INTRODUCTION

There is now considerable evidence that organisms attacking plants have acted as selective agents causing evolutionary changes of the plants that they attack. Such changes are most obvious when they are morphological, phenological or chemical (Janzen 1969, Cook et al 1971, Fraenkel 1959).

This paper discusses the consequences of such natural selection for the biological control of weeds.

THEORETICAL CONSIDERATIONS

As well as acting in past geological periods natural selection is still occurring. The organisms best adapted to their environment survive better and leave proportionately more of their progeny to contribute to future generations whereas those with less adaptive characters decline in proportion as time passes (Darwin 1859).

A simple model can be used to explain the effect of this situation on a weed and its biological control organisms. Consider one weed, with only one organism which attacks it (representing a large number of attacking organisms), and consider all other selective factors as a whole acting as a single selective agent. Two extreme cases can now be examined :- in the first the organism is by far the major selective agent and the other environmental factors of minor importance. In this case there will be heavy selection for those attributes that in one way or other help to avoid attack by the organism. At the same time however the organism itself will be under selection pressure. The weed, as its food, is always an important selective force so characteristics that assist the organism to overcome the new attributes of the weed will be strongly selected. This process will continue until a balance is set up which is apparently an ecogenetic homoestasis where the organism is able to utilise only part of its host plant or host plant population and the host plant does not suffer so much from the attack by the organism that its existence is threatened (Pimentel, 1961). In the second extreme case the environmental factors are the overriding selective agents and the organism plays only a minor role. In this case no apparent homoestasis between organism and weed would evolve. This is the case when the other environmental factors restrict to negligeable levels the damage that the organism can do. For instance, the organisms attacking Chondrilla juncea L. are not adapted to acting effectively against this plant under conditions of frequent cultivation. It is equivalent to the case when the weed species and the organism have evolved apart (Pimentel, 1963). It is also the case when a weed is introduced into a new region without its organisms. Any apparent homoestasis that existed between the weed and its organism in the original habitat, would, as generations pass, tend to disappear because a new regime of selection without the organism is imposed. The rate of breakdown of the original position would depend on the importance of the other selective agents in the new environment the extent to which the other environmental agents differed from those that imposed selection in the original habitat, the previous importance of the organism and the conservativeness of and amount of variation within the plant's biochemical and morphogenetic system. However, it would be expected that weeds which have been separated from their important selective organisms for a considerable number of generations would have lost a considerable amount of their adaptability vis-a-vis the organism. In the same way the organism which is still evolving in its original habitat with the weed will not be faced with the selective adjustments necessary as the weed evolves in its new habitat and will evolve only to the weed forms with which it is in contact. Little selective change will occur if the same other factors are of greatest importance and act to the same extent in the old and new habitats. Thus Chondrilla juncea plants in the same frequent cultivations in Australia and Europe would be under very similar selective pressures and would not be exposed to selection by organisms in the original habitat because of ineffectiveness or in the new because of their absence.

THE IMPORTANCE OF ECOGENETIC HOMOESTASIS TO BIOLOGICAL CONTROL

At first sight it would appear that the mutual selection which leads to a balanced ecogenetic homoestasis produces a plant which is only affected in a minor way by the organisms which attack it continuously in the same habitat. Pimentel (1963) considered this to be the case and on examination of the 66 cases of successful biological control listed in Sweetman (1958) found that in 39% of them control had been achieved not by parasites and predators of the pest species but by parasites and predators of allied species and genera. He suggested that the search for biological control agents should therefore also include organisms attacking allied species and genera, since these had not developed a homoestatic relationship with the weed species.

However, there are important practical difficulties when one widens the search to related genera especially when these are numerous as in the relatives of Chondrilla juncea among the Cichoriaceae. Moreover, in most cases most organisms will be better adapted in a general way to their original host. The specific insect species will be adapted to dealing digestively with and responding to the plant's secondary substances (Fraenkel, 1959) which could be very different in related genera. Such organisms as the Puccinia fungi and the gall makers have very close biochemical relationship with their host (Mani, 1964) which does not allow them to attack or produce the characteristic symptoms on other, often quite closely related, plants.

The importance of such adaptation is borne out by Sweetman's (1958) list since the remaining 40 out of 66 pests were controlled by biological control agents collected from the pest species in its original habitat. One has therefore almost double the chance of discovering a biological control agent by investigating the organisms attacking the pest species than by investigating a much larger number of related species and genera. Moreover, the very fact that an ecogenetic homoestasis has built up is because the organism has and is damaging and destroying those plants with a certain genetic constitution which are more readily injured than those whose genetic constitutions allow them in one way or another to escape or be less attacked or damaged. Ecogenetic homoestasis implies a continuous preferential mortality produced by the organism and the more effective the organism is as a biological control agent in its original habitat the more effective the selection for ecogenetic homoestasis.

This is well seen in the case of Chondrilla juncea and its rust Puccinia chondrillina Bubak & Syd. In certain cultivated fields where the rust cannot act as a selective agent plant populations are very high (100-300 plants/M^2). If cultivation stops, the rust immediately attacks most of the C. juncea plants and kills many. The population declines in a few years to 1-10 plants/M^2 at which level it stabilises but the proportion of rusted plants also declines suggesting that the Chondrilla population consists of mainly rust-resistant plants. There are however still a certain number of plants continually being attacked and destroyed by the rust, thereby maintaining the selection. Presumably, in the absence of the rust, populations of the plant would be higher and contain a smaller proportion of resistant plants. This might well be the case in Australia at the present time, where C. juncea populations remain high in abandoned situations.

This discussion suggests two ways of selecting biological control organisms. The first is by comparison of the plant in its new habitat where it is a weed with the plant in its original habitat. The second is a comparison in the original habitat of situations where the biological control organisms cannot act with those where they have acted for some time. In this way it may be possible to discover the organism which is having the greatest selective effect and which is therefore reducing more than any other the population level and habitat range of the plant (Wapshere, 1970). An effective organism can be quite rare in situations where it has achieved its maximum effect and where only a low density of relatively very resistant plants remain. Such resistant plants can be less palatable and smaller in size or of slower growth rates. They could occur in habitat situations within which the organism is ineffective. For example, Hypericum perforatum L. occurs now more abundantly in shady situations where Chrysolina quadrigemina (Suffr) is ineffective although previous to the beetle's introduction the plant was widespread and abundant on open range lands (Huffaker, 1962). The resistant plants could be chemically different and so less attrative to the biological control agents or they could be different in phenology and so avoid at least partly the maximum activity of the organism. Indeed the plant would have been selected for any characteristics which would in one way or another avoid the effective selecting organism and would appear to be very different from the plant observed as a weed in the new habitat where the selective organisms are absent. Many authors have commented on the enhanced troublesomeness, large size, high density and broad habitat ranges of weeds in new habitats (Huffaker 1957, Wilson, 1950, 1964). Indeed weeds in new habitats are behaving in much the same way as cultivated plants. These are also large, luxuriant and grow at high density when protected from insects and fungal diseases which attack them readily but soon revert to small, poorly growing but resistant wild types at low density once proper cultivation stops. Puccinia chondrillina would be selected as an effective biological control agent for C. juncea on these criteria.

The second way of selecting an effective organism is to select those organisms that are clearly well-adapted to the plant and that damage the plant severely under laboratory conditions but which, because of the attack of parasites or because of other factors not present in the new habitat, remain scarce in the original habitat of the weed. Also, as Pimentel (1963) suggests, this might also apply to those organisms that do not occur with the actual weed species but attack other species of the same or closely related genera, in other parts of the world. In both cases the organism would not have caused the production of resistant forms of the plant since, in the first case the organism was never important or common enough to exert a strong selection pressure, and in the second case it could not do so because it was not in contact with the plant. Chondrillobium blattnyi Pint., which is a very damaging aphid in the laboratory and clearly well adapted to C. juncea would be an organism of the first type if its insect and fungal parasites were the main cause of its low and infrequent occurrence. Sphenoptera foveola Gebl. which occurs on Chondrilla ambigua Fisch. in parts of Kazakhstan where C. juncea does not occur widely might be an example of the second case.

An ineffective biological control agent would be one which occurs frequently with the weed at levels clearly sufficient to have induced selective effects but which does not affect the plant sufficiently for selection to have occurred. The aphid, Uroleucon chondrillae, and the Eriophyid gall mite might be such organisms. Several authors have noted that it is not the most common insects or fungi that are necessarily the most effective agents and the above discussion suggests that there are important biological reasons for such observations, especially where it can be assumed that the biological control organisms have had their full effect.

DISCUSSION

The above is a discussion of the importance of evolutionary selection to biological control organisms. Unfortunately our knowledge of many of the organisms used for biological control of weeds in their original habitats is so slight that comparisons cannot be made which would test the above ideas. Even in the case of Hypericum perforatum L. and its chrysomelid species whose effects have been studied in some detail after release in Australia (L. Clark 1953 and N. Clark 1953) and in California (Huffaker and Kennett, 1959) were not studied in the same way in their country of origin (Wilson, 1943). It is to be hoped that studies similar to those undertaken with the Chondrilla organisms in Europe and followed by detailed studies on release will be made in any future biological control programmes. If the conclusions reached above are confirmed this would help to hasten an understanding of the factors underlying the successful use of organisms for the biological control of weeds.

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DISCUSSION

ZWOLFER Our study of the Balsam Wooly Aphid (Dreyfusia piceae Ratz.) has provided a fine example of such an ecogenetic homeostasis. In Europe this species is associated with Abies alba which controls the population dynamics of the aphid by a density-dependent defense reaction (formation of necrotic tissues which leads to breakdown of the aphid population). This homeostasis between D. piceae and A. alba is obviously the result of a long-lasting association of the two partners. After its accidental introduction to Canada D. piceae came into contact with Abies balsamea, a tree which does not exhibit this ecogenetic homeostasis and which, hence, can be severely damaged and even killed by the aphid.

There is another interesting phenomenon: In Europe a diversified complex of predators is associated with D. piceae. The studies carried out by members of the European Station of the CIBC showed that these entomophagous insects have biologically specialized to exploit the surplus population of D. piceae, and that they are inversely density-dependent. As a matter of fact a number of these species have been established in North America against D. piceae but they are not able to control the aphid. I think Margaleff expressed the idea that two different density-dependent control mechanisms cannot coexist in the same system. Applied to the Abies-D. piceae predator system we may conclude that as the ecogenetic homeostasis of the plant-phytophage system has led to a density-dependent control mechanism, there was no chance for the entomophagous insects to become regulating factors.

HARRIS It may be as you say, the effective biological control agent will tend to eliminate its host and hence make itself rare. However, an agent may also be rare because it is not a good doer as it has very strict ecological requirements which aren't met very often. I think among the Hypericum insects there is less competition than first apparent because they stratify themselves ecologically. Apparently in North America and Australia the species have sorted themselves out in spite of all we could do to release them in the wrong habitats.

WAPSHERE I agree completely with you Dr. Harris. I think all one can say is that if an organism is rare because it is being kept down by its parasites, and this is the only factor one could choose an organism on its rarity. Since this does not affect its ecological adaptability. In the case when man himself is acting as a factor reducing the occurrence of a particular phytophagous organism, and man is not operating in a population destructive way in the new environment under these circumstances you could also choose an organism on its rarity. If, however, you were pretty sure that it was ecologically ill-adapted, or had special ecological requirements reducing effectiveness and causing the rarity it still is not going to be all that useful to introduce it.

HARRIS I think the apparent effective control of the agent by parasites may be a very good indication that it will be useful for biological control as it is likely to lack a homeostatic mechanism as we escape the parasites by introducing the agent to a new habitat.

END OF DISCUSSION

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