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ASPECTS OF WEED BIOLOGY IMPORTANT TO BIOLOGICAL CONTROL

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ABSTRACT

Two plant factors of importance in the success of biological control programs are considered. The first is the evolutionary flexibility of the target weed. We argue that the greater the genetic variability of weed populations and the more open the recombination system, the less likely are the chances for successful weed control.

The second factor discussed is the availability of alternative control mechanisms based upon the use of competing plants. If this alternative method is integrated with the use of natural enemies then ecological control of the weed is more likely. Control of several Australian weeds is discussed in relation to these two factors.

INTRODUCTION

Success or failure of biological control programs, like attempts to control pests and diseases in agricultural situations, can be traced ultimately to the outcome of interactions between target species (host), control agents (natural enemies) and the environment. The importance of interactions between weeds and their environment (e.g., the existence of climatic ecotypes of a weed), between control agents and their environment (e.g., the occurrence of suitable aestivation or hibernation patterns in the control agent), and also between control agents and their hosts (particularly with respect to their overall host range and general dietary habits) has been generally recognized (Harris 1974, Wapshere 1975). However, only limited attention has been paid to the potential or actual evolutionary response of weed populations to attack by natural enemies or to the interaction of weed populations with co-occurring plant species. In this paper we consider these two relatively neglected aspects of the biology of weed species, especially in relation to the choice of appropriate weed candidates in future control programs.

BIOLOGICAL CONTROL AND THE REPRODUCTIVE MODE OF WEEDS

The display of genetic variation within a population of a species depends on the breeding system, which in turn controls the relative roles of repetition and experimentation that occur in the production of progeny (Harper 1977). Plants may reproduce by seed alone or by seed production and clonal replication. Apomixis is the process of reproduction in which no sexual recombination takes place and includes both clonal replication and agamospermy. Agamospermy is the process of asexual reproduction through seed formation and it results in seeds which are all genetically identical to the maternal parent. For most plant species reproducing by seed, however, seed production is preceded by a sexual process which results in a variety of recombinant genotypes. Even in these species though, opportunities for recombination of genes from different parents vary considerably. Some species (e.g., *Trifolium repens* L., Leguminosae) are obligate outbreeders, whilst other species are heavy inbreeders and rarely recombine genes with other individuals. Despite these restraints, considerable

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variation may occur within a natural population of strongly inbreeding or apomictic species (Allard *et al.* 1968, Solbrig and Simpson 1974, Harper 1977).

In some circumstances, however, such plant populations may show an extremely depauperate genetic structure. This is particularly true of weed species which have colonized new habitats through accidental or deliberate movement of a few seeds by man. Populations which arise from such small inputs, almost invariably show considerably less genetic variation than that found within naturally occurring populations of the same species (Harper 1977), because of so-called 'genetic bottleneck' or 'founder' effects (Mayr 1963). For agamospermous plants and those reproducing clonally the genetically limited nature of the original introduction may result in weed populations which are genetically uniform. In species reproducing sexually, on the other hand, although the establishment process reduces the genetic variability of the population, the recombination of genes from different parents usually results in stands containing a range of different genotypes.

The importance of genetic diversity in protecting plant species against parasite attack has been widely recognized in recent years (Browning and Frey 1969, Tahvanainen and Root 1972, Day 1977, Burdon 1978). This suggests that where introduced weeds successfully establish large-scale monocultures, the genetic diversity occurring within and between such populations may be an important factor influencing the ability of introduced natural enemies to have sufficient impact on that species as to substantially reduce stand density. In particular, it could be expected (other things being equal) that genetically uniform species might be easier to control biologically than species which exhibit wider genetic diversity. Unfortunately, the paucity of quantitative information available on the population genetic structure of weeds precludes any attempt to directly pursue the question of the relationship between the degree of success of weed control and the genetic diversity of host plants. Whilst a knowledge of the reproductive mode of a plant does not provide direct information concerning its population structure, it is reasonable, as a first approximation, to assume that apomictic species will be far less variable on average than species which undergo sexual recombination every generation, particularly if they have gone through a severe genetic 'bottleneck'. In this section we examine the relationship between the level of success achieved in weed control by deliberately introduced natural enemies from the native range of weed species (i.e., classical biological control) and the predominant mode of reproduction of the target species.

A comprehensive world-wide listing of projects involving the biological control of weeds for which at least preliminary results have been published concerning the effectiveness of released agents in the field is presented in Table 1. This table was compiled using a number of recent reviews as guides (Nat. Acad. Sci. 1968, Andres and Davis 1973, Laing and Hamai 1976, Goeden 1978). Wherever possible, estimates of the degree of control achieved were taken from the original reports. Results available for release sites only were excluded as these may not reflect the ultimate success of particular programs.

It is evident from this data base, that a preponderance of species which rely heavily on asexual reproduction have been selected as targets for biological control programs. Of the 45 species listed, 24 are obligate or facultative agamosperms or rely almost exclusively on clonal reproduction and only 16 species reproduce sexually. If the five species whose breeding systems are unkown are all allocated to the sexual group, the proportion of species relying heavily on asexual reproduction still exceeds 50 per cent.

Table 1. A worldwide list of projects for the biological control of weeds together with a list of the predominant means of reproduction of the target species (for documentation see Burdon and Marshall 1981).

Target species	Predominant means of reproduction[1]	Location of infestation[2]	Degree of control achieved[3]
Alternanthera philoxeroides (Mart.) Griseb.	A (C)	Aust., U.S.A.	S, S
Baccharis halimifolia L.	S('SI')	Aust.	P
Carduus nutans L.	S (SC)	U.S.A.	S
Chondrilla juncea L.	A (A)	Aust.	S
Cirsium arvense (L.) Scop.	S (SC)	Can.	P
Clidemia hirta (L.) D. Don	U	Fiji	C
Cordia macrostachya (Jacquin) Roemer & Schultes	S('SI')	Maur.	C
Cyperus rotundus L.	A(C)	Haw.	N
Cytisus scoparius (L.) Link	S (SC)	U.S.A.	P
Eichhornia crassipes (Mart.) Solms-Laubach.	A (C)	U.S.A.	P
Elephantopus mollis Hamboldt	U	Haw.	P
Emex australis Steinh.	S (SC)	Aust., Haw.	N, C
Emex spinosa (L.) Campd.	S (SC)	Aust., Haw.	N, S
Eriocereus martinii (Lab.) Ricc.	A (C)	Aust.	C
Eupatorium adenophorum Spreng.	A (A)	Aust., N.Z., Haw.	P–S, S–C, S
Hypericum perforatum L.	A (A)	Aust., Can., Chile, Haw., N.Z., S.A., U.S.A.	P, P–S, C, S, P–S, C, C
Lantana camara L.	S (SC?)	Aust., EA, Fiji, Haw., Maur., Norf.	P, P–S, P, S, P, C
Leptospermum scoparium Forst.	U	N.Z.	S–C
Linaria vulgaris Mill.	S (SI)	Can.	P
Melastoma malabathrium L.	S (SC?)	Haw.	P
Opuntia aurantiaca Lindley	A (A + C)	Aust., S.A.	S, C
Opuntia dilenii (Ker. Gaul.) Haw.	A (A + C)	EA, Ind., New Cal.	S, C, S–C
Opuntia elatior Mill.	A (A)	Cel., Ind.	S, S
Opuntia imbicata (Haw.) D.C.	A (A)	Aust.	C
Opuntia inermis D.C.	A (A + C)	Aust.	C
Opuntia littoralis (Engel) Ckll.	A (A?)	U.S.A.	S
Opuntia megacantha Salm-Dyck	A (A + C)	Aust., Haw., S.A.	C, S–C, S
Opuntia monocantha Han.	A (A + C)	Maur., S.A.	C, C
Opuntia nigricans Haw.	A (A + C)	Cel.	C
Opuntia oricola Phil.	A (A + C)	U.S.A.	P–S
Opuntia streptacantha Lem.	A (A + C)	Aust.	S–C
Opuntia stricta Haw.	A (C)	Aust.	C
Opuntia tomentosa Salm-Dyck	A (A + C)	Aust.	P–C
Opuntia tricantha Sweet.	A (A + C)	WI	S–C
Opuntia tuna Mill.	A (A)	Maur., Re.	C, C
Opuntia vulgaris Mill.	A (A + C)	Aust., Ind., Maur., S.A.	S–C, C, C, S–C

Table 1 (cont.)

Target species	Predominant means of reproduction[1]	Location of infestation[2]	Degree of control achieved[3]
Pluchea odorata (L.) Cassina	S (SC?)	Haw.	N
Rubus constrictus Lef. & M.	A (A)	Chile	S–C
Rubus penetrans Bailey	U	Haw.	P
Schinus terebinthifolius Raddi	S (SI)	Haw.	P
Senecio jacobaea L.	S (SC)	Can., N.Z., U.S.A.	P–S, P, S
Tribulus cistoides L.	U	Haw., St. K.	S–C, S
Tribulus terrestris L.	S (SC)	Haw., U.S.A.	C, P–S
Ulex europaeus L.	S (SC)	Haw., Maur., N.Z. U.S.A.	P, C, P, P
Xanthium pungens L.	S (SC)	Aust.	N

[1]A = Asexual; (C) clonal, (A) agamospermy
S = Sexual; (SC) self-compatible, (SI) self-incompatible, ('SI') functionally dioecious - self-incompatible
U = Unknown

[2]Aust. = Australia; Can. = Canada; Cel. = Celebes; EA = East Africa; Haw. = Hawaii; Ind. = India; Maur. = Mauritius; New Cal. = New Caledonia; N.Z. = New Zealand; Norf. = Norfolk Island; Re. = Reunion; St.K.= Saint Kitts; S.A. = South Africa; U.S.A. = United States of America (Continental); W.I. = West Indies

[3]N = none; P = partial; S = substantial; C = complete

The data in Table 1 can be analysed in a number of ways. The simplest of these is to compare the degree of success achieved at every location into which control agents have been introduced with the predominant means of reproduction of the target species (*sexual* cf. *asexual*). However, such an analysis contains two possible sources of bias. The first of these is the differences found between species in the number of locations at which control has been attempted. Species which have been controlled successfully in one area (e.g., *Eupatorium adenophorum* Spreng., Compositae) are more likely to be selected as targets at other locations than species for which control programs have failed. Such a source of bias may be eliminated by determining the degree of success of each species as a mean for all locations. A second source of bias arises from the preponderance of species of *Opuntia* (Cactaceae) in the category reproducing asexually (16 of the 24 species). This effect may be overcome by reducing the number of *Opuntia* species to two (*O. megacantha* Salm-Dyck and *O. vulgaris* Miller, the two most troublesome weeds), in line with the number of species in three other genera considered (*Emex*, Polygonaceae; *Rubus*, Rosaceae; and *Tribulus*, Zygophyllaceae).

If these changes are made, the significance and importance of the mode of reproduction of the target species can be shown by comparing the average degree of success achieved with the predominant means of reproduction of the target species (Table 2). The columns of this table were grouped ('non' plus 'partial' control cf. 'substantial' plus 'complete' control) and a Chi-square test carried out on the resultant 2 x 2 contingency table. The null hypothesis that the degree of control achieved was independent of the predominant means of reproduction of the target species is rejected when the results of this test are considered ($\chi_1^2 = 4.94$; $0.025 > P > 0.01$). If the alterations and exclusions made to the data to eliminate the two possible sources of bias are not made, this

Table 2. Ratings of biological control of weeds comparing the average degree of control achieved with the predominant means of reproduction of the target species.

Predominant means of reproduction	Degree of control achieved			
	None	Partial	Substantial	Complete
Agamospermy or	1.00	1.45	4.20	3.35
clonal reproduction	10.00%	14.50%	42.00%	33.50%
Sexual reproduction	3.00	8.08	2.50	2.42
	18.75%	50.50%	15.63%	15.13%

relationship is even stronger ($\chi_1^2 = 23.66$; $P < 0.005$)[2]. We conclude that the distribution of the degree of control achieved in these cases was significantly affected by the reproductive mode of the target species.

The present findings show that plants which reproduce primarily asexually have been successfully controlled more often than those which reproduce sexually. This indicates the importance of breeding system and population structure in determining the vulnerability of plant populations to pests and diseases. The greater effectiveness of biological control agents against asexually-reproducing weeds may be due to their greater genetic homogeneity particularly after dispersal over long distances, and/or their limited capacity to evolve resistant strains when heavily attacked by natural enemies.

Whether the increased level of variation which is likely to occur in sexually-reproducing species is sufficient to protect the species against serious damage by introduced natural enemies or to enable it to adapt to changing circumstances will be determined by the amount and type of variation present and the selectiveness of the control agent involved. Species which have been deliberately introduced on numerous occasions as garden plants and which have since become major weeds (e.g. *Lantana camara* L., Verbenaceae, in Australia) will present greater problems for control than species which have been introduced only once. The effectiveness of genetic hetergeneity in dissipating the impact of control agents will also be determined, in part, by the specificity of those agents. The more narrow the host range of natural enemy, the more likely the existence of resistant or tolerant genotypes in the host population. Thus it might be expected that pathogens would be less effective as control agents than insects, because of their usually greater host specificity (Norris 1970, Day 1974). However, the difference between insects and pathogens in their host specificity is a matter of degree rather than kind. Many examples are documented in the literature of highly specific interactions between insects and their hosts (Maxwell *et al.* 1972) and host plant resistance has seen increasing use in insect control over the last decade (Maxwell *et al.* 1972). In fact, the results shown here indicate that insects may be more host specific than previously suspected.

BIOLOGICAL CONTROL AND COMPETING PASTURE PLANTS

Biological control of cacti, such as *Opuntia* spp. and *Eriocereus martini* (Lab.) Riccob. (Cactaceae) has generally been substantially or completel successful in Australia (Table 1) using introduced insects and the classica methods of applied entomology (e.g., Mann 1970). In this section we point ou that rarely has this been the case with biological control programs on othe weeds in Australia. More often, and with other groups of weeds, success owin to the effects of entomological (or mycological) control has been confounde with reductions in weed growth because of the presence of competing pastur plants.

Consider the example of *Chondrilla juncea* L. or skeleton weed (Compositae) for which quantification of growth reduction is available in terms of both th reduction due to a competing pasture species as well as to the presence of biological control agent. *C. juncea* was a particularly intractable weed o Australian cereal-growing areas (Cullen and Groves 1977). Soon after intro duction, its density increased under a regime of regular cultivation and it canno be controlled satisfactorily in a cropping-pasture system by existing herbicide Moore and Robertson (1964) showed that in a pasture dominated by *Trifoliun subterraneum* L. (subterranean clover) the density of skeleton weed could however, be decreased by up to 60 per cent if a 4-year period of pasture wa included between successive cereal crops, whereas for a 2-year pasture period density was decreased by only 18 per cent. Since 1971, the release of severa insects and especially of the rust fungus *Puccinia chondrillina* Bubak & Syd. ha led to effective control of at least the most widepread form of the weed ir southeastern Australia (Cullen and Groves 1977).

Results of an experiment in which the pasture plant (*T. subterraneum*) an the weed (*C. juncea*) were grown alone and together in a glasshouse with an without *P. chondrillina* are summarized in Table 3. By 146 days after sowing weed growth was decreased by 70 per cent through competition with sub terranean clover and by about 50 per cent after infection with the fungus. Ir terms of the present argument, however, the combined effect of both com petition from subterranean clover *and* infection by the rust is the importan result and in this case the synergistic interaction of these two factors reduce growth of skeleton weed by up to 94 per cent of the uninfected control plants

Table 3. Total dry weights of *C. juncea* plants per pot, as influenced by rust infection an competition from subterranean clover (abridged from Groves and Williams 1975) Values are expressed as a percentage of the total dry weight of uninfected plant grown in the absence of competition from subterranean clover.

Days from sowing	Without rust Competition	Total dry weight (per cent uninfected wt) With rust No competition	With rust Competition
63	84	53	35
106	51	59	26
146	30	49	6

In the field, the situation is somewhat more complex, depending on the favourability of the area for both weed and pasture plant. For example, in harsh environments for the weed, the rust may be effective alone. In less severe environments and where subterranean clover grows well, the effects of the rust and competition with subterranean clover act synergistically, as described by Groves and Williams (1975).

Success in the control of skeleton weed has been achieved over a large part of southeastern Australia by manipulating the cereal-pasture ecosystem using both biological control techniques and agronomic methods of weed control (Cullen and Groves 1977). We suggest that in choosing candidates for biological control the chances of success for a large group of Australian pasture and crop weeds will be enhanced if they are also able to be controlled by competing pasture plants. Known examples of such weeds include *Echium plantagineum* L. (Boraginaceae) (Piggin 1978), *Hypericum perforatum* L. var. *angustifolium* DC. (Guttiferae) (Moore and Cashmore 1942, J.D. Williams, pers. comm.), and the thistles, *Onopordum* (Michael 1968a) and *Silybum marianum* (L.) Gaertn. (Compositae) (Michael 1968b). Several other thistles are likely additions to this group of important Australian weeds. These examples, all procumbent weeds in winter, suggest that the chances of success in southern Australia will be greater if the pasture species is winter-growing and therefore able to shade the weed through winter.

DISCUSSION

The approaches used in programs on biological control of weeds have, in large part, been based on concepts developed in applied entomology. Only recently, it seems, have attempts been made to review the relevance of both the approaches and the concepts to weed control (e.g., Wapshere 1974). In this paper, we have sought to emphasize two criteria which are based on characteristics of the host candidate; specifically, the genetic variability of the weed population and the susceptibility of the weed to control by economically desirable plants.

Based on our review of past records of success and failure in biological control programs, we conclude, firstly, that in many cases the greater the genetic variability of weed populations and the more open the recombination system, the less likely the chances for successful weed control. The potential value of this criterion for determining in advance the likely success of a weed control program seems to have been given relatively little attention by entomologists. Clearly a great many other factors, such as the activities of predators, parasites and pathogens, which may interfere with survival and persistence of insects imported for biological control of weeds (Goeden and Louda 1976) and the genetic diversity of the control agents themselves may also be of considerable significance in determining the final level of success achieved in the field. We do not consider the genetic constitution of the weed to be of sole importance, but make the point that it should be given greater consideration than has been the case previously. From the viewpoint of weed control the correlation discussed above strongly suggests that the biological control of genetically highly variable species will be a more costly process than the control of weeds which are genetically highly uniform.

Our second conclusion concerns the availability of alternative control mechanisms based upon the use of competing pasture plants. If this alternative method of control, of which some examples are known for major Australian weeds, can be integrated with the release of natural enemies then ecologi control of the weed is more likely. We have used control of one form of *juncea* as an example of this enhanced level of success achieved in over control. Other methods of control, such as by strategic timing of cultivation of herbicide application, may also be able to be integrated with biologi control and the chances for success thereby enhanced even further. In t contribution we have considered mainly terrestrial weeds of the pastu cropping regions of southeastern Australia, but the same concept could w apply to aquatic weeds by the planned integration of several methods of cont (D.S. Mitchell pers. comm.).

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