult to exchange results on field trials between mainland and island experiment stations. Further, it may mean that undisturbed forest on tropical islands is even more severely threatened than on the mainland.

CONCLUSION

I will not summarize the brief account given above but to stress that the complexity in tropical agroecosystems is quite high enough to require that optimal solutions to the animal pest (and weed) problem be worked out as a unique solution for each major area of the tropics. We have some feeling for the ecological generalities that are of importance. What we seem to lack are detailed case studies for particular agroecosystems. If I were to allot further research funding to understanding the agroecosystem, it would be primarily in the area of detailed field studies of functioning-misfunctioning agroecosystems rather than in "basic" studies of natural systems (with hope that by "spin-off" this will increase our ecological understanding.)

LITERATURE CITED

Janzen, D. H. 1973. Effects of seasons, vegetation types, elevation, time of day and insularity on tropical foliage insects. Ecol. Mon. (in press).