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The British Ecological Society

Biology in Pest and Disease Control

edited by
D.Price Jones and
M.E.Solomon



Biology in Pest and Disease Control

The 13th Symposium of
The British Ecological Society
Oxford, 4-7 January 1972

edited by

D. Price Jones MSc, PhD, FIBiol

Formerly of Plant Protection Ltd
Jealott's Hill Research Station
Bracknell, Berks

and

M. E. Solomon MSc, FIBiol

Long Ashton Research Station
University of Bristol

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Preface

This book comprises the papers presented at a Symposium at Oxford in January 1972 on the subject 'Increasing the Biological Contribution to the Control of Pests and Diseases', organized jointly by the British Ecological Society, the Association of Applied Biologists and the Society of Chemical Industry (Pesticides Group). The origins of the Symposium, and the part played by the Biological Control Subcommittee of the British National Committee for Biology, are outlined by Mr F. Wilson in the opening paragraph of his contribution, which constituted a keynote address at the Oxford meeting.

The aim of the organizers was to achieve a broad and principled account, as well as practical examples and assessments, of the role of biological factors and biological methods in the control of pests, weeds and plant pathogens. The intention was to look at the past and the present with an eye to the future.

Although pesticides have long been predominant in this field, biological factors, such as the resistance of pest to pesticide and of host-plant to pest, have of course always been relevant, and neglected only at the cost of later trouble. Biological agents, such as predators, parasitoids and pathogens of pests, are the chief means of regulation of the abundance of many pests, as has been demonstrated, for example, by the outbreaks of fruit tree red spider mite following the reduction of its natural enemies by pesticides, and by the numerous successes in pest control achieved by the introduction of predators, parasites or pathogens. A number of new methods of pest control, some entirely biological, some partly chemical, have been put forward and tested in the past ten or twenty years; these are discussed in some of the contributions to the Symposium. Some authors discuss combinations of appropriate husbandry with chemical and biological measures of control. With a few exceptions, attention is concentrated on British problems and conditions.

The plan of the book generally follows that of the Symposium meeting. A few opening contributions deal with some aspects of ecology relevant to the control of pests and weeds (Janzen, Varley, Sagar, Sarukhán). There follow eleven papers dealing with different approaches to the control of pests, weeds and plant pathogens: the principles of biological control of pests are discussed by Wilson; other contributors deal with the control of pests,

chiefly insects, by the exploitation of insect pathogens (Tinsley & Entwistle), behaviour (Cherrett & Lewis), hormones (Ruscoe), genetical manipulation (Davidson), selective insecticides (Price Jones), diversification of the crop habitat (Dempster & Coaker) and integrated control (Way); others deal with plant breeding for resistance to pests (Knight & Alston) and disease (Lupton), and with biological control of weeds (Cussans).

A third section comprises estimates of the applicability of biological methods of control to vertebrates (Murton), to nematodes (Jones), to pests and diseases of sugar beet (Hull) and vegetable crops (Wheatley), to pests of glasshouse crops (Wyatt) and of forest trees (Bevan), to plant diseases (Rishbeth) and to water weeds (Stott).

The topic of the final section is 'The Future of Biological Control in Britain', from the viewpoint of the grower (Gair, Strickland), the research worker (Hussey), the manufacturer (Jepson) and the conservationist (Melanby).

The appendix contains summaries of the opening remarks of two of the Chairmen of Sections of the Symposium, and a special contribution to the Symposium made by L. Brader on the development of biological control under the influence of the Organisation Internationale de Lutte Biologique contre les Animaux et les Plantes Nuisibles (OILB or, in its English equivalent, IOBC).

The discussions at the meeting are not included in this volume. One point, however, was raised by Professor G. C. Varley and referred to the editors for their attention, namely the possibility of confusion arising from the different meanings attached to the word 'control'. We hope that, in its context, the significance of this term will always be clear to the reader. The only example we feel may require our comment is the use of 'integrated control'. Professor M. J. Way, in his contribution to this Symposium, follows the very general usage in which integrated control means primarily the control of a pest by a combination of different methods. Dr. N. W. Hussey and Mr. I. J. Wyatt include, and indeed emphasize, the integration of control measures aimed at different pests of a single crop.

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Section 1
Ecological background

The role of the seed predator guild in a tropical deciduous forest, with some reflections on tropical biological control

DANIEL H. JANZEN *Department of Biology,
University of Chicago, now at Department of Zoology, University
of Michigan, Ann Arbor, Michigan 48104, U.S.A.*

General theory

What effect does the array of animals that kill seeds (and seedlings), henceforth termed the seed predator guild, have on the community structure of the plants in a forest? In north temperate forests, one of the major impacts of the seed predator guild appears to be in the generation of mast year cycles in seed production; this occurs through the mechanism of natural selection against those individual trees that are not synchronized in their fruiting with the majority of their conspecifics or even other unrelated members of the community (Janzen 1971a). I have also argued that it is the generation of mast year behaviour on a population and community-wide basis that prevents the seed predator guild from lowering the density of the dominant tree species to a level where other tree species may invade and thereby increase the richness and diversity of tree species in the forest (Janzen 1970a, 1971a). These arguments, as well as those discussed in the remainder of this presentation, can be applied to foliage-eating animals as well, but will not be discussed further here in that context.

Let us now move to the other end of the gradient of climatic harshness and unpredictability, the lowland tropical evergreen and deciduous forest. Here, we enter habitats where the seed predator guild can be maximally effective at preventing population recruitment by any particular species of forest tree. The result should be that no one forest tree species may competitively displace a wide array of others. This postulation assumes that, given the absence of plant-eating animals or given immunity to them, some small subset of the trees in any complex tropical habitat will be able to multiply to where they competitively displace the others that would also grow there (Janzen 1970a).

In short, I am postulating that the population size of a tree species in a mixed forest is regulated by 'density-dependent' processes just as are animal populations. Further, I am assuming that the phytophagous animal populations in these forests are resource-limited during significant portions of their contemporary (and evolutionary) histories. Finally, I assume that the more favourable are the conditions for the seed predator guild in respect to any particular tree population, the further will that tree's population density (= proximity) have to be depressed by the seed predators before the individual seed crops are so far apart in time and space that the animals can no longer find juvenile plants at a rate that prevents an increase in the population of the tree. The obvious density-dependent mechanism need not be discussed further here. We may, however, recognize that in the case of both seed- and foliage-feeders, a major method of escape by the plants in time and space is through chemically generated inedibility (e.g. Janzen 1971b). We are then confronted with the question of why cannot the animals, and particularly the insects, 'out-run' the plant in the biochemical coevolution game, since they have so many generations during the lifetime of the tree? A formal generalized answer is still in the formulation stage (Janzen & Wolff, unpublished manuscript) but, in short, it appears that it is probably the fate of the average tree population in the lowland tropics to lose the biochemical evolutionary game in a moderately short time to the animals on a local habitat basis. This should result in a high rate of local tree species extinction (and immigration) for any particular habitat over evolutionary time (a rate which is much higher than that to be expected in temperate zone habitats of equivalent geographic size). This higher extinction and immigration rate should also be associated with a higher rate of host-switching in evolutionary time for the more host-specific insects. Incidentally, it must be remembered that all such statements are to be viewed as stochastic in nature, and thus single examples that seem contradictory may simply represent the tails of frequency distributions.

The general postulations set forth in the previous three paragraphs have been generated from a very broad miscellany of data gleaned from the literature, and from my own field work and that of my colleagues in the Central American tropics. Until very recently, almost all the relevant data were gathered for reasons other than the direct examination of these ideas and are not definitive for any given forest or set of ecological conditions. The postulations are put forth for the express purpose of encouraging other workers to gather data on seed and seedling predation, and on foliage parasitization.

In considering these general questions, I have found it always useful to start with a model of the reproduction by a single tree in a single population, and focus my ecological attention primarily at that level. In doing this, I

have found a useful working model (Janzen 1970a). In most generalized terms, this model explores the idea that, on the average, an adult tree in a lowland tropical forest should be most likely to produce another adult at some intermediate distance from its crown. This follows from two observations. Reproduction close to the parent tree is very unlikely, owing to the attacks of incoming and reproducing predators on the seeds and seedlings concentrated below the parent. Reproduction is unlikely far from the parent owing to the low immigration rate of seeds. These two processes should generate an adult spacing pattern far from the contagion expected if only the seed shadow is considered. Now these considerations are of course only relevant if there is any reproduction at all. This proviso is added for the following reason. For any host-specific set of seed predators, a primary source of the seed predators at a specific crop are conspecific crops nearby (in time as well as space); there is a system of mutual infection by all the trees in the area that the insect regards as one 'species' of host. This means that, on the average, the closer a tree is to other conspecifics (with distances measured in ecological rather than metric units), the less likely it is to produce even one new adult. This type of reproductive heterogeneity may also mean that most of the adult trees of a given species may be effectively sterile (despite heavy seed production).

At this point in our brief résumé we could turn in either of two major directions. We could examine the theoretical outcomes, with particular population structures and with aggregate community structures, of modifying the behaviour or abilities of the dispersal agents, the seed predators, and/or the adult trees' reproductive behaviour. Except for a few cases, such as mangroves and some species of *Dipterocarpaceae* that can persist as pure stands in tropical forests, at present this would be a rather sterile exercise owing to the lack of hard data on the necessary parameters. We have just begun to build a data pool on what the seed shadow of an individual tropical tree looks like. We have almost no information on how tropical seed predators respond to an individual tree's seed crop, nor what is the effect of inter-tree spacing in time and space on tropical herbivores. Finally, we have almost no information on how individual tropical trees modulate their seed production. Some starts in these directions may be found in the following embryonic studies: Janzen (1969, 1971b, 1971c, 1971d, 1972a, 1972b), Wilson & Janzen (1972).

It is probably more profitable at this point to examine some of the more conspicuous assumptions underlying the general model. Data are now beginning to accumulate from a study of deciduous tropical forests in Costa Rica. I may add that, throughout the following discussions, it is evident that an understanding of the systems being described is relevant to the theory of applied ecology (= biological control of insect and weed pests), though

not necessarily to its practice, in tropical countries; I shall, however, save discussion of this area until last.

Host specificity of seed predators

A major background assumption of this study is that the degree and kind of host specificity will influence the predator-prey interaction. Let me immediately add that it is often not clear how it will do so. I have found the seed predator guild of a deciduous forest in Guanacaste Province (Pacific coast lowlands of Costa Rica) to be subdivisible into several major groups on the basis of their type of host specificity. The most host-specific are the beetles (Bruchidae and Curculionidae) whose larvae eat the contents of seeds, usually while the seeds are still within the fruit. They may kill as much as 50 to 99% of a seed crop before it has been dispersed. To date, each of 66 of these species of seed predators (59 bruchids and 7 weevils) has been reared from only one species of host plant (in over 1000 samples of seed crops). Only five species (all bruchids) occur on two hosts (a *Mimosestes* on two *Acacia*, one *Amblycerus* on two *Cassia* and another on two *Cordia*, a *Caryedes* on two *Bauhinia*, and an undescribed bruchid genus on two *Lonchocarpus*) and none on three. These observations should be viewed in the context of a habitat containing about 300 species of woody plants, over half of which have been surveyed in the study. It appears that seed chemistry and fruit behaviour-morphology (e.g. Janzen 1969, 1971a) are the primary traits preventing broader host selection and preferences by the bruchids; it is also tempting to postulate that past millennia of plant-bruchid coevolution have resulted in rather strong character displacement among those traits that are important in defence against these insects. The plant appears to have played the evolutionary game through predator satiation of its host-specific seed predators and chemical-morphological exclusion of its potential seed predators.

There is also an array of insects that feed on fruits, immature seeds, damaged mature seeds, and even mature seeds on occasion. The amount of damage they do is unpredictable and may involve such complex things as destroying the attractiveness of a fruit to a dispersal agent, thereby causing its seeds to be found still on the tree by a seed predator at some later date. Such insects are often highly variable in their host specificity, and will not be considered further here. I should, however, point out that they may be of great importance agriculturally while having little impact on the biology of the plant.

Vertebrates may be divided into at least two groups on the basis of their host specificity. I must add early in this discussion that an individual animal may be classed in either of these two groups at different times, depending on

such things as time of year, reproductive condition of the animal, and site of foraging in the habitat. The first group is made up of those vertebrates that subsist on the seeds of those tropical plants that escape through predator satiation. As in temperate forests, such trees generally produce highly edible (and often wind-dispersed) seeds during a very short period (and sometimes at long intervals, e.g. *Dipterocarpaceae*). Many vertebrates appear to subsist in great part on such seeds during those times of year when they are produced. Here, the vertebrate may be described as a 'polyphagous' or 'generalist' species, if we measure host specificity by the number of Latin binomials on the host list. I should point out, however, that this is quite different from the generalist that is capable of eating a wide variety of toxic plants. The epitome of escape through predator satiation is probably represented by grasses and palms, neither of which appear to have seeds toxic to seed-eating vertebrates.

On the other hand, there is another kind of polyphagy that appears to be practised by phytophagous vertebrates in tropical vegetation. A large number of tropical seeds contain high concentrations of alkaloids, uncommon amino acids and other poisonous compounds, probably as a primary result of co-evolution with insects. For example, the large seeds of the vine genus *Mucuna* contain 4–8% L-dopa and are not attacked by any insects (cf. Bell & Janzen 1971). Yet such seeds may be eaten in small amounts by small tropical rodents. For example, the seeds of the large forest vine *Dioclea megacarpa* contain 5–10% canavine (a potent arginine competitor in protein synthesis) yet are eaten by squirrels (*Sciurus variegatoides*) in quantities far below their stomach capacity. The result is that during the lifetime of a seed crop, the vine generally loses less than 10% of its seeds to this animal (Janzen 1971b). It appears that small rodents such as this eat only small amounts of a wide variety of toxic seeds during any one period, and thereby do not get enough of any one to overcome their internal detoxication system for that class of compounds (irrespective of whether detoxication is done by the gut microflora or their own biochemical system). This behaviour is probably functionally identical to the habit that ruminants have of browsing small amounts of foliage from each one of a wide variety of dicotyledonous plants, each of which is likely to contain a toxic dose of phenols, alkaloids, cyanogenic glucosides, etc. if eaten in large quantity.

The polyphagous phytophagous rodent that subsists on toxic seeds during all or part of its life cycle is clearly quite a different beast, from the plant's viewpoint, from the polyphagous rodent or other vertebrate that subsists primarily on seeds produced by predator satiators. The former rodent can never move into a local area and eliminate a medium-sized seed crop of toxic seeds, nor can it build up a large population on a locally abundant tree species (as could a host-specific insect). Yet such a rodent exerts a

constant selective pressure against trees that find themselves evolving in the direction of producing a very small number of very large seeds. To stay in the game, such a tree would have to have ever-increasingly toxic seeds. Finally, such rodents (or even larger animals such as deer and peccaries) clearly have less potential as density-dependent population regulators of the trees than do insects or those rodents subsisting primarily on the seeds from trees on the 'predator satiation' adaptive peak.

I might add at this point that most immature fruits appear to be protected by their chemistry alone, and both the rodents and birds (especially parrots) tend to take immature tropical tree seeds in regular but small amounts. Again, this suggests a system where satiation is achieved not through filling the stomach of the predator but through nearly overloading its detoxication abilities.

Parasitization of seed predators

A second major area of background assumptions is associated with the assumption that the seed predators are for the most part resource-limited on both an evolutionary and a contemporary time scale. For the insects, this is suggested by several indirect lines of evidence from the deciduous forest study cited earlier. For the vertebrates, no direct leads have been obtained, but much anecdotal and circumstantial evidence has convinced me that they are likewise resource-limited.

One of the most conspicuous aspects of rearing bruchids and weevils from tropical seeds crops is that many appear to have no parasites. Of the 71 beetle species alluded to earlier, I have reared parasites from only 20. Further, the parasitization is at a level of 1-5% of the emerging adult beetle population, strongly suggesting that the parasites are just 'riding' their host population and having little density-dependent impact on them. A second conspicuous trait of the parasites is that they appear to be highly polyphagous in respect to bruchid species (and probably in respect to other insects as well); one is left with the distinct impression that, to survive in a community where most of the prey species are widely scattered in space and time, the parasite must be polyphagous. It is this observation that suggests why many of the bruchids lack parasites. The parasite is probably not capable of simultaneously possessing the wide array of host-finding behaviours and morphologies that are needed to attack a high number of bruchid species (each with a low density). A high number would be necessary in order to accumulate enough prey individuals to sustain a parasite population. The process is probably the same as that underlying the fact that only a