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BIOGEOGRAPHY, APPARENCY AND EXPLORATION FOR BIOLOGICAL CONTROL AGENTS IN EXOTIC RANGES OF WEEDS

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ABSTRACT

Recent literature is used to evaluate the possibility that exploration in exotic, as well as native, ranges of weeds may discover organisms useful for biological control in regions where the organisms' own limiting agents are absent.

The native range should remain, for the present, the first priority for exploration because a margin of theory and evidence suggests a larger proportion of host-specific agents might be found there. If the native range proves unprofitable, or the aim is to control a native weed, then prospects for finding host-specific and effective agents in other parts of the exotic range do not seem greatly inferior.

INTRODUCTION

Most weeds are plants which have been released by man from limiting effects of the competitors and primary consumers in whose presence they evolved. Most native and some exotic species have been released by creation of new habitats, such as cropland, to which they but not their limiting agents were preadapted. Most exotic weeds have also been released by their dispersal into geographic regions where their limiting agents do not exist. A great upsurge in these processes started about 400 years ago with the development of ocean-going sailing ships, international trade and travel. It is probable that the majority of exotic weed problems started within the last 200 years at the same time as large scale planting of crops outside their native ranges (Purseglove 1965).

Many weeds have acquired new primary consumers in parts of their new, exotic ranges. These primary consumers might have potential as 'classical' biological control agents (*sensu* DeBach 1974) in regions where their own limiting agents are absent, either in the native ranges or in other parts of the exotic ranges of their weed hosts. This paper examines in turn the four main factors which determine that potential using some of the exciting patterns emerging from studies of the biogeography and coevolution of plants and primary consumers. Gilbert (1979) and Rhoades (1979) discuss the causes of these patterns.

The term 'primary consumer' includes pathogens and herbivores, predators, parasites and symbionts. It is used here almost as a synonym for 'natural enemy' but without the connotation that such organisms always reduce the fitness of their host plants (Pimentel 1961, Harris 1973*a*, Owen and Weigert 1976).

ORIGINS OF PRIMARY CONSUMERS IN EXOTIC RANGES

A primary consumer of a weed in part of the weed's exotic range must have a distribution which includes either:

(a) all parts of the weed's range, native and exotic; or
(b) the native and some parts of the exotic range of the weed; or
(c) all exotic parts of the weed's range but not the native range; or
(d) some but not all of the weed's exotic range only.

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Primary consumers having distribution type (a) cannot be used for classical biological control, while those with types (b) and (d) might be useful in parts of the exotic range where they do not already occur, and those with types (c) and (d) might be useful in the native range of the weed.

There is abundant evidence, for insects at least, that most species which feed on exotic plants are of type (d) and restricted to a single part of the exotic range. Goeden (1974) found none of the 28 insects identified to species feeding on Italian thistle in California present among the 58 identified species on the same plant in its native Europe. Similarly for milk thistle, only 1 of the 43 identified species from the plant in California (Goeden 1971) was among the 87 identified species on the plant in its native Europe (Goeden 1976). More than 85 per cent of 1905 insect pests of cocoa were reported from only 1 out of 31 geographic regions (Strong 1974*a*), and 60 per cent of 1645 insect pests of sugarcane were reported from only 1 out of 51 regions with only one per cent from 10 or more regions (Strong *et al.* 1977).

These data suggest that most primary consumers found by exploration in part of the exotic range of a weed would not be present already in the region where biological control is to be attempted, whether that be in the native range of the weed or a different part of the exotic range.

THE NUMBER OF PRIMARY CONSUMER SPECIES PER PLANT SPECIES

It is assumed in this section that the probability of finding a useful agent is correlated with the number of primary consumer species found; the following sections examine the validity of this assumption.

Time in exotic range

Contrary to earlier hypotheses (e.g., Fischer 1960), Strong *et al.* (1977) reported 'the unanimous result [of relevant studies] has been that, beyond an initial few hundred years, younger host populations have a number of parasite species per unit host range that is indistinguishable from the number supported by older host assemblages'. Evidence includes studies of insects (Strong 1974*b*) and fungi (Strong and Levin 1979) on trees and insect pests of cocoa (Strong 1974*a*) and sugarcane (Strong *et al.* 1977). However, using Feeny's (1976) concept of apparency (see later), Gilbert (1979) has pointed out that the majority of plants in these studies would be expected to have quantitative defences to which many polyphagous insects should be preadapted. Herbs, with more qualitative defences, might take longer to become fully colonized, though the speeed at which insects have become resistant to insecticides (man-made plant defensive poisons) suggests otherwise.

There is some evidence that the time needed for the number of primary consumers to reach an asymptote can be tens rather than hundreds of years. Milk thistle was first recorded from California in 1854 and 117 years later it was being attacked by 47 species of insects (Goeden 1971), while Italian thistle was first recorded from the same State in the 1930s and only 40 years later had a fauna close in size to milk thistle's of more than 40 species (Goeden 1974). Similarly, numbers of insect pests per unit range of cocoa in Brazil, Papua New Guinea and Sabah appeared to reach asymptotes in less than 60, 30 and 10 years, respectively, after large increases in areas planted (Strong 1974*a*). Ten years is probably close to the minimum time possible for cocoa because trees take about eight years to become reproductive.

Range within exotic region

Strong (1979) and May (1979) reviewed the extensive evidence that the range of a plant within a geographic region is the most important determinant of the number of primary consumer species feeding on the plant in the region. The data of Lawton (1976), Futuyma and Gould (1979), Strong (1979) and Ward (1977) suggest that at any one locality, number of species is not related to the range of the plant throughout the region, each locality having an assemblage of species which incompletely overlaps assemblages at other localities. However, Opler (1974) showed that species richness of leaf-miners at a locality was correlated with the geographic range of oaks. Strong and Levin (1979) showed for fungi of trees, shrubs and herbs that at least part of the importance of geographic range stems from its correlation with ecological range expressed in terms of vegetation zones.

Local abundance

In a particular locality, the number of primary consumer species increases with population density of the host plant (Root 1973, Cromartie 1975, Tepidino and Stanton 1976, Ward and Lakhani 1977). Since most weeds are more abundant in exotic than in native parts of their ranges, they would be predicted to have more primary consumers per unit range in exotic than in native ranges. This prediction does not appear to have been tested.

Local dispersion

The number of species of primary consumers is greater if a host plant is growing interspersed among other kinds of plants rather than growing as a monoculture (Root 1973). The maximum number of primary consumers is expected where the positive effects of increasing host density balance the negative effects of an associated tendency towards monoculture. Effects of particular patterns of dispersion and combinations of neighbouring plants will depend on the dispersal characteristics of the primary consumers which are present in the locality (Atsatt and O'Dowd 1976, Cromartie 1975).

Growth form and predictablility through time

Size, structural complexity, longevity and probability of a plant being contacted by a primary consumer are all strongly correlated. Strong and Levin (1979) concluded, as did Lawton (1978), that 'trees tend to have more pest species than do shrubs, which in turn have more than herbs, per unit of geographical distribution'. Similarly, Lawton and Schroder (1978) and Strong and Lefin (1979) found that annual herbs had smaller insect faunas and fungal floras, respectively, than perennial herbs. Plants which are weeds in their exotic but not their native ranges are probably larger and longer-lived in their exotic range due to less competition from other plants, less effective natural enemies, or other variables. Whether such differences exist and whether they may be large enough to result in significantly more primary consumers in exotic ranges do not seem to have been investigated.

Isolation from similar species of plants

The number of primary consumers in native and exotic ranges should be related to the number of species preadapted to a plant, which should in turn be related to the presence of other species of plants having similar defensive, nutritional and other properties. Similarity of plants as hosts has been assumed to be correlated with their taxonomic relatedness (Ehrlich and Raven 1965). That assumption appears to be only partly valid as many closely related, sympatric plants seem to have evolved to escape from each others' spectra of primary consumers (Janzen 1973, Meeuse 1973).

Powell (1980) found that evolutionary radiation in microlepidoptera had occurred more within specialized feeding niches, such as leaf mining, than along botanical evolutionary lines. Except for monocot herbs other than grasses, Lawton and Schroder (1977) found no evidence that taxonomic isolation influenced the number of species of insects associated with a particular species of plant. Futuyma and Gould (1979) also found little correspondence between faunal similarity and taxonomic affinity among woody plants in a forest, though their result may have been influenced by the polyphagous nature of most consumers of apparent, woody plants.

These three studies examined long-term associations of plant species whose community structure might reflect selection for diversity to prevent destructive increases in primary consumer populations (Atsatt and O'Dowd 1976). Future studies using measures of similarity based on biochemistry, pilosity and other attributes and studies of recently introduced plants would still be expected to show that similar, sympatric plants support similar arrays of primary consumers.

Island biogeography

The patterns described above 'explain' about half of the variability in the number of primary consumer species on plants (May 1979). Janzen (1968, 1973) suggested that MacArthur and Wilson's 1967 theory of island biogeography might summarize the patterns in terms of the sizes of host 'islands' and their physical and defence mechanism 'distances' from sources of immigrants. However, Connor and McCoy (1978), Strong (1979) and Strong and Levin (1979) have pointed out difficulties in such use of the equilibrium biogeographic model on its own. A more realistic model will have to take account of habitat heterogeneity and passive sampling effects as well as the sympatric distribution and evolution of host plants in contrast to the allopatric distribution and independent evolution of true islands. Even then, there will be unexplained variability due to historical accident in evolutionary and ecological time, an example of which might be the lack of insects preadapted to feed on eucalypts in California (Strong 1979) but not Brazil.

Assuming growth form and life cycle of a weed are similar in different parts of its range, there is a high probability that it will have at least as many primary consumers per unit range in exotic regions as in native regions. Time since introduction and the taxonomic affinity of other plants in the region appear to be unimportant, but detailed studies of herbs are needed to confirm these two generalizations for most weeds. More species of primary consumers should be found in regions in which the weed has a large range and in localities where the weed is abundant and interspersed among other species of plant.

HOST-SPECIFICITY

Finding many species of primary consumers is of no value for biological control unless some of them are acceptably host-specific. Discussion of this topic is difficult because no scale has been devised to quantify host-specificity which is biologically meaningful and can be used to define what is 'acceptable'. In most

Exotic weeds have discontinuous distributions because they have been dispersed over barriers such as oceans. On arrival in a new geographic region, an exotic weed will fall at the extreme left of Figure 1 because there has been no time for coevolution with local primary consumers and because there is little chance of coevolved primary consumers following the weed from its native range (see 'ORIGINS OF PRIMARY CONSUMERS IN EXOTIC RANGES', above). Thus, the probability of finding useful control agents in an exotic region might be largely a function of the time since the weed arrived and the rates of evolution of the poorly defined attributes of 'acceptable' host-specificity and effectiveness.

CONCLUSIONS

The native range should remain for the present the first priority in exploration for organisms to control a weed in part of its exotic range. The sole reason is some evidence suggesting greater probability of finding organisms there with acceptable host-specificity. If the native range proves unprofitable, or the aim is to control a native weed, then prospects for finding host-specific and effective agents in other parts of the exotic range do not seem greatly inferior. Further information is sorely needed on the host-specificity and effectiveness of primary consumers from different parts of the ranges of herbs to refute or support these conclusions.

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Isolation from similar plant species

The data of Wapshere (1974) relating host-specificity to supposed centres of host evolution may be interpreted in terms of the presence of taxonomically related plants as well as in terms of coevolutionary time. However, use of taxonomic affinity as an index of similarity suffers from the problems discussed earlier. It seems unlikely that presence of plants similar to a weed in a region where an agent is discovered can have much effect on the acceptability of the host-specifity of the agent in another region. The presence of plants similar to the weed in the region where the agent is to be released would seem to be far more important and that of course, is independent of where an agent is discovered.

Apparency and defensive strategies

The relation of the likelihood that a plant will be found by herbivores (apparency) to quantitative and qualitative defences (Feeny 1976, Rhoades and Cates 1976) summarizes much of the variability in host-specificity of primary consumers. They suggested that large, long-lived plants are more apparent than small, ephemeral plants and that selection has favoured different defensive strategies in the two extremes. Apparent plants generally have quantitative defences, such as tannins or silica which reduce digestibility, act according to concentration and are relatively expensive to produce. Unapparent plants generally have qualitative defences such as poisons, which are effective at low concentrations and are less expensive to produce. Primary consumers of unapparent plants tend to be more stenophagous than those of apparent plants because they must be adapted to specific, uncommon defence mechanisms.

Many weeds are probably larger and longer-lived, and therefore more apparent, in exotic than in native regions and Rhoades (1979) has suggested that apparency is at least as important as phylogeny in determining plant defensive chemistry. Whether this might lead to evolution of significantly different defences in native and exotic regions in less than 200 years is not known.

Practical implications are not immediately clear because of insufficient data on the time needed to evolve host-specificity and on the results of changes in apparency. At present, it seems safest to assume a greater proportion of host-specific organisms in the native than the exotic ranges of weeds. In native and exotic ranges, there may be cases where establishment of an extensive monoculture of a weed could be the best method of discovering host-specific organisms.

EFFECTIVENESS

Finding many species of host-specific primary consumers is of no value unless one or several in combination, can maintain populations of a weed at tolerable densities. Pimental (1961), Harris (1973*b*) and Winder and Harley (1978) have discussed the need for control agents which, though acceptably host-specific, are not so coadapted with their hosts that their relationship approaches symbiosis. As with host-specificity, effectiveness depends not only on the degree of coadaptation between primary consumer and host but also on the context in which they interact.

Time in exotic range

Pimental (1963) reported that 39 per cent of successful cases of biological control, mostly of insect pests, involved use of organisms collected from species other than the ones controlled. Rather than increasing with time, he suggested that effectiveness should decrease as agent and host coevolve. In practical biological control this seems to have occurred only to a limited extent for reasons which are not understood (Green 1975).

Local abundance

Abundance of a weed can give no indication of how effective local primary consumers might be in other regions where their own limiting agents are absent and others may be present (Goeden and Louda 1976).

Race formation in weeds

Populations of exotic weeds have usually started with narrow genetic bases and it is established that different selection pressures and barriers to gene flow usually result in different gene frequencies over quite short distances in plants (Levin 1979). Mutation aside, genes in exotic populations must be present in the native range while genes in one exotic population will not necessarily be present in another. However, there is no obvious relationship between genetic similarity of hosts and effectiveness of control agents which can suggest where exploration might be most profitable. Pimentel's (1963) examples of lack of ecological homeostasis associated with great genetic differences appear to clash with the need for strains of rust fungus adapted to particular strains of skeleton weed in Australia (Cullen 1973), for example.

Environmental similarity of infested regions

Several authors have stressed the importance of carrying out explortation in regions ecoclimatically similar to the region where control is to be attempted (Harley 1979). Environments may be more similar between exotic parts of a weed's range than between exotic and native regions, making discovery of appropriate organisms sometimes more likely in an exotic region. For example, the floating fern, salvinia, has a restricted native range in subtropical Brazil but is causing major problems in tropical Africa, Asia and Australia. However, race formation in many weeds may make it impossible to find the same plant phenotype in any two areas with the same ecoclimate.

Relation of effectiveness to host-specificity

The evidence referred to above suggests that host-specificity of primary consumers generally decreases with distance and increases with time from the evolutionary origin of a plant, while effectivness peaks at some intermediate distance and time. Figure 1 illustrates these trends and the implications for exploration. Note that 'evolutionary origin' refers to the time and place of origin of a *single* new taxon of plant, as distinct from the more nebulous concept of 'centre of evolution' which refers to the area in which a *group* of related plant taxa differentiated. Broad bands of probabilities are shown which might accommodate many trajectories, each unique to a particular host-agent pair. At zero time or infinite distance, some organisms might have a degree of host-specificity through preadaptation while others may have none. At infinite time or zero distance the probability of finding host-specific organisms should be higher. Effectiveness might be low at zero time or infinite distance because of an association with host-specificity, despite the examples given by Pimentel (1963). Effectiveness might also be low, or even negative due to symbiosis, at infinite time or zero distance, with maximum effectiveness at some intermediate time or distance.

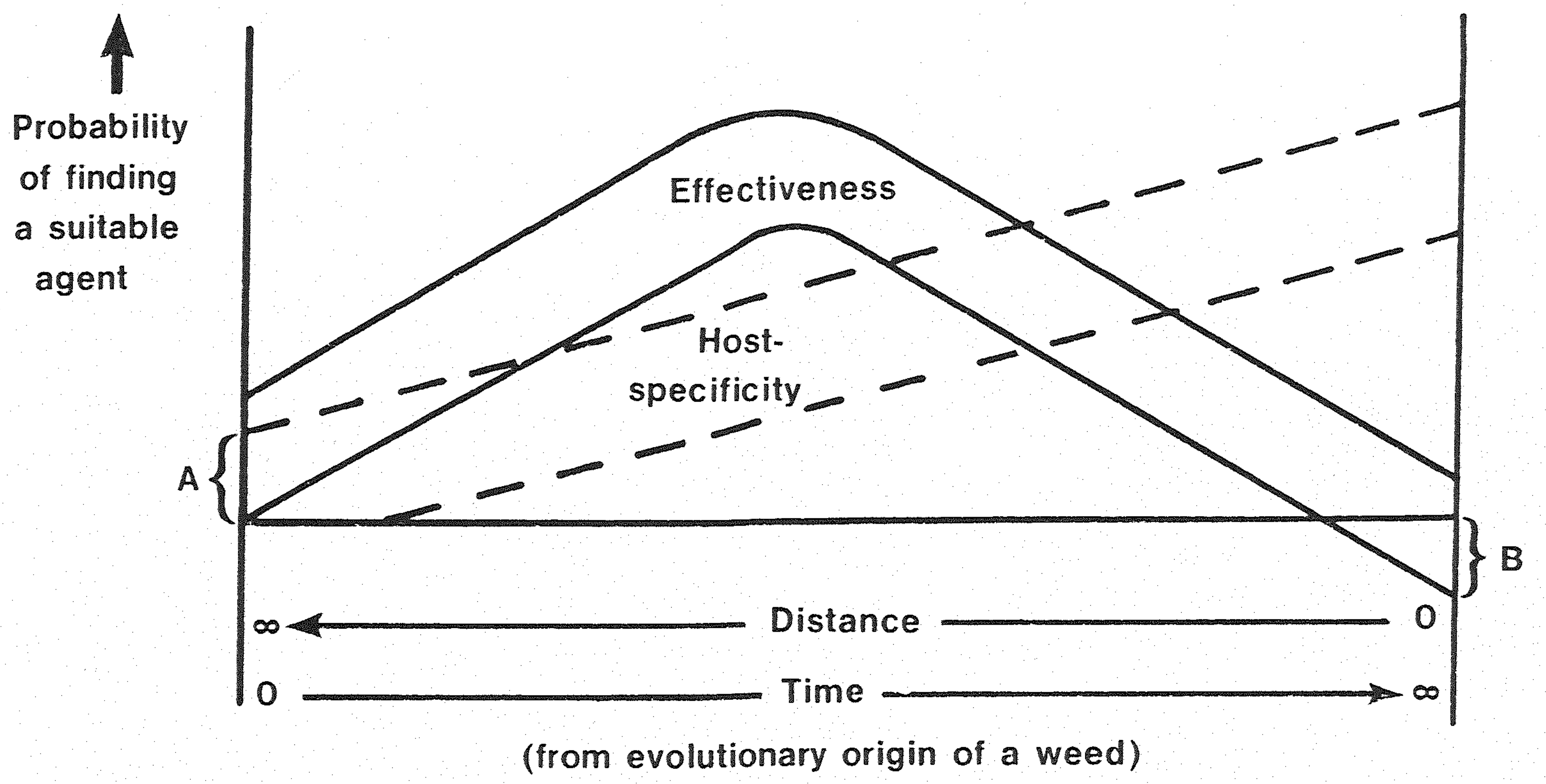

Figure 1. Hypothetical model of the probabilities of finding host-specific and effective control agents with respect to the time and distance from the evolutionary origin of a weed. (a = probability of limited host range through preadaptation; b = probability of symbiosis).

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