An Overview of Biological Control, with Particular Commentary on Biological Weed Control

by
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INTRODUCTION

Biological control has had largely an empirical origin, starting strongly with the outstanding success in control of cottony cushion scale in California in 1888-89, and blossoming out from that in many directions. Each success has in some way helped to encourage and obtain support for other attempts. The practice, however, had at its inception a basis in theory. The cottony cushion scale attempt itself was made on the basis of a theory that stood in sharp contrast to an opposing theory advanced some years before by perhaps the leading U.S. insect ecologist of his time. Stephen A. Forbes of the University of Illinois, had written in 1880, "... the annihilation of all the established 'enemies' of a species would, as a rule, have no effect to increase its final numbers."

The contrary theory of C. A. Riley and others who espoused the introduction of natural enemies for biological control held that an alien insect which becomes much more abundant in its new home than in its native region has probably escaped from its natural enemies and that discovery in the native area and introduction of those enemies might well bring about natural control in the invaded region. The truth of this basic ecological theory—that natural enemies may in fact have a profound impact on the abundance of their hosts—has been verified over and over again - i.e., for some 170 or more examples of at least partially successful introductions for control of insect pests and weeds. These successes have done much to remove the doubts of this generation of people like Forbes, although negativism about biological control persists in many circles, particularly among those who stand to gain by sales of pesticides or who have concerned themselves mainly with use of pesticides.

Yet we have not progressed as far as we would like from this basic theory and its verification by empirical events toward prescribing precisely those natural enemies that might be best to introduce for specific pests and situations. The record of successful projects in biological control, in relation to the funds and efforts expended suggests, in fact, that the rather *ad hoc* method of making introductions has not worked so badly. This is not to say, that no science is used and none is needed. Quite the contrary.

Biological control in the strict sense of action of natural enemies cannot be expected to solve every pest problem of a crop; it may present excellent control possibilities for one or a few such pests and help to control others. However, biological control, together with plant resistance (nature's chief agencies for containment of excessive abundance in otherwise favorable environments) form the central core around which pest control should be developed. The current world emphasis on integrated control of pests (or pest management) is built largely upon this concept, with use of supplementing cultural methods everywhere possible, and of disrupting but essential chemicals as little as is consistent with the needs.

Several world developments have recently emerged which offer widened opportunities for biological control. The first was the widespread development of resistance in pest insects to the broad spectrum insecticides being used against them; up to 1973 over 200 insect species representing over 70% of the major pests of the world were resistant to certain insecticides (Georghiou 1971, 1972), and a few cannot be controlled by any (Adkisson 1971). The second was the increased world consciousness of the quality of the environment and the adverse impact of pesticides on this quality, especially on our terrestrial and estuarine wildlife and on man himself (e.g. Carson 1962, Council on Environmental Quality, 1972). The third was the realization that man is rapidly exhausting his most strategic fossil fuel reserves, especially oil. A fourth has been the realization that industry cannot produce, and the consuming developing countries cannot afford to buy, the amounts of pesticides that would be needed if sole

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reliance were placed on this tactic (Furtick 1974). In all four respects, greater use of biological control is viewed as the most viable alternative (DeBach 1974). Biological control has not entailed development of resistance to appropriate natural enemies, for the enemies have, in general, means of countering moves in that direction; it offers no hazards to the environment where appropriate enemies are used; it would require much less fossil fuel energy; and would stretch and conserve our chemical control potential. Greatly increased use of plant resistance should come in time, but such improvements are slow, and this tactic, too, cannot be the solution for every pest. A combination of tactics, which should include much more effort in biological control, habitat management and resistance to pests, will be required.

Currently, biological control has been utilized mainly for control of insect and mite pests and weeds. One exceptional case involves the European rabbit. Insects have been the principal agents used for both insect pests and weeds. Extensions into control of animal and human diseases and of plant diseases, have largely just begun, the former via biological control of the vectors, including snails (Bay *et. al.* 1976), and the latter, especially via extensive studies of the inter-species interactions among soil organisms relative to possibilities of biological control of soil-borne plant pathogens (Baker and Cook 1974, Snyder *et al.* 1976). The possibilities of manipulating the habitat of the natural enemies to obtain better biological control by existing natural enemies also offers significant horizons. Biological control of weeds offers many prospects, because it is here that the greatest disparity exists between the damage caused by the pests (which far exceeds that caused by insects) and the funds and effort expended for biological control (Wilson and Huffaker 1976).

TYPES OF PROBLEMS

The type of problem may greatly influence the chance of success with classical biological control (Huffaker 1957). Successes for both insect pests and weeds have been disproportionately centered on pests of long-lived habitats of relatively limited disturbance—i.e. pests of range, forests and tree crops (Andres *et al.* 1976, Huffaker 1959, Turnock *et al.* 1976, Waters *et al.* 1976), and particularly for tropical tree crops (Bennet *et al.* 1976). Successes with pests of short-lived, highly disturbed habitats, as with annual row crops, have been quite limited (Clausen 1956, van den Bosch *et al.* 1976). Pests of aquatic habitats are relatively little known in terms of their natural control factors. A principal difference between aquatic habitats and crop habitats is that the latter are cultured by man while the former in general are not. Disturbance by human cultivation, rotation, irrigation, etc. does not apply, although other disturbances caused by human interference or alterations with the natural water resources and water flow have actually created many of our worst aquatic pest problems, e.g., mosquitoes, snails and weeds. Until we know far more about the aquatic ecosystems, we will not make the most of our opportunities for biological control.

If the problem is a multiple one, as with extensive and obstructive growth of aquatic vegetation of a mixture of species, or of a mixture of aggressive weeds in row crops, the opportunities for a biological control solution are reduced. One may in fact only trade one pest for another, as critics have been wont to apply much too broadly concerning our field. (Of course, the removal of one pest species by use of chemical or cultural means may also only 'trade one pest for another'.) As Huffaker (1957, 1964) noted, the special opportunity for biological control of weeds is in those situations where a single highly aggressive species is overwhelmingly dominant, e.g., in a range or forage or grain crop situation where the forage or crop plants can compete rather well with other resistent claimants of weedy character. Biological control of St. Johnswort in California (Huffaker and Kennett 1959, Huffaker 1967), and of prickly pears (Dodd 1940) in Australia and *Chondrilla* (Cullen in press) are good examples. In neither case has there been any flat trading of one pest for another, although, of course, some portions of the space formerly occupied by these weeds are now utilized by other weeds. This claim of only trading one pest for another has also recently been made with respect to biological control of olive parlatoria scale in California because now that it is under perfect biological control on some 200-odd host plants, another scale insect, black scale, has increased on olives. It does not, however, present nearly the problem parlatoria scale did even on olives, and it does not even occur on most of the other 200-odd hosts of parlatoria scale. This is a sample of the unreasoned criticism we sometimes face.

The possibilities of biological control of weeds carries at least one major advantage over those of biological control of insect pests. This is that weeds are engaged in a very direct inter-species competition with the crop or range plants to be protected, and even slight damage to the weed by an introduced agent may be enough to tip the competitive advantage to the crop plants. Insect pests feed as predators on the crop plant and are not engaged in a direct competition with them for soil nutrients, water and sunlight; hence the natural enemy pressure on the insect population must be sufficient to *directly* reduce its numbers. On the other hand, biological control of weeds present many more problems involving conflicts of interest which may deny this possible solution of a problem.

TYPES OF NATURAL ENEMIES

The types of natural enemies used for weed control and insect control have been similar; in both areas insects have been most used, Predatory mites are very successful agents in control of the important spider mites all over the world and one species has even been successfully mass produced and commercially used in glasshouse cultures in several countries of Europe, including the U.S.S.R. (Rabb *et al.* 1976). A phytophagous mite was introduced into Queensland, Australia and established for control of prickly pears, but its action was soon dwarfed by that of *Cactoblastis* introduced later.

The most efficient natural enemies of insect pests do not attack plants (therefore, weeds), for these are the highly host specific parasitoids. The most nearly comparable insects that attack weeds are the gall-forming insects among the Hymenoptera and Diptera, for example, and these too commonly exhibit high host specificity and have been introduced for biological control of weeds in a few instances, but without the general success we have had with the highly host specific parasitoids in insect control. The insects introduced for weed control are for the most part predators, and they too must possess a very high degree of host specificity; they must not endanger economic plants. Hence, in weed control, we can only utilize a small spectrum of the full complement of these natural enemies. These near-generalists (which are quite effective in control of some insect pests - e.g. *Chrysopa, Geocoris*, nabids, spiders, etc.) are not available for introduction to serve similar roles in weed control. In fact, for some insect pests, especially in frequently disturbed annual row crops, the near-generalists (predators) have proven to be more important than the more host specific parasitoids (Ehler and van den Bosch 1974) for they have greater mobility, a high prey consumption rate and ability to switch or transfer to many different prey, and some to feed on plant juices. The greater availability of alternate prey, combined with their mobility and a good intrinsic rate of increase, make them especially useful in short-term, frequently disturbed habitats—they have a high factor of opportunism or r-strategy. They cannot, however, compete with good K-strategists—the specialists—in stable, long-term habitats. The only generalists that could be admitted for weed control, however, would be those that would be spatially confined in areas where a general removal of other than target vegetation would be acceptable.

Pathogens have been used for insect pest control in two ways, (1) for introduction and distribution with the hope that once established, multiplication and perpetuation would be sufficient to maintain continued control, and (2) use as microbial agents like insecticide applications. The first is exemplified by the milky spore disease bacterium which attacks the Japanese beetle in the U.S. For a decade or so a single distribution program was considered effective (Hall, 1964). The inadvertent introduction of a virus disease of the European spruce sawfly in Canada and its natural distribution and multiplication was credited with a major role in suppression of widespread outbreaks, and together with action of the deliberately introduced parasitoids, with continuing good control over many years (Munore). For weed control, an early example is that in Hawaii reported by Fullaway (1954) wherein spores of *Fusarium oxysporum* Schlect were sprayed on the prickly pear *Opuntia megacantha*, apparently with little success. Dodd (1940) also reported occasional primary attack by several fungi on prickly pears in Queensland, but he considered the secondary organisms . . . "the bacterial soft rot or rots" . . . to be of more importance in assisting *Cactoblastis* than were the primary parasites.

It was not until recently, however, that introduction of a plant pathogen from one continent to another to control a weed was attempted, and sucussfully so. In this effort entomologists and plant pathologists have for the first time fully cooperated. The introduction of *Puccinia chondrillina* for control of skeleton weed, *Chondrilla juncea*, in Australia thus stands as a landmark.

It is probable in my view that introductions of plant pathogens for subsequent natural interaction with and regulating control of weeds will prove more successful than has been the case with such introductions of insect pathogens for control of insect pests. This belief is based on my view that plant pathogens are in general more effective competitors against the insects which attack their host plants than are the insect pathogens in competition with the primary entomophagous parasitoids and predators which attack *their* hosts, the phytophagous insects. In any event there are many plant pathogens that exhibit high degrees of host specificity, exemplified by *Puccinia* and other rusts, and these offer untouched horizons for biological weed control, whereas the insect pathogens have been much more fully studied with respect to their biological control potential, and in general they have proved much less effective as self-generating agents than the highly specific parasitoids. This is not to say that they have no role in insect control. Quite the contrary; they have proved to be quite useful as selective insecticides, particularly *Bacillus thuringiensis*, and to a degree in China, *Beauveria bassiana* (Nat. Acad. Sci. in press). Others should come into use as the problems of their development, registration and commercial acceptance are solved. One point is that there should be a lower mortality expectation by both government registration officials and the farmers than that expected of a chemical insecticide, as the two are not comparable. With the selective microbial pesticide, mortality by natural enemies (which are thus not killed) could easily make up for the deficiency, or even greatly more so.

Introduction of a complex of different kinds of natural enemies for control of a single pest species has been customary in both insect and weed control projects. Some theoretical objections to this practice for insect control have been posed by a number of authors (Turnbull and Chant 1961; Turnbull 1967) but other theoretical as well as empirical considerations widely support the practice (Varley *et al.* 1974, Huffaker, Luck and Messenger in press). No significant criticism has been leveled at this practice in weed control so far as I know; I see no significant differences in the two areas regarding this question. The advantages of introducing a complex of natural enemies where a single one does not suffice would seem to be similar in both cases except that attack of the insect host by even one individual parasitoid or predator means its death, while many attacks may be required to kill a weed or prevent seed maturity. Considering the whole terrain infested by a pest species, in both cases use of several natural enemies clearly offers advantages in scope of adequate adaptation.

INCREASING THE SCIENCE AND IMPROVING THE CHANCES OF SUCCESS?

Whether or not biological control specialists can increase the level of science employed in introductions and improve the chances of success in a project, as distinct from success with a given species being introduced, has been much considered recently.

We need first to look at the properties a natural enemy must possess to be a good biological control agent. This in turn depends on the type of problem (above) and the use expected of the natural enemy. Thus, the requirements of a natural enemy that is expected to become a permanent, self-generating and truly regulating component (without additional releases) in the crop-pest ecosystem are often quite stringent. On the other hand, if such a natural enemy is unavailable for the given situation, the requirements may be relaxed if control can be achieved by adequate periodic or annual releases (Rabb *et al.* 1976), say, each spring following the winter period, if winter kill of the parasite prevents the natural enemy's overwintering, or its general effectiveness, as shown by Sailer (in press) in control of Mexican bean beetles in Florida by early season releases of *Pediobius*. In annual row crop situations where mobility and opportunism in prey acceptance are important features, effective natural enemies would not require the high host specificity commonly desired in a natural enemy for a stable habitat. W. W. Murdoch and associates are among the few workers who have attempted to model the benefits from such near-generalist natural enemies, and they have extensively considered their switching behavior (e.g. Murdoch and Oaten, 1975, Oaten and Murdoch, 1975). Since the near-generalist cannot be considered for biological control of weeds, and since the main stream of modeling research has dealt essentially with host specific parasitoids as natural enemies for self-sufficient permanent biological control, we will here consider only the latter. We recognize also that the parameters and models of value in appraising the roles of such parasitoids may be different from those needed in appraising the action of insects and pathogens which attack weeds. Huffaker *et al.* (in MSS) have just reviewed these developments, and this synopsis is drawn from their account.

The model of exponential growth of a population in an unlimited situation ($\frac{dN}{dt}=rN$) has, of course, no basis in reality. However, this model has been incorporated in certain other models. The model for logistic growth (Verhulst 1838; Pearl and Reed 1920) of a population ($\frac{dN}{dt}=rN\frac{(K-N)}{K}$) adds only a factor representing density-dependent restriction in growth by increase in the population itself $\frac{(K-N)}{K}$. [1]But this is not a model for a two species, host-parasite or predator prey interaction. Thomson (1922a,b, 1924, etc.) was the first to develop generalized models of host parasite interactions. But he only incorporated the comparative fecundities of host and parasitoid; no density dependent component was utilized. Only extermination or complete lack of control of the host was provided.

Lotka (1925) and Volterra (1926), however, developed models of predator-prey interaction which did incorporate a density- dependent or negative feed-back factor, and for the first time we had a model which produced a sustained state of balance about an equilibrium position for both populations. The model consisted of a pair of coupled equations describing change in predator/prey densities in terms of modified exponential growth, with prey increase suppressed by predator feeding, and predator increase by starvation. No lag effect was incorporated. For this and other reasons, Nicholson (1933) and Nicholson and Bailey (1935) developed models which included this important feature. However, this still gave us a very unsatisfactory model for explaining events observed in nature. The model generates oscillation about an equilibrium position, but with increasing amplitude—leading to extincition. It also failed to explain how two or more host specific natural enemies may co-exist in the same interacting situation. A breakthrough came as a result of work by Hassell and Huffaker (1969). Studying data I collected over 36 host generations, Hassell and Huffaker found that not only searching capacity (a) of the parasite and the fecundity (f) of the host are important, but also the effect of parasite density on searching effectiveness of the parasite. Hassell and Varley (1969) then modified the Nicholson and Bailey model to include this mutual interference factor (m) in the model. With appropriate values for m, this model gave us for the first time theoretical basis for sustained host population regulation by a host specific parasitoid, and it also provided for coexistence of two or more such parasitoids.

Hassell and Rogers (1972), Hassell and May (1973), and Varley *et al.* (1974) developed a number of extensions from this model and others which I will not deal with, except to say that they added a feature representing parasitoid aggregation at places of higher host density. Hassell and May (1973) and Murdoch and Oaten (1975) also brought in host and natural enemy distribution patterns as a significant factor affecting stability. Hassell and May (1975) suggested that:

"Parasites with the following characteristics are the more likely to stabilize their host populations at low levels:

1. A high intrinsic searching efficiency (a^1). This is necessary to attain the low equilibrium populations.
2. A low handling time (T_h) relative to total time T. This minimizes the inability that results from parasite functional responses.
3. Some degree of parasite interference (m). This contributes to stability if the interference constant falls within the range $0 < m < 1$.
4. A high level of parasite aggregation (μ). This too can contribute markedly to stability but depends very much on the host distribution".

Yet, they also stated, "*Of course the success of biological control depends in the first place on the suitability of the chosen natural enemy or enemies within a broader context* [Italics ours] (Messenger 1971; van den Bosch 1971; Zwolfer 1971)."

After considering the highly theoretical nature of these models and their laboratory determined values, and the fact that many other factors extrinsic to the models may contribute controlling and stabilizing features (e.g. Huffaker *et al.* 1971; Huffaker and Stinner 1971), Huffaker *et al.* (in MSS) doubted whether such laboratory determined values of a, m, p and μ should be used to deny introduction of any otherwise promising natural enemies. Perhaps superior to this method would be studies conducted in the field in the home environment over 2 to 4 host generations to ascertain which of several local host specific parasitoids are most effective (or capable of effectiveness if freed from their own parasites) at low host density and most responsive to changes in host density and maintenance at low host densities. This would furnish the best assurance of good searching capacity combined with adequate intrinsic stablizing aspects.

Before leaving this question, there are many characteristics of a natural enemy than high searching capacity and some stabilizing behavior, that are of major importance. Huffaker *et al.* (in MSS) listed the various characteristics of a good parasitoid or predator of insect pests as: (1) fitness and adaptability, (2) searching capacity, (3) power of increase, (4) host specificity and/or host preference, (5) synchronization (in time or place), (6) density-dependent response to host density increase, (7) detection of and responsiveness to the condition of the host and (8) competitiveness with other natural enemy species. Good disseminative quality of a pathogen is somewhat comparable to searching capacity, and responsiveness to infection court condition has its counterpart in item (7). Any of these features can be very important in a given situation. For weeds, the ability to kill the host or greatly retard its competitiveness by accumulation effects of many attacks is a distinct feature, for the successful insect parasitoid or predator always kills its host or sterilizes it, mostly the former.

Extensive ad hoc studies are usually required if the full potentialities of proposed agents are to be learned. For natural enemies of weeds, for safety reasons, this must be done in general before introductions, but for insect pests, introductions of their enemies are commonly made before extensive studies are conducted. For these cases I doubt that extensive prior-to-introduction modeling or life table studies are justified while the problem continues unabated and biological control funds are so badly needed for other purposes. Also, denial of otherwise promising species other than the best one, or of, say, 2 or 3 best ones, as ascertained by the modeling parameters is not currently feasible, I believe, if for no other reason than that a large regional area is often diverse in conditions and a natural enemy that is superior in one part may be superseded by others in certain areas. For weeds especially, the empirical record suggests that the more collective stress put on the weed - i.e., by a complex of natural enemies - the better. Moreover, modeling of effects of attack would require extensive modifications from the 1 on 1 relationship employed in host/parasitoid modeling. There would seem to be much more that can be done with funds for biological control of weeds than expending it in *extensive* modeling approaches to predict eventual outcome and determine by this means primarily which natural enemies should be introduced. The safety feature alone commonly puts severe constraints on what can be introduced, anyway. Ability to kill the host is another constraint. These are primarily determined by detailed research and experimentation.

There is also another aspect of utilizing more science in our biological control work. This embraces both evaluation of the results of introductions and the possibilities for manipulating the environment, the host populations, or the natural enemies in ways to increase biological control effectiveness. Evaluations are a highly important aspect, because sound documentation supports other efforts and gives us insights useful in adding to effectiveness by discovering wherein additional enemies might supplement one(s) already introduced, or wherein manipulations may be made to improve effectiveness. Extensive life-table studies form a good basis for evaluation in some respects but not in others (DeBach *et. al.* 1976). For example, life table data will not tell us how high a host population would reach in the absence of given natural enemies. This, however, is answered reasonably well by use of various "check methods", and by "before" and "after" introduction documentation, which is a form of experimental comparison. However, to avoid the objection that change(s) in *other* factors may have accounted, coincidentally, for the reduction in the pest's status use of a series of widely separated plots extending over a number of different years in timing (relating to when releases were first made) will help to reduce criticism, especially if good data are accumulated on the specific effects of the natural enemies on the pest population at various phases following introduction (for 8 to 10 years at least).

Habitat manipulations for improving biological control of pest insects have varied from classical one-time, inoculative colonizations to mass inundative or periodic releases, through various crop management techniques such as adding alternate foodstuff or refuges, and use of strip planting or strip harvesting (to preserve or augment natural enemies), to release of the *pest species itself* at critical times in the year in order to allow for continuity of the natural enemies. Any of these methods can have successful outcomes, depending upon the situation (see Rabb *et al.* 1976). Way (1973) has cautioned that there is no substitute for detailed specific biological and ecological studies on the many behavioral and life-history features of the various organisms involved. It is interesting that Frick and Garcia (1975) and Garcia and Frick (1975) have developed a mass production program for releases early each year of *Bactra verutana*, hopefully to improve the synchrony of attack and improve effectiveness in other chrony of attack and improve effectiveness in other respects for control of purple nutsedge in Mississippi.

FUTURE PROSPECTS AND LIMITATIONS

The future of biological control has been opened up in recent years by the world developments noted above. The prospects for biological control of insect pests associated with expanded employment of integrated control are very substantial if the movement retains its ecological approach and philosophy and does not become gradually shifted over to greater emphasis on different aspects of chemical control, to the detriment of biological and other ecological approaches. The legions of the chemical control industry are indeed many and nowhere is this more apparent than in the enormous expansion of herbicidal control of weeds. It is significant that there is no fundamental and organized activity to foster integrated control of weeds. Biological control of weeds, then, is likely to continue to strive in some isolation to solve those weed problems most amenable to this approach.

Yet weed control, whether by the hoe, herbicides or natural enemies, must surely come under the promising and highly pragmatic systems analysis approach now being developed for crop production and crop protection. Analysis of all areas of crop production, pest damage and pest control will be, I think, the wave of the future. The primary focus must necessarily be on crop growth and development, secondly on the pests, and thirdly on the ways by which the pests are naturally controlled or can be artifically controlled. All types of pests and their natural enemies, the effects of weather, irrigation, fertilization and other cultural practices, etc. must be included in holistic perspective. This will put each phase of the problem in perspective and give us a means of setting priorities as to the importance of pursuit of any particular tactic for control, of any and all of the pests, as well as all other tactics to increase yield and net gain to the grower.

Systems analysis will not itself accomplish what is needed by research on tactics. It can point more effectively to needs and indicate areas where effort would be (and is being) largely wasted. Suitable *tactics* will be required to control the pests! Such tactics will include new natural enemy introductions, manipulations in the target area (above), new methods of monitoring pest damage and evaluating economic impact and establishing economic levels, use of selective pesticides and selective use of pesticides, use of resistant crop varieties, etc. Thus, much expanded effort will be needed in the development of specific *tactics* within, hopefully, the umbdella of a broad strategy of pest *containment* rather than total *prevention* or eradication, using ecological means wherever possible and employing chemicals only as truly needed, allowing for crop capacities to compensate for early season *apparent* damage by pests.

There must be expanded biological control effort in many problem areas. Fortunately this is already underway—witness the expanded efforts in weed control (of aquatic weeds, use of plant pathogens, and strategic releases of weed feeding insects). Various possibilities exist in problem areas hitherto neglected, for example, looking toward biological control of plant pathogens and snails (e.g., as vectors of schistosomiasis), or in elimination of cow dung or other feces or materials which produce vectors of human and animal disease, or may be noxious in other ways.

To accomplish this expansion and obtain the support needed, several general needs must be broadly met. There must be more effective "selling" of the special advantages of biological control. This includes education of administrators, bureaucrats and politicians controlling funds. Biological control *organizations* need to be strengthened. Simmonds *et al.* (1976) have said that often it is lack of a proper organization and well trained and motivated specialists rather than lack of funds, that limits biological control programs. On the other hand, successes on a worldwide basis have been more or less correlated with the financial support received. It is not contradictory to say that the support in funds has also been highly correlated with existence of highly trained and motivated, largely autonomously structured organizations for biological control. I suggest that a largely autonomous status is the number one priority. This effort must have considerable control of its own future; else it is invariably relegated to second or third place in the allocation of funds by administrators who favor more conventional tactics or disciplines with which they are more familiar. Those working in biological control, whether they be entomologists, plant pathologists, zoologists, weed scientists, public health specialists, etc. should, I think, join forces under the general banner of biological control and form Departments of Biological Control wherever possible. It is the philosophical and ecological approach that is unique, not the specific disciplinary background.

There are certain limitations and problems in biological control, some of which were treated above, which must be squarely faced (e.g., it is not a solution to every problem). An especially difficult one for biological weed control is the matter of conflicts of interests. Cattle and sheep growers, grain growers etc. have interest in control of many plant species which landscape beautification (or appreciation) and wildlife advocates, soil conservationists or beekeepers, for example, may want to retain. Examples are yellowstar thistle, scotch broom and even poison oak, to some degree, in California. On the other hand, the shoe is sometimes on the other foot, as for example with saltbush or tamarix in the U.S. Southwest which some ranchers and especially beekeepers want to keep it for its cattle and bee forage value, while certain water resource conservationists want it brought under biological control. Preponderance of interest has usually been used to solve such conflicts, but complete resolution it not always possible.

We desperately need an increase in the taxonomic expertise that can be concentrated on problem pests and potential biological control agents relative to biological control possibilities. Biological control specialists should promote and foster support of systematists. We are learning more and more that sibling species ,and subspecific and strain differences in both pest species and their natural enemies are vitally important to successful biological control programs. The different strains of *Chondrilla juncea* are not equally subject to successful biological control by *Puccinia chondrillina*. In the genus *Aphytis* complexes of sibling species exist which have different potentialities for control of several species of diaspine scale insects. Only recently have some of the "old" species been separated into their sibling components, with appropriate new siblings then having been successfully introduced in various parts of the world (DeBach and Rosen in press, Bennett *et al.* 1976).

Lastly, major training programs are needed to expand the number of well trained specialists. This is especially needed for personnel in developing countries, and for personnel who may be highly trained in the areas of weed control, plant pathology, insect pathology, entomology, forestry or public health who are entering this field but who have had limited exposure to the ecological and philosophical fundamentals of the field of biological control. A greater degree of drawing together of these distinct disciplinary elements will itself help solve this problem.

Satisfying these needs is a big order, but with motivation, imagination and perseverance, much can be accomplished in the next few decades.

FOOTNOTES

r — intrinsic rate of increase
N — population size
K = saturation in size

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