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BIOLOGICAL CONTROL IN THE MANAGEMENT OF PESTS

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ABSTRACT

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In this paper the author reviews the broad general picture of developments in biological control in relation to the increasing opportunities presented for its employment in developing programmes of integrated pest control worldwide. Included are not only the classical examples of biological control of insects and mites and of weeds but such other areas as biological control of vertebrates, of plant diseases, and of dung accumulations, and as well the development of crop plant varieties resistant to plant disease. The review is developed as a means of illustrating that biological control offers real potential as a major manipulatable tactic for central use and maximization in a strategy of integrated control of pests in a great variety of situations — on land and in water, from the tropics to cold, temperate and sub-arctic regions, in forests and range and in cultivated crops and ornamental plantings. It is noted that the employment of these biological control tactics are often self-sufficient but they are not expected to broadly replace the use of chemical pesticides, for chemicals remain necessary in most crop situations and are still our most reliable *immediate* solution to such a problem. The two types of tactics are to be used together where necessary, with the chemicals being used only where really required and in ways to supplement the use of biological controls in the broad sense.

INTRODUCTION

Modern society is converging in two respects to produce a dilemma of no little import. It arises from the worldwide human population explosion and the need to produce an ever increasing supply of food and fiber while maintaining a desirable, even a livable environment. Meeting these increased needs threatens the very resource base upon which all life and the food base itself rests. The dilemma arises from the fact that the control of human births remains an unsolved problem, in spite of massive worldwide scientific, technical and social efforts to that end, and from the fact that the very means man employs to match in food production the needs of the world's hungry will in the long view be self-defeating unless he can stop his own population increase. The massive unilateral use of broad-spectrum biocides, the chemicals with which we commonly control the pests of our forests and fields and those causing disease, pose major problems for their continued use in this way. For one thing, there is currently an acute worldwide shortage of appropriate pesticides, and this is not likely to be corrected for several years (Furtick, 1974). Consequently we must now use them in the most effective way possible, that is, to augment rather than to replace other methods. Under the old system, some soils in the Pacific Northwest (U.S.A.) have become so loaded with arsenic compounds that some crops can no longer be grown on them (Benson, 1968) and the accumulated effects of DDT in world food chains and the environment generally have occasioned the banning of its use in a number of countries. Dieldrin and aldrin have now been banned for use on crops in the U.S. Moreover, the use of these and various less residual toxins have caused rapid resurgences and resistance in some pests and the inducement of previously innocuous species to pest status through the destruction of their natural enemies (Ripper, 1956; Doutt and Smith, 1971) and sometimes by physiological stimulation of the reproduction of the pests themselves (e.g., Huffaker and Spitzer, 1950; Chaboussou, 1963, 1965; Huffaker, 1971).

The other major means by which man has sought to increase his supply of food and fiber in the more deprived areas of the world, where indeed hunger is common, is by the development of varieties of higher yielding food crops. Success in this effort has been termed the "Green Revolution". While this method has, indeed, had some resounding success, already warning signals are seen. There has been a massive narrowing of the general genetic base of the crops used in these and similar programs (Horsfall, 1972). Some 600 varieties of rice have been grown in Indonesia. A Green Revolution program would utilize only a few of these, with corresponding loss of this great pool of genetic factors for resistance to pests and diseases, of both known and unknown economic potential. The great U.S. catastrophe of 1970 due to Southern corn blight is attributed to the extreme narrowing of the genetic base of our corn plantings. Our common crop plants have historically and unconsciously been selected partly because of their resistance to pests, as this has affected their yield potential in the presence of pests in the situations at hand. It is interesting that in the Philippines some 10 000 world rice varieties were tested under "traditional" methods of culture, and the highest yielding variety proved to be one already popular among Philippine farmers (Wortman, 1968).

The pests themselves comprise an enormous complex of species — insects, nematodes, bacteria, fungi, viruses and weeds — the last as direct competitors of our crops, the former as natural enemies, in great variety, causing all manner of distress and destruction. Each species often possesses a great capacity to adapt to changed conditions in the crop plants, or to our methods to combat them, such that complete freedom from pests is a virtually unattainable goal. The very measures used to achieve the elimination of one pest problem often engender another. "Disease trading" is a term that arose from the emergence of a "new" disease with the chemical control of a former one.

As Huffaker (1970) previously noted: "Our strategy in pest control would ideally be one of complete eradication of pests. Achievement of this state was suggested by some entomologists when DDT first arrived on the scene. Among other difficulties, as we are now aware, however, pests often counter-attack and develop resistance to such toxicants. More recently, it has been suggested that we may eventually be able to eradicate from producing areas all forms of life other than the ones involved in production (Beirne, 1967). Such views tend to ignore the complexity of nature, the environment, and the forces tending to sustain life, even under great adversity. Is it likely that we can really grow field crops completely free of pests? The answer seems clear and the conclusion from it is indicated. A more realistic strategy would seem to be one simply of control of pest species at noneconomic densities." With this goal, man has at hand a vast arsenal of the tools for such a war. He can use a crop species' own factors for inherent tolerance or resistance. He can use the pest's own natural enemies against them — first simply by stopping the unnecessary measures now used that harm them, by introducing new ones from other lands, and by artificially augmenting their numbers and by making the crop environments more favorable for them. We must learn to accept minor damage from pests and manage them so as to optimize the yield to ourselves while not attempting the unattainable which, in fact, causes all manner of problems, and in the long run is self-defeating with respect to the purely economic motive itself, to say nothing of the ethical and cultural.

Nor can we feed the world's teeming millions, no matter what science may discover to increase our food production potential, unless we learn also how to check our own population increase. Thus, the *real* problem is this. The most the agriculturist can do is to buy *time* by developing rational methods of agricultural production to meet the increasing needs for the short time that this will be possible in the absence of a solution to the population problem. In the meantime we can only hope that the current trends to reduced birth rates can be spread to the areas of the world where this is most needed. To buy this needed time, as agriculturists we must produce higher yielding crops, without damaging the environment and the productive base itself by excessive use of potentially damaging chemicals, including excessive use of fertilizers as well as pesticides in great variety. The pest control specialist's job is to devise means of pest control that will be effective, and adaptable enough to be "enduring", with minimum adverse effects on the environment, the crop environment itself and the environment generally.

What is emphasized here is only one tactic of a promising solution in our short-term effort to buy that time and to feed mankind without seriously damaging the basic productive capacity of our environment. This is the use of biological control. Its potential, however, cannot be realized except as it is used as a central part, but by no means the only part, of a broader ecological approach to pest control. This broader approach is that of integrated control, or integrated pest management, as some now refer to it. Biological control in its broadest context would include what I have termed "nature's own principal means of pest control" — i.e., the development of resistance to pests in the plants themselves and the control of the pests by their own natural enemies.

These two forces protect the world's natural plant cover to a mighty degree. Indeed, it is not common for the natural vegetation of any part of the earth to be drastically smitten by pestilence and destroyed, except when some alien pest (e.g.,some insect pest or disease pathogen) has arrived, usually inadvertently, in the former instance without its own complement of natural enemies that evolved with it, and especially in the latter case, where the new host plants with which the pest organism did not co-evolve present an uncommon degree of susceptibility to it.

It is not meant that in order to use these forms of natural biological control, around which we can build an ecologically sound system of crop protection, that we will need to accept undue losses from the pests. Indeed, the degree of biological control enjoyed from introduced natural enemies is virtually complete for some 40-odd species of major pests, and for over 300 examples, by pests and countries, substantial protection has been afforded by this means alone (Huffaker et al., in press). By this classical method the natural enemies of a foreign invader are located in its native home area and introduced into the pest invaded area for control of the alien pest. The majority of our serious insect pests and weeds are in fact aliens and likely subjects of this method of control. Plant resistance factors have also been much used in modern agriculture, mostly against diseases but also against a number of insect pests. The use in the U.S. of varieties of wheat resistant to Hessian fly (*Phytophaga destructor* (Say)), of apple resistant to woolly apple aphid (*Eriosoma lanigerum* (Haus.)), of corn resistant to European corn borer (*Pyrausta nubilalis* (Hubner)), and e.g., in Europe, of grape rootstocks resistant to grape phylloxera (*Phylloxera vitifoliae* (Fitch)), are widely known. Research in these general areas is now being intensified.

Integrated control uses these two natural control forces as a central core, and then adds another dimension of major consequence. It recognizes the crop's own power of compensation for pest attack, and by considering the crop system or agroecosystem as a unit, it seeks a solution to all the pest problems or potential pest problems as a complex. A pest is not considered in isolation of the other pests of the crop. Rather, the consequences of measures taken to control one pest upon the natural control factors operating in the control of other pests are taken into consideration. Above all, potentially disturbing and costly pesticides are not used in a prophylactic fashion, but only when really needed, and this is judged by proper assessment of the economic damage to be expected, rather than being fixed by calendar date(s). When such pesticides are used they are used at minimal necessary dosage and at times and in coverage so as to protect the natural enemies when possible. Next, maximum use is made of cultural practices by which pests are destroyed physically or exposed to inclement weather, or the natural enemies or the crop's tolerance are thereby favored. Lastly, chemicals, the most reliable *immediate* solution on a broad basis, are definitely used but only when really needed. Their useful life is thus extended and the limited supplies will more nearly suffice.

It is useful now to turn more specifically to some outstanding successes of biological control, sufficient to indicate that its success is more than a rare and lucky event.

SUCCESS IN BIOLOGICAL CONTROL

Perhaps the best way to convince the "Doubting Thomases" that biological control is a very real and feasible means of pest control is to present something of the scope of factors and the kinds of organisms that have been used successfully in biological control, and, as well, the scope of problems that have yielded to this method. These are discussed under three topics: (a) host plant resistance factors; (b) natural enemies used against various types of pests; and (c) the kinds of habitats where natural enemies have proved successful.

Host plant resistance factors

As I am not a plant breeder nor one who has worked in this area, I will not attempt a technical discussion of the types of resistance factors available nor the finer genetic manipulations in plant breeding to develop resistant or tolerant plants. This discussion is of a more general nature.

Over the eons of time plants have developed a great diversity of means of warding off attack by plant feeding animals and disease organisms. A vast pool of such resistance factors exists in domesticated and wild plant stocks which can be used to develop crop varieties more resistant to pests.

Plant pathologists have extensively used plant breeding for disease control. Early success in the U.S. with wilt diseases of cotton, cowpea, watermelon etc., in France with downy mildew and powdery mildew of grape, and with wheat stem rust and crown rust of oats in various countries, led on to many successes of greater or less duration (Coons, 1953). In the case of wheat stem rust, crown rust of oats, tobacco·mosaic virus on tomato and a number of others, continued success is dependent upon continued breeding to meet the counter development of resistance-breaking new biotypes of the pathogens (Coons, 1953; Day, 1972). Borlaug (1965) considered that the average useful life of a stem rust resistant variety of wheat is about 5 years. In general, however, even in the 1950's a large percentage of our main crops were comprised of varieties that had been improved with respect to some resistance to disease (Coons, 1953). This trend has increased since then and the dollar value would be very difficult to estimate.

Entomologists have only recently begun extensive efforts in this area in spite of there having been several notable early successes — e.g., with the development of Hessian fly resistant wheat, a woolly apple aphid resistant apple, Winter Majetin, and use of American grape rootstocks resistant to grape phylloxera (Painter, 1951). This inattention has been due in part to the effectiveness and simplicity of using the new insecticides developed for the post World War II era. The increased recent effort has produced promising results, not only in developing new varieties resistant to plant pathogens but also to insects, nematodes and other types of pests. Horber (1972) has noted that already some 25 vegetable crops have been developed which fend off 35 species of insects, and for some, combined resistance to both insects and disease is being sought, e.g., in the cucurbits, wheat, maize, soybean, and alfalfa (e.g., Smith et al., 1975).

Significant expansion of effort is needed to develop such multiple pest resistant varieties. Yet it is well again not to expect the impossible. This solution will probably not be available for whole complexes of pests for very many crops, rendering other methods unnecessary. This is because a resistance factor for one pest may predispose to attack by another (e.g., Zink and Duffus, 1969; Beck and Maxwell, in press).

Natural enemies used against various types of pests

Among the kinds of natural enemies found useful or promising are the insects, mites, snails, nematodes, microbial pathogens and antagonists, plant parasitic higher plants and vertebrates, with the latter groups having been little used.

Use of insects against insects

Biological control by use of insects has had a long history — even a prehistory about which we have only legend. Ants were used in China from very early times to control stored grain insects and in Yemen around 1200 A.D. to control date-palm pests (Simmonds et al., in press). While many examples of the movement of parasitic and predaceous insects from one place or country to another antedated it, the introduction of the Vedalia beetle, *Rodolia cardinalis* (Mulsant), from Australia into California in 1888 and its striking success in control of the cottony cushion scale, is generally regarded as ushering in the modern world effort in biological control that has continued ever since.

Cottony cushion scale, Icerya purchasi (*Maskell*). — For the control of this pest, which was threatening the young citrus industry in California with ruin, two natural enemy species were introduced. In addition to the coccinellid beetle, *R. cardinalis* (above), a parasitic fly, *Cryptochaetum iceryae* (Williston) was also introduced. The beetle multiplied at a fantastic rate and by 1889 had brought about control of the pest in southern California. To this day, however, the fly remains the dominant control factor in cooler coastal areas (Quezada and DeBach, 1973). Together, they keep this pest under such complete control that it is difficult to find. We were reminded of its catastrophic damage potential, however, when in the late 1940's DDT was used in some citrus groves for control of other citrus pests. The destruction of *Rodolia* occasioned again massive general outbreaks of the scale that threatened destruction of the groves until the DDT treatments were stopped and the groves were restocked with the beetle (DeBach and Bartlett, 1951).

Olive parlatoria scale, Parlatoria oleae (*Colvée*), — One of the world's best documented examples of biological control by introduced insects is that of olive scale in California. This example also illustrates two basic principles of some importance. The first is that a better natural enemy — one that is better adapted and a better searcher for hosts — may so reduce the abundance of its host (the pest) that other natural enemies will die out. This is termed "competitive displacement". Biological control specialists have been in the forefront in demonstrating such ecological displacement. In this case the host species was so reduced by the two introduced parasitic wasps that the pest remains year after year under perfect biological control — as good as can be achieved by any insecticide. A thousand or so leaves, on average, will harbor only a single unparasitized scale plus the five or six parasitized ones needed to maintain the parasite populations and the control.

The second principle is that two or more partially competing natural enemies may co-exist and achieve a higher degree of biological control than the best one could achieve alone. Although the first effective species, *Aphytis maculicornis* (Masi), did completely displace a number of other indigenous and previously introduced natural enemy species, another good one that was later introduced, *Coccophagoides utilis* (Doutt), was able to establish, to co-exist with *Aphytis*, and to greatly improve the overall degree of biological control, even though *Aphytis* is clearly the better of the two (Huffaker and Kennett, 1966).

It should be said here that these parasites have completely controlled this devastating scale insect, not only in olive groves where some US$7 $\times 10^6$ has already been saved (to 1973), but on *all* of its host plants — some *200* kinds — in many types of situations, the length and breadth of California, being an inestimable benefit of far greater value.

Rhodesgrass scale, Antonina graminis (*Maskell*). — This example of biological control of rhodesgrass scale in Texas is used to illustrate an interesting consequence of adaptation of a parasite to its host and its habitat which, however perfect can, paradoxically, make it difficult for man to use the parasite over a vast region recently invaded by its host species. This pest scale invaded Texas sometime prior to 1942 and has since spread over some 60 000 miles^2 of grazing lands in that state (Schuster et al., 1971). To make a long story short, a wingless parasitic wasp, *Neodusmetia sangwani* (Rao) was introduced from India into infested Texas grasslands in 1959.

The grasslands of the world are notoriously windy places. For a parasite co-evolved with a grassland host, the rhodesgrass scale, *N. sangwani*, found it an advantage to be wingless for it could readily be blown far away from the colonies of its hosts if it flew normally. Since the pest scale also has very limited mobility, moving only in the crawler stages, there was no need to take such risks to keep up with its host in its native infested habitat. However, when the scale became inadvertently established thousands of miles away in Texas and quickly spread, with the aid of man and other means, over vast expanses of Texas grassland before the parasite arrived, a major problem was posed as to how adequate spread of the wingless parasite over such a vast area could be obtained in a reasonable period of time. Biological control workers in Texas (see Schuster et al., 1971) devised a cheap method to do this. They also established the effectiveness of the parasite as a control agent of the scale. They devised methods by which the parasites could be collected on the grass culms in the field. These then were dropped from an airplane, at a cost of 39¢/mile^2 on a drop at 1×2 mile intervals. The wingless parasites would then spread naturally in about 4 years over the intervening infested areas. While this program has not yet been fully exploited, the potential benefits are nevertheless obvious.

Use of insects against weeds

No story of the use of insects in biological control should omit the classic cases of biological control of weeds by use of introduced insects. Examples are numerous, and indeed some of the world's most extensive and notorious weeds have yielded to this method when no other means sufficed. The partial control of the alien lantana in Hawaii shortly after the turn of the century by various insects introduced from Mexico was not followed by a spectacular success until in the 1930's when the moth *Cactoblastis cactorum* (Berg.) was introduced from Argentina into Australia to control a weed that had become a national catastrophe. This was prickly pear, *Opuntia* spp., which virtually rendered useless some 60 000 000 acres of grazing lands in Queensland and New South Wales. Within 3 years from the time of introduction Dodd (1940) was able to write that transformation from utter economic ruin to prosperous enterprise had been effected, and Dodd himself was given highest acclaim by a grateful nation.

I was fortunate in being able to participate in a case equally spectacular in effect but of less geographic scope. In this case also, economic ruin threatened a ranching industry over some 5 000 000 acres of land in California and other western states. As with the prickly pears, the alien Klamath weed, *Hypericum perforatum* Linn., was not controllable by any other economically feasible method. Again, within 3 years from the time of introduction of a chrysomelid beetle, *Chrysolina quadrigemina* (Suffrian), which feeds exclusively on it, the potential of biological control was demonstrated at the initial release sites. Within 6—8 years, as a result of extensive human distribution and natural spread of the beetles this toxic and economically devastating weed was completely controlled as an economic problem in California, and essentially so in other western states as well. Land values rose sharply and banks no longer refused loans for the purchase of land in the infested region. To 1973, savings in California alone are estimated at US $\$66 \times 10^6$.

An insect has also been used with striking results against a major water weed in southeastern U.S. The alligator weed (*Alternanthera phylloxeroides* (Mart.) Griseb.) grows so extravagantly there that it blocks passage by small boats and is detrimental to fishery. A small flea beetle (*Agasicles hygrophilia*

Selman and Vogt) which attacks it in its native home area in Argentina was introduced and has already greatly reduced the problem in some areas and others are coming under its influence. This result has encouraged scientists to seek out natural enemies of another far more serious weed of the world's waterways, water hyacinth *Eichhornia crassipes* (Mart.) Soln. An initial introduction has been made in Florida (Andres et al., in press).

Use of mites against mites

Spider mites are among the major pesticide-induced crop pests of the world. Their fecundity and population increase is known to be affected favorably by a number of pesticides, e.g., DDT, Carbaryl, and some fungicides (Huffaker and Spitzer, 1950; Chaboussou, 1963, 1965). More importantly, with the appearance and extensive use of broad spectrum organo-synthetic insecticides subsequent to World War II these spider mites have become major pests on many crops where previously they were of secondary or no importance. The destruction of indigenous predators by the new materials has been the major factor in this change. Some of these predators have now developed their own resistance to some of these materials and two at least are being used in conjunction with use of modified spray programs against other pests of apples (Hoyt and Caltagirone, 1971; Asquith and Hull, 1973). Moreover, one predatory species (*Phytoseiulus persimilis* Athias—Henriot), also a mite, has been widely introduced into other countries from Chile and is mass produced and released on a very large scale in greenhouse cultures of cucumbers, tomatoes and other crops for control of spider mites (Hussey and Huffaker, in press).

Use of snails against other snails, aquatic weeds, and human disease

Two examples of the use of snails are interesting. One is the successful control of the Giant African snail, *Achatina fulica* Bow., in Hawaii by an introduced predatory snail (*Gonaxis quadrilateralis* (Preston)). The Giant African snail had become a major pest of various plants and was sometimes so abundant that the slime left by their crossing roadways and being crushed by cars proved to be a traffic hazard. The other example is the use of the snail, *Marisa cornuarietis* (L.), in Puerto Rico for control of aquatic weeds. Interestingly and of profound public health importance, *Marisa*'s effect has been to so reduce or displace another snail (*Biomphalaria glabrata* (Say)) which is an intermediate host of the pathogen causing schistosomiasis in man, that this latter problem is considerably reduced (Bay et al., in press).

Use of microbial pathogens against insects, vertebrate pests, weeds and plant diseases

Many examples exist of the worthwhile role of microbial pathogens in the control of pests, i.e., against vertebrate pests, insects, weeds, and also against plant parasitic pathogens.

The phenomenon of microbial disease in insects has long been known, and the Italian, Agostini Bassi (1773—1856) is credited as the giant among those who laid the first foundations of infectious disease science, and especially of insect pathology (Steinhaus, 1956).

The practicality of introducing pathogens from foreign areas for the control of indigenous or alien pest insects and of their use as microbial insecticides received its modern impetus from two inadvertent introductions in North America. One was the milky disease bacterium causing milky disease of the Japanese beetle in eastern U.S.A., and the other a virus causing a granulosis disease in the European spruce sawfly in eastern Canada. Both were probably inadvertently admitted in the programs of importing various insect parasites of these alien insects, the one from Japan and the other from Europe. The sawfly virus had a remarkable natural effect, spreading naturally and causing a rapid cessation of the sawfly outbreaks, and, coupled with the effects of the introduced parasites, this status still holds (Neilson et al., 1971). The milky spore disease inoculum of the beetle had to be mass-produced and spread in Japanese beetle infested areas of the eastern states, but not without substantial success. These results, together with the remarkable additional stimulus given the field by the late E.A. Steinhaus, ushered in a large world-wide effort to exploit disease in the control of insect pests (Burges and Hussey, 1971).

Two examples of the use of pathogens against entirely different kinds of pest organisms, one a vertebrate and the other a weed, in an opposite corner of the world, Australia, are noteworthy. The first is the introduction of the myxomatosis virus of the South American rabbit into Australia for control of the plagues of the European rabbit that were rampant over vast areas of the country. The interesting popular book, "Flying Fox and Drifting Sand", by the late naturalist-author Francis Ratcliffe (1938) gives a vivid account of the utter devastation wrought by the rabbit hordes. No one remotely knows the former size of these rabbit populations, but soon after the myxomatosis virus was introduced and spread widely, accelerated by natural mosquito vectors, the rabbit populations drastically declined (Fenner and Ratcliffe, 1965). So great was the relief that a euphoria developed and the customary precautions of rabbit fencing and baiting were largely abandoned. Later, however, there was some attenuation of the virulence of the virus and an increase in the resistance of the rabbit populations, such that the rabbits have somewhat increased again. Some such effect is to be expected over time with the employment of such pathogens against vertebrates, but the immunity reactions are weaker in insect pests (Stephens, 1963) and resurgences because of this are rare. Moreover, even in the case of the rabbit in Australia the numbers now are reportedly only a small proportion of the hordes that were characteristic prior to their biological control by the virus (Davis et al., in press).

The other Australian example is that of control of an extremely noxious plant, skeleton weed, *Chondrilla juncea* Linn. in wheatfields of southeastern Australia. The native home of this weed is the Middle East and the Mediterranean. It is relatively uncommon there, is not regarded as a weed, and is attacked by many organisms. After prolonged study in Europe, a species of rust, *Puccinia chondrillina*, was introduced in 1971. By 1973 it had resulted in extensive and effective epidemics. In the very wheatfields where the wheat stem rust organism, *Puccinia graminis*, form *tritici*, had been so devastating in earlier years, this other *Puccinia*, i.e., *chondrillina*, has been dramatically used by man to protect the wheat crop (Waterhouse, 1973). This rust is so host-specific that it will not attack other than *Chondrilla* and in fact does not attack two other strains of *C. juncea* itself which occur in but are of less importance in New South Wales. Noteworthy, this is the first example in the world of a plant pathogen being scientifically selected and deliberately introduced into a new country for weed control.

We have all become accustomed to a form of biological control of human and animal diseases, so greatly expanded after the discovery that common bread mold, *Penicillium*, inhibits growth of bacteria in its vicinity. This development has led to the discovery and use of many such microbe-produced antibiotics, and they are widely used, not only in medicine, but in the control of plant diseases.

Scientists at California and colleagues elsewhere have recently reviewed the prospects for biological control, especially of soil-borne pathogens which cause disease in our crop plants (Baker and Cook, 1974; Snyder et al., in press).

Chemical control of such diseases or use of steaming or flooding can be effective, but unfortunately, these measures are often not economic. Such treatments also affect the whole soil biosphere rather than just the pathogens, and reinvasion and resurgences often occur quickly. Sometimes there is simply a "disease trading", i.e., of a formerly dominant pathogen for a minor one that then becomes a problem (Kreutzer, 1965).

Biological control of plant pathogens, observed in both field and laboratory, include the viruses, fungi, insects, nematodes and various types of microbial antagonists. Virus "cross-protection" has been noted, e.g.,wherein peach trees infected with a strain of peach mosaic virus which caused only very slight symptoms were thus protected from the much more virulent closely related strains (Stout, 1950), and it has been shown that potato plants pre-infected with the H-strain of the X-group of potato viruses causing no disease symptoms, are protected subsequently from all X-viruses.

The nematode *Thornia* sp. has been observed to feed on the plant parasitic nematodes *Tylenchus semipenetrans* and *Aphelenchus avenae* (see Boosalis and Mankau, 1965). The authors felt that under certain conditions this predation, plus other parasite feeding, may account for a significant degree of natural control of these nematodes in California citrus groves.

Predaceous nematophagous fungi (primarily *Hypomycetes*) are a well defined ecological group in the soil. Trapping structures, e.g., of short sticky lateral branches or constricting rings are effective in capture of nematodes. Although no one seems to have claimed a controlling effect, their abundance in soils seems to be correlated with the density of nematode hosts (Snyder et al., in press).

Bacteria, actinomycetes and other fungi that produce substances antibiotic to plant pathogens in vitro have been isolated from soil. Production of antibiotics antagonistic to *Pythium* species by addition of organic matter has been obtained and lessening of damping off disease has temporarily resulted in soils infested with organisms antagonistic to *Pythium*, but such effects seem to be very temporary and therefore discouraging. Certain rotation practices greatly reduce the problems with some plant pathogens.

Finally, while some of the reasons are known for these various manifestations, much more needs to be learned about the whole complexity of soil microfauna and microbe interrelationships, as associated with the growth of various crops, before we can use pathogens and microbial antagonists against the organisms causing plant disease. The book by Baker and Cook (1974), first of its kind, should help to stimulate the needed investigations.

Use of vertebrates against weeds, insects and vertebrate pests

Various vertebrates have been employed as effective biological control agents on occasion. Thus, carp and manatees have been used to reduce obstructing and otherwise injurious growths of aquatic vegetation in special situations. Goats and geese have been used likewise on land. The mongoose was introduced into sugar producing islands in the Caribbean to control rats, and while it is recognized to be a good rat predator, it also has had damaging effects as a predator of lizards, ground nesting birds, and chickens. This is an example wherein too little attention was given to prey (or host) specificity in making an introduction, a carelessness that is no longer permitted. Lastly, the woodpecker is an excellent predator of overwintering codling moths in Nova Scotia and is a key factor in the integrated control program for control of pests of apple there, and the placing of nesting boxes in woodlands in Europe has been used to increase the populations of insectivorous birds as a natural control of woodland pest insects.

Use of insects against dung in pastures

As a last and unusual example of the use of biological control, another Australian success is cited. It seems that the long geological isolation of Australia from the rest of the world — indeed from a time before the origin of true mammals — lies at the root of this case. There are no large native grazers there except kangaroos. The dung of these animals is quite unlike the heavy wet pads of cattle. Consequently, the native Australian insects that breed in and dispose of the small dry kangaroo droppings are not suited to the utilization of "cow pads".

Thus when the Australians began an intense husbandry of cattle the pads of these animals lay where they fell and dried, but became ever more abundant, disappearing only very slowly in a decade or more. The result was an accumulating loss each year of some 6×10^6 acres of grazing lands. In the past 10 years Australia's Commonwealth Scientific and Industrial Research Organization (CSIRO) has conducted an intensive research effort to redress the imbalance in Australia between dung and dung beetles by importing into their country dung beetles from Africa. The dung beetle and its services to mankind are steeped in history. The scarab *Scarabaeus sacer* Linn. was sacred to the early Egyptians. They even represented the Sun God, their most important deity, as a scarab in their art and hieroglyphics (Waterhouse, 1974). A range of coprid beetles have been introduced in Australia beginning in 1963. In areas where one species, *Onthophagus gazella* F. became established dung disposal has been almost complete, large wet pads being buried underground in 24 h during the season of this species' activity. But while this and other introduced species have already had considerable success, it is now apparent that a larger complex of dung insects will need to be introduced in order to satisfy the needs in all seasons and areas and to avoid the disruptive effects of toads which feed on the smaller species of dung beetles, such as *O. gazella*. Moreover, the Australians are studying the feasibility of introducing certain mites that are carried from pad to pad by the beetles and which attack muscid flies which compete with the dung beetles. The possibilities of biological control, not only of the dung problem but of the frightfully annoying Australian bush fly and other dung breeding muscids, are thus suggested and are being studied.

The kinds of habitats and problems where biological control has proved successful

From the foregoing and from consideration of other examples, we can say readily that biological control may not only be accomplished by a wide variety of organisms, but that this method has proved to be efficacious for a very wide range of habitats and problems. No longer can it be casually dismissed as a method that works only in special situations of great rarity. It has worked on land, in water, in forests and in fields, in long lived tree crops and in natural forests of great longevity. It has worked on islands and over vast continental areas, in geographic climes from the salubrious situations at the equator into our great coniferous forest formations far northward in Canada, for example. Succulent tropical fruits, windswept grasslands and range,orchards, woodlands, and field crops of great variety have all benefitted by the deliberate introductions of natural enemies for control of their pests (Huffaker and Messenger, in press).

Unheralded, almost ignored, yet more important, surely, than all these introductions is the "invisible" naturally-occurring biological control that exists all around us, and which, to a large degree must account for the fact that only a small proportion of the insects that feed upon our crop plants ever become pests. DeBach (1974) has likened this "invisible" biological control of potential pests to the submerged part of an iceberg, some 80—90% of the total, noting that the visible part of the iceberg is represented by those phytophagous species that do not in the given habitat have effective natural enemies. Many of these potential pests that were formerly under biological control have recently become "visible" pests because of the destruction of their natural enemies by intensive use of broad-spectrum organosynthetic pesticides. This usage has dramatically revealed the existence of this "invisible" biological control, which is not seen until it is disturbed.

CONCLUSION

By way of conclusion, it is emphasized, that in my view and that of the small but enlarging group of workers in this field throughout the world, the main limitation to greater use of biological controls is the ignorance of its potentials in the public area and the consequent lack of the necessary support to develop it. For years biological control has been almost non-existent as a significant research endeavor in most of our world universities and experiment stations, and in the various federal governments it has had only limited support while at the same time suffering in being administratively dismembered as to its various functional aspects, thus lacking the necessary cohesiveness for maximum effectiveness.

It is heartening to see that at least in places this situation is beginning to improve, and that the general worldwide trend to favor ecologically oriented, integrated pest control is creating a climate favorable not only to integrated control but to biological control in its broader sense as a central feature of integrated control. It is only through the pursuit of integrated control as well as biological control by a large corps of well-trained enthusiastic specialists from a spread of disciplines working together that the maximum rewards can be had. The application of systems analysis techniques is rapidly making this goal realizable.

Thus in the U.S.A., a team of specialists from 18 universities and the U.S. Department of Agriculture, including not only entomologists but agronomists, extension specialists, plant pathologists, ecologists, plant breeders, plant physiologists, engineers, mathematicians, and economists have combined their talents in a single major effort to develop multidisciplinary systems of crop production for six major U.S. crops, centered on pest control in this case. They are using systems science and modeling as a uniting and catalyzing force to develop schemes to manage the pests in such a way that a maximum reliance is placed on natural or biological controls, and other methods are employed only with proven need. Thus, costs and energy use are reduced, profits increased, and the environment is subjected to less abuse (Huffaker and Smith, 1973).

REFERENCES

Andres, L.A., Davis, C.J., Harris, P. and Wapshere, A.J., in press. Biological control of weeds. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 19.

Asquith, D. and Hull, L.A., 1973. *Stethorus punctum* and pest population responses to pesticide treatments on apple trees. J. Econ. Entomol., 66: 1197—1203.

Baker, K.F. and Cook, R.J., 1974. Biological Control of Plant Pathogens. W.H. Freeman, San Francisco, Calif., 433 pp.

Bay, E.C., Berg, C.O., Chapman, H.C. and Legner, E.F., in press. Biological control of medical and veterinary pests. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 18.

Beck, S.D. and Maxwell, F.G., in press. Use of plant resistance. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 25.

Benson, N.R., 1968. Can profitable orchards be grown on old orchard soils? Wash. State Hort. Assoc. Proc., December 1968, pp.109—114.

Beirne, B.P., 1967. Biological control and its potential. World Rev. Pest Control, 6: 7—19.

Boosalis, M.G. and Mankau, R., 1965. Parasitism and predation of soil microorganisms. In: K.F. Baker and W.C. Snyder (Editors), Ecology of Soil-Borne Plant Pathogens. Univ. of California Press, Berkeley, Calif., pp. 374—391.

Borlaug, N.E., 1965. Wheat, rust, and people. Phytopathology, 55: 1088—1098.

Burges, H.D. and Hussey, N.W., 1971. Microbial Control of Insects and Mites. Academic Press, London, New York, N.Y., 861 pp.

Chaboussou, F., 1963. Multiplications des populations de deux espèces de tétranyques (*Panonychus ulmi* Koch et *Eotetranychus carpinus vitis* (Boisd.) sur vigne à la suite de l'utilisation de certains insecticides dans la lutte contre l'eudemis (*Lobesia botrana* Schiff.). Résultats de trois années d'experimentation. C. R. Seances Acad. Agric. Fr., 49: 187—199.

Chaboussou, F., 1965. La multiplication par voie trophique des tétranyques à la suite des traitements pesticides. Relations avec les phénomènes de résistance acquise. Biol. Zool. Agric. Bachic, Ser.II, 7: 143—184.

Coons, G.H., 1953. Breeding for resistance to disease. In: Plant Diseases, Yearbook of Agriculture 1953. U.S. Dept Agric. Wash., D.C., pp.174—192.

Davis, D.E., Myers, K. and Hoy, J.B., in press. Biological control among vertebrates. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 20.

Day, P.R., 1972. Crop resistance to pests and pathogens. In: Pest Control Strategies for the Future. Nat. Acad. Sci., Washington, D.C., pp. 257—271.

DeBach, P., 1974. Biological Control by Natural Enemies. Cambridge Univ. Press, London, 323 pp.

DeBach, P. and Bartlett, B., 1951. Effects of insecticides on biological control of insect pests of citrus. J. Econ. Entomol., 44: 372—383.

Dodd, A.P., 1940. The Biological Campaign Against Prickly Pear. Commonwealth Prickly Pear Board, Brisbane, Qld., 177 pp.

Doutt, R.L. and Smith, R.F., 1971. The pesticide syndrome — diagnosis and suggested prophylaxis. In: C.B. Huffaker (Editor), Biological Control. Plenum Press, New York, N.Y., pp. 3—15.

Fenner, F. and Ratcliffe, F.N., 1965. Myxomatosis. Cambridge Univ. Press, London, 379 pp.

Furtick, W.R., 1974. Insecticides in food production. In: Insecticides for the Future: Needs and Prospects. Proc. Rockefeller Found. Conf. (Bellagio, Italy), April 22—27, 1974.

Horber, E., 1972. Plant resistance to insects. Agric. Sci. Rev., 10: 1—18.

Horsfall, J.G., Chairman, 1972. Genetic vulnerability of major crops. Nat. Acad. Sci. Nat. Res. Counc., Washington, D.C., 307 pp.

Hoyt, S.C. and Caltagirone, L.E., 1971. The developing programs of integrated control of pests of apples in Washington and peaches in California. In: C.B. Huffaker (Editor), Biological Control. Plenum Press, New York, N.Y., pp. 395—421.

Huffaker, C.B., 1970. Life against life — nature's pest control scheme. Environ. Res., 3: 162—175.

Huffaker, C.B., 1971. The ecology of pesticide interference with insect populations. In: J.E. Swift (Editor), Agricultural chemicals — harmony or discord for food, people, environment. Univ. Calif. Div. Agric. Sci., Berkeley, Calif., pp. 92—104.

Huffaker, C.B. and Kennett, C.E., 1966. Biological control of *Parlatoria oleae* (Colvée) through the compensatory action of two introduced parasites. Hilgardia, 37 (14): 533—561.

Huffaker, C.B. and Messenger, P.S. (Editors), in press. Theory and Practice of Biological Control. Academic Press, New York, N.Y.

Huffaker, C.B. (Project Director) and Smith, R.I. (Associate Project Director), 1973. Integrated Pest Management: The Principles, Strategies and Tactics of Pest Population Regulation and Control in Major Crop Ecosystems. Progress Report and Renewal Proposal for National Science Foundation Grant GB-34718. Volumes I and II. Int. Cent. Biol. Control, Univ. of California, Berkeley, Calif.

Huffaker, C.B. and Spitzer Jr, C.H., 1950. Some factors affecting red mite populations on pears in California. J. Econ. Entomol., 43: 819—831.

Huffaker, C.B., Simmonds, F.J. and Laing, J.E., in press. Theoretical and empirical basis of biological control. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 3.

Hussey, N.W. and Huffaker, C.B. (Coordinators), in press. The biological control of spider mites. In: International Biological Program Cooperative Studies in Biological Control. Cambridge Univ. Press, London.

Kreutzer, W., 1965. The reinfestation of treated soil. In: K.F. Baker and W.C. Snyder (Editors), Ecology of Soil-Borne Plant Pathogens. Univ. Calif. Press, Berkeley, Calif., pp. 495—508.

Neilson, M.M., Martineau, R. and Rose, A.H., 1971. *Diprion hercyniae* (Hartig), European spruce sawfly (Hymen.: Diprionidae). In: Biological Control Programmes against Insects and Weeds in Canada 1959. Tech. Commun. No.4: 136—143. Commonwealth Institute of Biological Control.

Painter, R.H., 1951. Insect Resistance in Crop Plants. Macmillan Company, New York, N.Y., 520 pp.

Quezada, J.R. and DeBach, P., 1973. Population biology of the cottony cushion scale, *Icerya purchasi* Maskell (Homoptera: Coccidae) and its natural enemies in Southern California. Hilgardia, 41: 631—688.

Ratcliffe, F.N., 1938. Flying Fox and Drifting Sand. McBride, New York, N.Y., 341 pp.

Ripper, W.E., 1956. Effect of pesticides on balance of arthropod populations. Annu. Rev. Entomol., 1: 403—438.

Schuster, M.F., Boling, J.C. and Marony Jr, J.J., 1971. Biological control of rhodesgrass scale by airplane releases of an introduced parasite of limited dispersing ability. In: C.B. Huffaker (Editor), Biological Control. Plenum Press, New York, N.Y., pp. 227—250.

Simmonds, F.J., Franz, J.M. and Sailer, R.I., in press. History of biological control. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 2.

Smith, R.F., Huffaker, C.B., Adkisson, P.L. and Newsom, L.D., 1975. Progress achieved in the implementation of integrated control projects in the U.S.A. and tropical countries. EPPO Conference on Integrated Control in Horticultural Crops (Kiev) August 27—31, 1974.

Snyder, W.C., Wallis, G.W. and Smith, S.N., in press. Biological control of plant pathogens. In: C.B. Huffaker and P.S. Messenger (Editors), Theory and Practice of Biological Control. Academic Press, New York, N.Y., Chapter 21.

Steinhaus, E.A., 1956. Microbial control — an emergence of an idea. A brief history of insect pathology through the nineteenth century. Hilgardia, 26: 107—160.

Stephens, J.M., 1963. Immunity in insects. In: E.A. Steinhaus (Editor), Insect Pathology: An Advanced Treatise. Academic Press, New York, N.Y. and London, 1: 273—297.

Stout, G.L., 1950. New method of plant disease control. Bull. Calif. Dept Agric., 39: 129—136.

Waterhouse, D.F., 1973. Insects and wheat in Australia. J. Aust. Inst. Agric. Sci., December 1973.

Waterhouse, D.F., 1974. The biological control of dung. Sci. Am., 230(4): 101—109.

Wortman, S., 1968. Toward the conquest of hunger. In: Strategy for the Conquest of Hunger. Proc. Symp. Rockefeller Found., pp. 2—3.

Zink, E.W. and Duffus, J.E., 1969. Relationship of turnip mosaic virus susceptibility and downy mildew (*Bremia lactucae*) resistance in lettuce. J. Am. Soc. Hort. Sci., 94: 403—407.