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Plant Life-history and the Success of Weed Biological Control Projects

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Abstract

Success in weed biological control in defined as the degree to which weed density is depressed below its pre-release equilibrium. Only subjective assessments of success are available for most biological control projects, because pre-release study and post-release follow-up assessments are not sufficiently quantitative. The most successful individual control attempts were against *Opuntia* in India and Ceylon and involved the cochineal insect *Dactylopius opuntiae*. The most frequently repeated success has been against lantana using a variety of different agents in different habitats. Frequent successes have also been obtained against the waterweeds waterhyacinth, *Eichhornia crassipes*, alligator weed, *Alternanthera philoxeroides*, and, more recently, against *S. molesta* (once taxonomic difficulties involving both the fern and the insect were resolved). The most frequently repeated failure of control also involves lantana. Other weeds frequently failed against include ragwort, *Senecio jacobaea*, leafy spurge, *Euphorbia* x *pseudovirgata*, *Cyperus rotundus* and salvinia (before the taxonomic difficulties were resolved). The most successful control agents against weeds other than *Opuntia* and lantana are beetles; weevils are successful in 26% of releases and chrysomelids in 23%. This is to be compared with average success rates per release of 15% for Diptera and 14% for Lepidoptera. Plant attributes associated with good control are genetic uniformity, lack of perennation or dormancy (both exhibited by *S. molesta*), and susceptibility to secondary infection (e.g., secondary rotting in many cacti of the genus *Opuntia*). Plant attributes associated with persistent failure of control are a rhizomatous perennial growth-form, high powers of regrowth, and low quality as food for insects. Recent information suggests a slight downward trend in success: pre-1980, establishment probabilities were 65% and success probabilities were 14% per release; since 1980, there has been a fall to 44% in establishment probability and 8% in successful weed control. This may be a genuine trend, suggesting that all the easy targets have already been hit, or it may be an artefact of frequent failed attempts to repeat controls that were successful elsewhere.

Introduction

The balance of trace between ecological theory and biological control practice is highly skewed. Biological control has given ecology some text-book examples of plant-herbivore and host-parasite interactions. For all their limitations, these studies provide some of the best large-scale, long-term data sets available. In contrast, ecological theory has made virtually no contribution to the way in which biological control schemes are planned or executed. It was one of the aims of the Silwood Project on Weed Biological control (Moran 1986) to begin to redress this imbalance, by attempting to extract ecological insights from a thorough analysis of previous biological control releases, both successful and unsuccessful.

I have described the factors influencing the probability of establishment of an introduced biological control agent elsewhere (Crawley 1986, 1987). Here, I describe the more subjective notion of the 'success' of a biological control project, and analyse the attributes of weeds and insects that are associated with high and low degrees of success in weed control.

Definitions

Success

An ecological measure of weed biological control success is q; the degree to which the biological control agent depresses the equilibrium weed population density below its pre-release levels (Beddington *et al.* 1978):

$$q = N^*/K$$

where N^* is the weed equilibrium following biological control and K is the pre-release equilibrium. When control is complete, $N^* = O$ and $q = O$; when the attempt fails completely, $N^* = K$, so $q = 1$. Other, more applied measures of success would take account of economic factors; e.g., benefit-cost ratios based on the revenue generated per hectare following control compared to the revenue (if any) generated prior to control. This paper however, is concerned only with ecological measures of success.

Success Rating

The Silwood Project employed two different measures for the success of an individual weed control project. The first was an all-embracing, but rather subjective measure of success, in which the outcome of the introduction was categorized on a scale of 0 to 4 (Table 1*a*). This scheme has the merit of great simplicity, but different authors are quite likely to classify the same outcome in different ways; what is moderate control to one person, may be marked control to another.

Table 1. Success ratings used by the Silwood Project on Weed Biocontrol. (a) The simplest measure uses only "degree of control"; (b) the more complex version uses S = DEGREE x EXTENT x COVER x AREA.

Degree	Extent	Cover	Area
0 = none	0 = imperceptible	1 = sparse	Log base 10 km^2 area of weed before control.
1 = slight	1 = local	2 = dense patches	
2 = moderate	2 = partial	3 = all dense	
3 = marked	3 = broad		
4 = complete	4 = complete		

A no less subjective, but rather more comprehensive measure of success involved taking account of the initial scale of the weed problem. Control of a minor weed on a small oceanic island was deemed to rate as less successful than a similar degree of control achieved over a major weed on a continental scale. For this, we produced a compound index of success by multiplying together four variables (Table 1*b*); degree of control, initial weed density, uniformity of initial weed infestation, and the area of the infestation (in $\log_{10} km^2$).

Results

The Most Successful Individual Releases

Using the second, more complex measure of success, it is possible to rank the 627 cases that were documented prior to 1980 (Table 2). Not surprisingly, the table of top releases is dominated by projects that were successful over very large areas, and 8 out of 11 involve large-scale control of *Opuntia* spp. (Cactaceae). It is heartening that recent control successes appear in this all-time list; e.g., *Carduus* (Asteraceae) in Canada. The spectacular and repeated successes of *Salvinia molesta* D.S. Mitchell (Salviniaceae) control since 1980, would almost certainly appear high up this list (Room, this volume). Note that the textbook example of successful weed control - *Cactoblastis cactorum* (Bergroth) (Lepidoptera: Pyralidae) in Queensland - does not make the top 10 on the criteria used in this rating.

The Weeds Most Frequently Controlled

If we define releases as successful when they achieved a score of 3 or 4 using the simple scheme (Table 1a), then we can ask which target weeds have been the most frequently controlled (Table 3). *Lantana camara* L. (Verbenaceae) had been successfully controlled on 21 occasions prior to 1980. This figure would have been surpassed by *Opuntia* had we added the cactus species together. *Teleonemia scrupulosa* Stål (Hemiptera: Tingidae) was successful in 31% of releases, and *Hypena strigata* (F.) (Lepidoptera: Noctuidae) in 43%. The second most frequently controlled weed was *Hypericum perforatum* L. (Clusiaceae); *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) was successful on half the occasions it was released. Note how many of the successfully controlled weeds are water plants or weeds of badly managed, semi-arid pasture.

Table 2. The top 10 most successful cases of weed biological control up to 1980, as judged by the more complex success rating (Table 1*b*). Recent successes (e.g., salvinia in New Guinea) would almost certainly figure in an updated version.

Rating	Plant	Insect	Place & Date
1	*Opuntia vularis* Miller (Cactaceae)	*Dactylopius ceylonicus* (Green) (Hemiptera: Dactylopiidae)	India, 1795
2	*O. vulgaris*	*D. ceylonicus*	Sri Lanka, 1795
3	*Opuntia dillenii* (Ker-Gawler) Haworth	*Dactylopius opuntiae* (Cockerell)	India, 1926
4	*Carduus nutans* L. (Asteraceae)	*Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae)	Canada, 1968
5	*Hypericum perforatum* L. (Hypericaceae)	*Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae)	USA, 1946
6	*O. vulgaris*	*D. ceylonicus*	South Africa, 1913
7	*Opuntia elatior* Miller	*D. opuntiae*	Indonesia, 1935
8	*Opuntia* sp.	*D. opuntiae*	Madagascar, 1923
9	*Opuntia tuna* (L.) Miller	*D. opuntiae*	Madagascar, 1928
10	*O. triacantha* (Willdenow) Sweet	*Cactoblastis cactorum* (Bergroth)	Nevis, West Indies, 1957

The Most Frequently Unsuccessful Targets of Weed Biological control

Just as nothing succeeds like success, so nothing is guaranteed to produce more biological control failures than the knowledge that a particular weed has been successfully controlled somewhere else. Thus, numbers one and two on the list of failures are the same weeds as headed the list of successes (Table 4). Eighty one releases against lantana were complete failures. The case of *Hypericum* represents another example of misguided optimism, based on the (almost certainly erroneous) logic that, because a weed is controllable by one agent, it must be controllable by others.

The first new plant species to appear on the list of failures are *Cirsium arvense* (L.) Scopoli (Asteraceae) and the 'world's worst weed', the nutsedge *Cyperus rotundus* L. (Cyperaceae). These plants have a number of traits in common: they all possess substantial powers of regrowth, and a number of them (e.g., *Euphorbia* and *Cyperus*) represent very low quality food for herbivores. The repeated failure to control salvinia was due to taxonomic confusion concerning both the fern and the insect (see below).

Weed Attributes Associated with Success

Why is that cacti and lantana have been successfully controlled more often than other weeds? Is it simply that biological control has been attempted more frequently against these plants, or is there something about their biology that makes them more likely to succumb to insect

Table 3. The most frequently repeated successes, showing the weed, the range of insects employed and the mode of feeding. S = number of releases rates as marked or complete success; E = numbers of releases becoming established; R = number of releases up to 1980; % S = percent of releases leading to marked or complete success; % E = percent of releases leading to establishment.

Weed	Agent	S	E	R	% S	% R	Agent Biology
1. *Lantana camara* L. (Verbenaceae)	*Teleonemia scrupulośa* Stål (Hemiptera: Tingidae)	9	26	29	31	90	leaf-feeding tingid
	Uroplata giardi Pic (Coleoptera: Chrysomelidae)	5	11	17	29	65	chrysomelid beetle
	Hypena strigata (F.) (Lepidoptera: Noctuidae)	3	6	7	43	86	noctuid moth
	three others	4	14	24	17	58	various
2. *Hypericum perforatum* L. (Clusiaceae)	*Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae)	4	7	8	50	88	chrysomelid beetled
	C. hyperici (Forster)	3	6	10	30	60	chrysomelid beetle
	Zeuxidiplosis giardi Kieffer (Diptera: Cecidomyiidae)	2	5	6	33	83	cecidomyiid midge
3. *Eichhornia crassipes* (Martius) (Solms-Laubach) (Pontederiaceae)	*Neochetina eichhorniae* Warner (Coleoptera: Curculionidae)	5	6	10	50	60	weevil
	Sameodes albiguttalis Warren (Lepidoptera: Pyralidae)	2	3	5	40	60	pyralid moth
	N. bruchi Hustache	1	2	3	33	66	weevil
4. *Opuntia vulgaris* Miller (Cactaceae)	*Dactylopius ceylonicus* (Green) (Homoptera: Dactylopiidae)	6	7	9	66	78	cochineal
	Cactoblastis cactorum (Bergroth) (Lepidoptera: Pyralidae)	1	20	22	5	91	pyralid moth

Table 3. Continued.

Weed	Agent	S	E	R	% S	% R	Agent Biology
5. *Cordia macrostachya* (Jacquin) (Boraginaceae)	*Metrogaleruca obscura* Degeer (Coleoptera: Chrysomelidae)	3	3	3	100	100	chrysomelid beetle
	Eurytoma attiva Burks (Hymenoptera: Eurytomidae)	2	3	3	66	100	eurytomid wasp
6. *Centaurea diffusa* Lamarck (Asteraceae)	*Urophora affinis* Frauenfeld (Diptera: Tephritidae)	4	6	6	66	100	tephritid fly
7. *Opuntia dillenii* (Ker-Gawler) Haworth	*Dactylopius opuntiae* (Cockerell)	2	16	23	9	70	cochineal
	C. cactorum	2	20	22	9	91	pyralid moth
8. *Alternanthera philoxeroides* (Martius) Griseb (Amaranthaceae)	*Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae)	2	2	2	100	100	chrysomelid beetle
	Vogtia malloi Pastrana (Lepidoptera: Pyralidae)	2	2	2	100	100	pyralid moth
9. *Tribulus cistoides* L. (Zygophyllaceae)	*Microlarinus lypriformis* (Wollaston) (Coleoptera: Curculionidae)	3	10	10	30	100	weevil
	M. lareynii (Jacquelin du Val)	1	3	5	20	60	weevil
10. *Linaria vulgaris* Miller (Scrophulariaceae)	*Gymnaetron antirrhini* Paykull (Coleoptera: Curculionidae)	2	3	3	66	100	weevil
	Brachypterolus pulicarius L. (Coleoptera: Nitidulidae)	1	2	2	50	100	nitidulid beetle

Table 4. The most frequently repeated failures of biological weed control. E = releases leading to establishment; R = number of releases; % E = percent of releases leading to establishment. None of the agents on this list ever achieved marked or complete control.

Weed	Agent	E	R	% E	Plant growth form
1. *Lantana camara* L. (Verbenaceae)	*Diastema tigris* Guenèe (Lepidoptera: Noctuidae)	1	11	9	Verbenaceae: perennial, straggling shrub with prickly seed, but regrowing vigorously after cutting
	Leptobrysa decora Drake (Hemiptera: Tingidae)	4	11	36	
	Ophiomyia lantanae (Froggatt) (Diptera: Agromyzidae)	13	20	65	
	Teleonemia elata Drake (Diptera: Agromyzidae)	0	5	0	
	17 others	13	34	38	
2. *Hypericum perforatum* L. (Clusiaceae)	*Agrilus hyperici* (Creutzer) (Coleoptera: Buprestidae)	2	7	29	Clusiaceae: proto-hemicryptophyte, rhizomatous perennial
	Chrysolina varians Schaller (Coleoptera: Chrysomelidae)	0	3	0	
	four others	2	5	40	
3. *Salvinia molesta* D.S. Mitchell (Polypodiaceae)	*Cyrtobagous singularis* Hustache (Coleoptera: Curculionidae)	1	5	20	Polypodiaceae: annual/perennial floating fern spreading by fragmentation
	Paulinia acuminata (Degeer) (Orthoptera: Pauliniidae)	7	10	70	
	Samea multiplicalis (Guenèe) (Lepidoptera: Pyralidae)	1	3	33	
4. *Cirsium arvense* (L.) Scopoli (Compositae)	*Altica carduorum* (Guèrin - Mèneville) (Homoptera: Dactylopiidae)	0	4	0	Compositae: geophyte with root buds, rhizomatous perennial spreading by seed and by rootstock fragments
	Urophora cardui (L.) (Diptera: Tephritidae)	2	5	40	
	Ceutorhynchus litura (F.) (Coleoptera: Curculionidae)	2	2	100	
	Lema cyanella (L.) (Coleoptera: Chrysomelidae)	0	1	0	
5. *Opuntia littoralis* (Engelmann) Cockerell (Cactaceae)	*Chelinidea vittiger* Uhler (Coleoptera: Chrysomelidae)	3	6	50	Cactaceae: spreading by seed and cladodes
	Melitara prodentalis Walker (Lepidoptera: Pyralidae)	0	9	0	
	four others	27	42	64	

Table 4. Continued.

Weed	Agent	E	R	% E	Plant growth form
6. *Cyperus rotundus* L. (Cyperaceae)	*Athesapeuta cyperi* Marshall (Coleoptera: Curculionidae)	1	7	12	
	Bactra minima Meyrich (Lepidoptera: Tortricidae)	0	4	0	
	B. venosana (Zeller)	2	5	40	
7. *Opuntia ficus - indica* (L.)	*Archlagocheirus funestus* (Thompson) (Coleoptera: Cerambycidae)	4	4	100	Cactaceae: spreading by seed and cladodes
	Melitara doddalis Dyar	0	3	0	
	M. prodenialis	0	9	0	
	three others	6	8	75	
8. *Chromolaena odorata* (L.) R. King & H. Robinson (Compositae)	*Apion brunneonigrum* Bèguin-Billecoq (Coleoptera: Apionidae)	0	5	0	Compositae: short-lived, scrambling perennial, spreading by seed
	Pareuchaetes pseudoinsulata Rego Barros (Lepidoptera: Arctiidae)	1	6	17	
9. *Senecio jacobaea* L. (Compositae)	*Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae)	4	9	44	Compositae: biennial or perennial, rosette-forming, hemi-cryptophyte, spreading by seed and root fragments
	Hylemya seneciella Meade (Diptera: Anthomyiidae)	2	4	50	
	Longitarsus jacobaeae (Waterhouse) (Coleoptera: Chrysomelidae)	3	3	100	
10. *Euphorbia x pseudovirgata* (Schur) Soo (Euphorbiaceae)	*Chamaesphecia tenthrediniformis* (Schiffermüller) (Lepidoptera: Aegeriidae)	0	3	0	Euphorbiaceae: rhizomatous perennial proto-hemicryptophyte
	C. empiformis Esper	0	2	0	
	Hyles euphorbiae (L.) (Lepidoptera: Sphingidae)	3	4	75	
	Oberea erythrocephala (Schrank) (Lepidoptera: Sphingidae)	2	2	100	

herbivory? It is clear that certain cacti are good targets for weed biological control (Moran & Zimmermann 1984); 8 out of the top 10 most successful releases are of *Opuntia* spp. (Table 2). It appears that secondary rotting, following initial attack by insects, may be important factor contributing to cactus control in a number of cases. Note, however, that *Opuntia* spp. also appear in Table 4, as repeated failures. The case of lantana is less informative about the relationship between plant life-history and control success; the plant is so polymorphic, and control has been achieved using such different numbers and different kinds of agent species in different habitats (with varying degrees of success), that no clear picture has yet emerged. It is from other species that we are likely to obtain a clearer definition of the nature of a "controllable weed".

Recent trends in control success can be guaged by comparing pre- and post-1980 releases (Table 5), allowing for the fact that the most recent releases may not yet have had sufficient time to allow a full assessment of their outcome. The greatest success story of weed biological control in recent years has been the repeated (and predictable) eradication of salvinia by *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae) (Room, this volume). Little is known about why *C. salviniae* makes such a good control agent, whereas the virtually indistinguishable *C. singularis* Hustache is such a failure. The fern, however, is extremely uniform in its genotype (indeed, the entire species may be represented world-wide by a single clone). High genetic uniformity appears to be a necessary condition for repeatable and predictable successful control using a single agent. Again, salvinia lacks any means of persisting through unfavourable conditions (it produces no spores), and is killed outright by desiccation.

Table 5. Success of weed biological control projects before and after 1980. Data pre-1980 from Silwood Project on Weed Biocontrol; post-1980 from Julien (1987). (a) percent of releases; (b) numbers of releases falling in each category.

Category	Pre-80	Post-80
a. Failed	35%	56%
Established	65%	44%
Achieved marked or complete success	14%	8%
b. Success 1		8
Success 2		7
Success 3		6
Success 4		5
Unknown		32
Failed		40
Total		72

We do not know anything about the relative genetic uniformity of *Opuntia* in the successful and unsuccessful control attempts, but I suspect that the successfully controlled species were less polymorphic than those which resisted attempts at control.

Insect Attributes Associated with Success

Leaving aside the *Opuntia* cacti (these tend to be controlled either by *Dactylopius* spp. of cochineal insect [Hemiptera: Dactylopiidae] or by *C. cactorum*), and lantana (generally controlled by several insects, often including *T. scrupulosa*), it is clear that beetles are conspicuously more successful than any other insect group. In particular, the weevils produce successful weed control following 26% of releases, and the chrysomelids in 23% of cases. Compare this with only 14% success for Lepidoptera and 15% for Diptera (Table 6). The biological attributes associated with this success are not yet understood, although the factors that correlate with a high probability of establishment (high rate of increase, long-lived adults, high voltinism, low per capita feeding rates associated with small individual size; see Crawley 1986) do seem, also, to correlate broadly with the decree of success obtained. While some successful weed control agents are local and uncommon as natives, like *Trichilogaster acaciaelongifoliae* (Froggatt) (Hymenoptera: Pteromalidae; Dennill & Moran, this volume), it appears that most successful agents are both widespread and abundant in their native lands (Crawley 1987).

Table 6. The relative success of different agents. (a) Insect orders compared; (b) insect families compared. Success ratings as in Table 1*a*. Mean = arithmetic mean success rating; % S = percentage of releases in which success > 2.

a. Insect order	0	1	2	3	4	mean	% S
Hemiptera	48	14	20	22	8	1.29	27
Coleoptera	100	30	20	40	3	0.90	22
Diptera	28	20	7	10	0	0.79	15
Lepidoptera	85	38	12	21	1	0.72	14
Hymenoptera	0	2	1	2	0	2.00	40
Thysanoptera	2	1	0	2	0	1.40	40
Orthoptera	4	3	1	2	0	1.10	20
b. Insect family							
Dactylopiidae	18	1	6	12	8	1.80	43
Curculionidae	27	10	6	19	2	1.20	26
Chrysomelidae	36	7	10	18	1	1.18	23
Pyralidae	29	12	0	14	1	1.04	24
Cecidomyiidae	3	1	0	3	0	1.29	33
Acrididae	4	3	1	2	0	0.60	20
Tingidae	22	9	12	10	0	1.19	17
Tephritidae	12	11	5	7	0	1.20	16
Noctuidae	15	5	1	3	0	0.67	11
Apionidae	11	6	0	2	0	0.63	11
Arctiidae	8	3	2	1	0	0.71	7
Tortricidae	6	4	2	0	0	0.67	0
Coreidae	8	4	2	0	0	0.57	0
Agromyzidae	10	8	1	0	0	0.53	0
Cerambycidae	17	5	3	0	0	0.44	0
Buprestidae	7	1	0	0	0	0.33	0

Discussion

It is relatively straightforward to determine whether or not a biological control introduction has established a viable population, and, given sufficiently close monitoring at the time of release, with a reasonable level of follow-up effort, it is usually possible to understand why failure of establishment came about. Thus, the search for correlations between demographic attributes of organisms and the probability of establishment is reasonably fruitful (Crawley 1986, 1987). As we have seen, however, biological control success is much more difficult to judge. In principle it should be straightforward to estimate pre-release and post release weed densities, and therefore to calculate q, the ecologist's measure of success. In practice, however, there is rarely sufficient information to do even this. Thus, any associations we uncover between the ecology of the organisms and the degree of success achieved, are likely to be a good deal more nebulous (and therefore less useful) than similar associations involving the probability of establishment of the agent.

One of the most important questions that remains to be answered about the ecology of successful biological control is this: to what extent is the continued, stable, low density condition that (by definition) prevails after a completely successful control attempt, due to the continued and continuous action of the introduced agent? Does the interaction represent a stable equilibrium in the classic Lotka-Volterra mould, or is it a non-equilibrium state, in which the agent has driven the weed to local extinction (Crawley 1983). Looked at another way, would the weed return to its former abundance if the plant community were now to be sprayed with insecticide to exclude the herbivorous insects? Although, for understandable reasons, this experiment is not routinely carried out, I suspect that the weed would not return to its former abundance in most cases. So many ecological factors change following successful weed control (increase in perennial plant cover, improved management practice, etc.), that post-control dynamics of the plant may be radically different from those that prevailed before introduction of the insect. In terrestrial communities, for example, interspecific plant competition may play a vital role in reducing recruitment of the weed following successful control, whereas a virtual monoculture of the weed might have existed prior to release.

An alternative explanation is that successful biological control does not involve a continuous insect-plant interaction, because the successful agent causes local extinction of the weed. For example, in several of the successful cases involving salvinia (Room, this volume), the weed population went extinct following control by *C. salviniae*; the remnants of the water-fern were blown into rafts by the wind, then desiccated when the water level was lowered, leaving the rafts high and dry. Whether or not all successful cases of salvinia control follow this model, remains to be seen. In rivers and lakes where the water levels are more stable, and there is a complex fringing vegetation, there may be some kind of "hide-and seek dynamics" between the beetles and the small, ephemeral, isolated pockets of the fern that survive. In any event, it is most unlikely that there is a spatially uniform, stable equilibrium, with the herbivore and the plant coexisting at low densities throughout the former extent of the weed population, in the manner described by Lotka-Volterra dynamics.

We are a long way from understanding the relationship between plant life history and the degree of success obtained in weed biological control. We know something about the correlates of successful establishment of insect agents, but we lack genuine predictive power. Faced with all the available information on the biology of *C. singularis* and *C. salviniae* there is no way that we could predict with better than 50% probability which (if either) would turn out to be the successful agent. If we hope to understand the ecology of weed biological control, we must carry out detailed, long-term research on the current status of previously successful projects, and put much more effort into pre- and post-release study of future releases.

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