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How Many Insect Species are Necessary for Successful Biocontrol of Weeds?

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Abstract

The conventional wisdom of classical biological weed control is that as more insects are established on weeds the damage to the plants increases and the goal of successful biological control is gradually approached. I test this hypothesis by comparing the reduction in seed production of knapweed achieved by several insects attacking the same plants, and by reviewing reported successes in the biological control of weeds. Observations don't support a model of cumulative insect attack leading to biological control. Multiple attack by different insect species introduced on knapweed in British Columbia varied from being slightly advantageous, to having little influence, to being slightly deleterious, as compared to attack by a single species. A review of 26 successful weed control programs shows that in 81%, success was achieved by a single insect species. These observations suggest that biological weed control is more frequently achieved by a single insect species rather than the cumulative effect of several insect species. I suggest that each insect introduction is a lottery and may lead to successful biological control.

Combien d'Espèces d'Insectes Sont-elles Nécessaires à la Lutte Biologique Efficace Contre les Plantes Nuisibles?

L'introduction de 107 espèces d'insectes a permis d'assurer une lutte biologique efficace contre 26 espèces de plantes nuisibles (moyenne de 4,1 introductions par plante nuisible). Parmi les populatoins d'insectes introduites, 74 (70%) se sont établies. L'efficacité de la lutte a été attributée à une espèce d'insecte dans 16 cas (62%), deux insectes dans 5 cas et 3 insectes dans un cas. Dans trois des cinq cas où une lutte efficace a été assurée par deux espèces d'insectes et dans l'unique cas où l'efficacité de la lutte a été attribuée à trois espèces d'insectes, les agents biologiques étaient *Cactoblastis cactorum* et *Dactylopius opuntiae* et les plantes hôtes, des cactus. Aucun des cas où le succès de la lutte a été attribué à plus d'un insecte n'a été suffisamment documenté. Le succès des méthodes repose sans doute davantage sur le hasard, car l'introduction de l'espèce d'insecte la plus appropriée au site donne de meilleurs résultats que l'essai cumulé d'un certain nombre d'insectes moins adaptés. Il est difficile d'identifier les espèces d'insectes les plus propices à la lutte biologique. Des insectes étroitement apparentés, présentant des phénologies et des comportements d'infestation similaires, n'ont pas nécessairement le même succès comme agents biologiques. L'étude donne comme exemple *Chrysolina quadrigemina* et *C. hyperici*, deux insectes étroitement apparentés, mais dont l'un est efficace, l'autre non.

Introduction

The aim of biological weed control is to decrease the population of weeds through the establishment of insect herbivores or plant diseases. Harris (1979) reports that an average of four species were established in successful biological control projects. This could be interpreted to indicate that the cumulative stress of several herbivore species was frequently required before control was achieved (Harris 1985). On the other hand, successful biological control is the exception and has been achieved in only approximately 30% of the attempted programs. This lack of success suggests that many insects have little effect on the population density of plants or that many plants are able to compensate for herbivore damage (for recent examples see Hendrix 1984; Islam and Crawley 1983; McNaughton 1983; Solomon 1983).

To test the generality of the conventional wisdom that more insect herbivory is better for weed control, I report observations of the seed reduction achieved in diffuse (*Centaurea diffusa* Lam.) (Compositae) and spotted (*C. maculosa* Lam.) knapweed by several introduced insects. In addition, information from Julien's (1982) review, 'Biological Control of Weeds' is summarized to determine the number of insect species involved in successful weed control projects.

Methods

The number of *Metzneria paucipunctella* Zeller (Lepidoptera: Gelechiidae) and *Urophora quadrifasciata* (Mg.) (Diptera: Tephritidae) in seed heads of spotted knapweed was scored in the late summer of 1979 and 1980 in plants collected from the release site near Westwold, B.C. The number of seeds in heads with no insects, one insect species, or both species was counted.

Table 1. Mean number (SD) of *Urophora* and *Metzneria* in heads attacked and not attacked by the other species.

		Metzneria			
		Present		Absent	
	1978	0.51	(0.94)	0.24	(0.63)
Urophora/head	1979	0.89	(0.93)	1.00	(1.39)
	1980	1.18	(1.64)	1.06	(1.89)
		Urophora			
		Present		Absent	
	1978	0.37	(0.44)	0.38	(0.45)
Metzneria/head	1979	0.65	(0.52)	0.56	(0.54)
	1980	0.70	(0.49)	0.48	(0.50)

To study the interactions between *Urophora* and a root-boring beetle, seed production of diffuse knapweed was assessed by counting the proportion of buds which developed to form seed heads in diffuse knapweed plants from the White Lake area south of Penticton, B.C. in 1981. *Urophora* attack was scored by counting the number of galls in five distal heads on each plant and plants were scored as to whether they were attacked by *Sphenoptera jugoslavica* Obenb. (Coleoptera: Buprestidae).

Results

Multiple Introductions on Knapweed

Six insects have now been introduced on knapweed, *C. diffusa* and *C. maculosa*, in British Columbia (Harris and Myers 1984). We have attempted to measure the interactions between pairs of these agents to determine if in general they are complimentary. Two species of gall-flies, *Urophora affinis* Frauenfeld and *U. quadrifasciata* have been introduced to B.C. Although the mean number of each species was lower in flower heads containing larvae of both flies, the total fly density was approximately 35% higher on average in the heads attacked by both species. We don't have enough information on well-established populations of one *Urophora* species to compare to populations with both fly species. In Europe the density of flies in areas where both species were present tended to be lower than in areas inhabited by only one species (Myers and Harris 1980). Therefore where several insect species have evolved together, interactions among species can reduce their combined impact on plants. This negative interaction has not yet been observed in B.C.

The seed feeding moth, *M. paucipunctella* has previously been reported to kill co-occurring larvae of *Urophora* (Englert 1971; Varley 1947). We found no evidence of a reduction of *U. quadrifasciata* in seed heads of spotted knapweed containing both insect species (Table 1). In Westwold, B.C., *Urophora* reduced seed production of spotted knapweed by 28–35% in the two years studied when they occurred in seed heads by themselves (Table 2). The percent seed reduction in heads with both *Urophora* and *Metzneria* was 20–41% in those same years. We calculated that *Metzneria* larvae eat approximately three to four seeds for larval development; this is approximately 20–30% of the average number of seeds/head.

Table 2. Mean number of seeds/flower head (SE) of spotted knapweed heads attacked and unattacked by *Urophora* and *Metzneria* in 1979 and 1980 at Westwold, B.C. Percent reduction in seed production is based on number of seeds in heads unattacked by either species.

	Metzneria			
	Present		Absent	
Urophora	1979	1980	1979	1980
Present	12.6 (0.6) −20%	9.9 (0.6) −40%	10.3 (0.8) −35%	12.1 (0.9) −28%
Absent	18.5 (0.8) +17%	13.4 (0.7) −20%	15.8 (0.8) Control	16.8 (0.6) Control

Harris (1980) records that *Urophora* densities of 1.9/spotted knapweed flower head reduced seed production by 67%. In 1980 the mean density of *Urophora* at the Westwold site was a little over 1/head and the density of *Metzneria* approximately 0.5/head. The combined reduction in seed numbers in attacked heads was approximately 40%, which is slightly below the total seed reduction in an area with a well-established *Urophora* population. These data indicate that two insects aren't greatly better than one.

At the White Lake area near Penticton three introduced insect species are now established on diffuse knapweed, *U. affinis*, *U. quadrifasciata*, and *S. jugoslavica*. In September 1981, samples of plants were collected to determine the level of attack of *Urophora* and *Sphenoptera*. Generally only one *Sphenoptera* larva develops in the root of the plant and previously-attacked plants can easily be identified from the damage. *Urophora* attack was determined by sampling five distal seed heads on the plants. The level of attack by *U. affinis* was the same in plants attacked by *Sphenoptera* and unattacked plants (Table 3). However, attack by *U. quadrifasciata* was significantly lower on plants attacked by *Sphenoptera*.

The density of *Urophora* at this site was 1.63 larvae/head (SE = 0.30) based on a count of all the seed heads of 23 plants. This is high as compared to previously sampled populations of *Urophora* on diffuse knapweed in B.C. and considerably higher than European densities (Myers and Harris 1980). The influence of insect attack was assessed by the proportion of total buds which developed to produce seed heads. In 1981 the actual number of developed heads was not reduced on plants attacked by *Sphenoptera*, 45.5 (*SE* = 4.9) for attacked plants and 35.1 (*SE* = 3.9) for unattacked plants, and the proportion of heads developed on attacked and unattacked plants was the same (Table 3). However when *Urophora* attack was considered, the proportion of seed heads which developed on plants attacked by *Sphenoptera* was actually greater for plants with a high level of *Urophora* attack (> 10 larvae in 5 distal heads) than in plants with a low level of *Urophora* attack (Table 4). This was not the case for plants unattacked by *Sphenoptera*.

Number of Agents in Successful Control Programs

In Julien's (1982) review, 26 weed species were recorded as having been successfully controlled. The average number of insect species introduced in each of these successful projects was 4.1 and the success rate of establishment was approximately 70% (2.8 insect species/plant). Eighty-one percent of the successes were attributed to a single species. In four cases success was attributed to two insect species, with *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) and *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae) being involved in two of these examples. A single case in which success was attributed to three insect species also involved the control of cactus with *Cactoblastis* and *Dactylopius*, but a cerambycid beetle was also thought to have contributed to control.

Table 3. Mean number of *Urophora* larvae (SE) in five distal seed heads of diffuse knapweed plants attacked by *Sphenoptera* and unattacked plants.

	Sphenoptera	
Urophora sp.	Attack	No Attack
U. affinis	9.9 (1.2)	9.3 (1.3)
U. quadrifasciata	0.9 (0.4)[1]	2.8 (0.8)[1]

[1]Means significantly different with a T-test ($P<0.05$).

Discussion

I conclude from the study of knapweed that the influence of several insect species attacking plants in the same vicinity varies from being slightly complimentary (two *Urophora* species) to making little difference (*Urophora* and *Metzneria*) to possibly being slightly deleterious (*Urophora* and *Sphenoptera*). The ability of plants to compensate for insect damage contradicts the assumptions of a simple cumulative model for insect attack. A little insect attack may stimulate plants rather than stress them. Knapweed cannot be considered to be successfully controlled in British Columbia at this time, even in sites where several insect species are well established.

The history of biological weed control indicates that a single species of insect most frequently is sufficient for successful control. This would indicate that only some insects are capable of reducing the density of their food plants. The challenge is to identify these species for introduction.

If biological control successes are achieved by the chance introduction of an effective species in the appropriate location, we might think of success in terms of a lottery model rather than a cumulative stress model as proposed by Harris (1985). With every introduction comes the possibility of success. Once the successful agent becomes established it will largely displace the other agents. Different agents may be successful in different environments, and successful control may only be achieved in certain environments.

It remains a question if successful agents can be selected in a manner to change the odds in the lottery. The example of *Chrysolina hyperici* (Forster) and *C. quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) shows that two very closely related insect species can vary in their ability to control *Hypericum* (Clusiaceae) even though they are very similar in their life cycles and the damage they do to plants (Williams, Myers and Edwards, unpubl. data). The important difference seems to be that the environment which selects for a preponderance of *C. hyperici* also is conducive to *Hypericum* seedling establishment. The reproductive pattern of the plant is the factor which determines the success of the biological control agent, not the characteristics of the agent itself.

Successful biological control programs show that insects can control the density of their food plants. The experimental removal of insect herbivores from native weed populations may be very helpful in identifying plants with potential for successful biological control.

It may be of little importance to the mechanics of biological control whether the cumulative stress or lottery model pertains. But preconceived notions can influence how data are collected and interpreted. We should avoid the assumption that all established species contribute to the control of a particular weed.

Table 4. Mean proportion (SE) of seed heads developed on plants attacked by *Sphenoptera* and unattacked plants with high and low *Urophora* attack.

Mean *Urophora*/head	Attacked by *Sphenoptera*	Unattacked
<10	0.38 (0.03)[1]	0.42 (0.07)
>10	0.51 (0.04)[1]	0.47 (0.05)

[1]Values significantly different from each other (P<.05, T-test).

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