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The Biological Control of *Centaurea* spp. in North America: Do Insects Solve the Problem?*

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Abstract: Spotted and diffuse knapweed, *Centaurea maculosa* Lam. and *C. diffusa* Lam., both of European origin, are two of the most important rangeland weeds in North America. Surveys for potential biological control agents started in 1961, and agents were first introduced in 1970. So far, 11 phytophagous insect species of European origin have been released in North America. Despite legislation (restricted transport), large-scale application of herbicides and reductions in seed production of up to 95% by the existing seed-feeding biocontrol agents established, knapweed infestation has further increased during the last decade, covering nearly 2·8 and 1·3 million ha for spotted and diffuse knapweed, respectively. In this paper, the biocontrol programme is reviewed critically and the present status analysed. To reach a break-through in knapweed control, a cumulative stress approach is now envisaged, by extending the stress imposed by the biocontrol agents to increasing competition by the other vegetation through grazing regimes and reseeding programmes. Four steps to optimize the biocontrol effect and which lead to the integration of biocontrol into range management are described and suggestions, both scientific and political, are presented to render biological control more efficient and predictive.

1 INTRODUCTION

Biological control of weeds is the deliberate use of herbivorous organisms and pathogens to reduce the population density of a target species below its economic injury level. We would like to emphasize this definition, because the term has been used recently for other non-chemical weed control methods, including grazing management, crop rotation, genetic engineering etc.

The *Centaurea* species targeted for biological control in North America are spotted knapweed (*C. maculosa* Lam.), diffuse knapweed (*C. diffusa* Lam.), yellow starthistle (*C. solstitialis* L.), Russian knapweed (*C.* (*Acroptilon*) *repens* L.) and squarrose knapweed (*C. virgata* Lam. ssp. *squarrosa* Gugler).[1] Some of the insects approved for release against these more serious weeds (particularly the first three) also attack purple starthistle (*C. calcitrapa* L.), cornflower (*C. cyanus* L.) and meadow knapweed (*C. jacea* × *nigra*).[1] All of these *Centaurea* species are introductions from Eurasia, as there are no native *Centaurea* spp. in North America (the native *C. americana* and *C. rothrockii* should be treated as *Plectocephalus americanus*).[2,3] This paper considers only spotted and diffuse knapweed, two of the most important rangeland weeds in Western Canada and the northern USA. The biological control of both species is being realized by the 'classical' approach, i.e. by the introduction of exotic agents from the weeds' native area for permanent suppression of the weed populations.

The evaluation of such 'classical' biological weed

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control projects and the understanding of underlying mechanisms pose a great challenge to ecologists as, compared with the use of chemical or biological herbicides, changes in weed density do not depend primarily on the impact of the agents released on individual plants. More important is the impact on succeeding generations and, hence, their establishment rate and population development.

Although biological weed control started nearly 200 years ago, the number of projects has particularly increased during the past 25 years, and over 17% of the total 729 releases of exotic invertebrates were carried out during the past five years.[1] The results are variously described as 'a few unequivocal and spectacular successes',[4,5] and, 'a fair number of qualified successes'[6] or 'a large number of disappointments',[4] the rating varying with the compiler.

2 EVALUATION OF SUCCESS IN BIOLOGICAL WEED CONTROL

Success in biological weed control is measured in terms of the degree to which target weed density is reduced below its pre-release equilibrium. In principle, it should be straightforward to estimate pre-release and post-release weed densities, but in practice assessments are generally not sufficiently accurate to demonstrate control success. Success also depends upon land quality, its value before the weed became a problem and prior to control attempts.[4] In addition, the validity of ascribing reduction in weed abundance to herbivore activity can be challenged since we do not know what the behaviour of the system would have been without herbivores. The assessment of herbivore impacts is generally masked by abiotic factors, particularly disturbance and rainfall, which vary between years and which may, by determining recruitment of seedlings, lead to substantial local population fluctuations.[7]

A further problem lies in attributing a continued, stable weed reduction to the action of the introduced agent(s). Many ecological factors, such as increase in perennial plant cover, may change following successful weed control, so that post-control dynamics of the target plant may be radically different from those that prevailed before introduction of the insect. It cannot, therefore, be expected that weed density would return to its former abundance if the control agents were to be excluded by insecticides. However, this would represent an appropriate test to indicate causality between density decline of the weed population and the effect of the introduced agents.[8] Interspecific plant competition, for example, may well play a major role in reducing recruitment of the weed following successful control. On the other hand, a continuous insect–plant interaction, with the herbivore and the weed populations both being at a stable, low density equilibrium, may not exist. Successful agents may cause local extinctions of the weed, creating a spatial mosaic of variable agent/weed assemblages ('hide and seek dynamics').[9] It is therefore not surprising that successful agents in one region produced failures in other regions.[4] Hence, predicting success before introductions, as well as success ratings of biological weed control projects, will remain subjective, until we understand better the ecology of weed biological control.

During the past five years comprehensive data bases on biological weed control projects have been set up[1,10] and several analyses have been published recently to determine attributes of plants and biological control agents associated with good control success.[4,9,11-13] In our analysis, we will be concerned mainly with ecological aspects of success, as recent economic factors are not available. According to Julien *et al.*[11] the overall success rate of biological weed control programmes is 39%, and *c*.48% of all target weeds have been controlled in at least one project. Crawley[4] lists about one in six cases giving satisfactory control. Although preparation of benefit/cost ratios is a complex task and open to various criticisms, a 200:1 benefit/cost ratio was calculated for the *Chondrilla juncea* L. project, a 10·5:1 to 48:1 for the *Echium* project and a 56:1 ratio for the *Salvinia molesta* Mitchell project. These values compare favourably to those of 4:1 and 5:1 commonly suggested for herbicides (cf. Ref. 14 and references therein).

In the following, we shall try to evaluate the outcome of a 30-year programme (20 years since the first agent's introduction) on the biological control of two rangeland weeds in North America. First, we shall briefly describe the problem and summarize non-biological control attempts and secondly, provide a brief review of the project and assess the present status of the agents. Thirdly, the question asked in the title will be considered. Finally, potential future strategies will be discussed and possibilities for rendering classical biological weed control more effective will be considered.

3 THE PROBLEM: KNAPWEEDS INTRODUCED FROM EUROPE TO NORTH AMERICA

3.1 Invasion, present distribution and forage reduction

Spotted and diffuse knapweed, a short-lived perennial and a biennial respectively, are both of Eurasian origin and were accidentally introduced into North America in the early 1900s. Groh[15] reported that diffuse knapweed was first recorded in Washington State in 1907, from where it spread into British Columbia. Spotted knapweed was first collected in North America at Victoria, British Columbia in 1883 and in the USA in 1935 in Montana. Groh[16] provides evidence that both species may have been introduced with alfalfa seeds from Turkestan. Both

TABLE 1
Infestations by *Centaurea maculosa* and *C. diffusa* Reported from Eight American States and one Canadian Province in 1988 (only Sites with Estimated Forage Reductions above 5% are Included; Adapted from Lacey[23])

State/Province	*Area (ha × 10⁴) infested by*	
	C. maculosa	C. diffusa
British Columbia (estimated)	1·01	3·04
Washington	1·18	17·31
Montana	191·05	0·42
S. Dakota	0·10	0·04
Oregon	0·12	48·56
Idaho	92·79	58·68
Wyoming	0·004	0·20
Utah	0·02	0·001
Colorado	1·01	1·21
Total (ha × 10⁴)	287·28	129·46

weeds have subsequently become important rangeland weeds in south-western Canada and the north-western United States[17] (cf. Refs 17–20 for further details on the invasion history, taxonomy and biology of the two knapweed species).

Harris and Cranston[21] reported that the two weeds had infested approximately 30000 ha of dry grassland in Canada by 1972, mostly in British Columbia, with forage reductions of up to 88%. When only reductions in hay production were considered, they calculated an annual loss of $350000 for the area infested in British Columbia in 1972. These authors further estimated that approximately 10 million ha were susceptible to invasion by the two weeds, with a potential annual loss to Western Canada of about $58 million (corresponding to 2·5 million tonnes per year of dry native pasture species). In 1976, minimum costs of initial chemical treatment of the infested 30000 ha in British Columbia would have been $900000, and $204000 was actually spent in 1976 by various agencies in that province just for knapweed containment. Despite spot-treatment, containment, and large-scale-herbicide programmes, the infested area has continued to increase. These figures compared favourably with an estimated total cost of $1.8 million for a biological control project, comprising the introduction of six control agents.[21]

The Third Knapweed Symposium was held in 1988 to determine the status of the knapweed problem and to identify new control programmes.[22] The number of states/provinces reporting infestations of spotted and diffuse knapweed, as well as the total area infested, had further increased between 1978 and 1988 (135% for spotted knapweed, and 54% for diffuse knapweed),[23] with spotted knapweed covering more than twice the area of diffuse knapweed, and occurring predominantly in Montana (Table 1). Only Alberta reported reduced infestations during the last decade as a result of a severe eradication programme started in 1980.[24]

Disappointingly, these figures contrast markedly with the enormous increase in control efforts during the past decade: several states have passed legislation to reduce the spread of knapweed in seed and hay, and intensive educational programmes on the knapweeds were initiated. In addition, knapweed received a higher priority from extension specialists and research scientists (from 14·9% in 1978 to 24·2% in 1988) and the number of full-time state employees involved with knapweed increased nearly fourfold.[23]

3.2 Chemical control

Commonly recommended herbicides to control spotted and diffuse knapweed selectively in grass include auxin-like growth regulators, such as the benzoic acid-type dicamba, clopyralid and picloram, and the phenoxy acid 2,4-D. On uncultivated soil, glyphosate is also being used.[25,26]

A study by Fay *et al.*[26] showed that annual applications of 2,4-D are necessary to provide satisfactory control of spotted knapweed, dicamba needs to be applied every two to three years, and picloram only every three to four years. Clopyralid gives long-term control similar to that by picloram and both are relatively selective and of minor impact on the native grassland species.[27,28] Beside the limited longevity of control, the use of these herbicides has a further constraint in that reseeding grass after herbicide application is problematic, as some grass species are susceptible to these herbicides during their early development.[29] Future large-scale application of picloram will not be permitted due to the risk of groundwater contamination, but could be reconsidered after new slow-release formulations have become available.[25] In addition, picloram-resistant *C. solstitialis* strains have been detected recently.[30] According to Fay,[25] new chemicals for knapweed control cannot be expected within the next ten years due to the relatively small market (see above). To summarize, aerial treatment is only justified in terms of increased yield on good quality range, whereas treatment of large areas with a persistent, broad-spectrum herbicide is generally not economic and ecologically highly undesirable. Spot application is very costly and only reasonable in case of small local infestations to prevent further spread.[25]

Recently, Stierle *et al.*[31] discovered the black leaf blight fungus *Alternaria alternata* Lam. on spotted knapweed, isolated a phytotoxin (maculosin, a dipeptide) from this native fungus, and synthesized the toxin in the laboratory. Maculosin seems to be highly toxic only to spotted knapweed, suppressing growth of seedlings and rosettes, but some biotypes seem to be resistant. Further research to determine field efficacy is being carried out currently.[32]

3.3 Cultural control

Neither knapweed persists under cultivation, but much of the knapweed-infested area consists of rough terrain, which is not cultivated.[18]

Nitrogen fertilization as a cultural approach to suppress knapweeds was recently studied by Story *et al.*[33] They found that nitrogen fertilization cannot be recommended, as it promotes spread of knapweed when used in some of the plant communities normally associated with spotted knapweed on rangeland in western Montana.

Grazing and reseeding programmes will be discussed below.

4 THE BIOLOGICAL CONTROL APPROACH

4.1 A brief review of the project

4.1.1 The European side: surveys, screenings and introductions

Between 1961 and 1964, surveys on both target species were carried out in France, Switzerland, southern Germany and eastern Austria.[34] From 1965 onwards, surveys were extended to eastern central Europe (Slovakia, Hungary) and the Balkans (former Yugoslavia, northern Greece, western Turkey, Bulgaria, Romania). Although the main distribution areas could not be surveyed for both species,[35] a total of two mites and 49 insect species were found to attack spotted and diffuse knapweed.[36] Of these species, one mite and 34 insect species were found on *C. diffusa* and two mite and 34 insect species on *C. maculosa*.

General field surveys were terminated in 1971. By this time the life history of 12 species had been studied and the host range of ten species screened. In view of the prolific seed production of the two target weeds (e.g. 36000 seeds m^{-2} at Chase, British Columbia, for spotted and 25000 seeds m^{-2} at Neds Creek, British Columbia, for diffuse knapweed),[37] the first potential control agents selected for study and screening (1967–71) were the seed-head-attacking species *Urophora affinis* Frfld. (released 1970), *U. quadrifasciata* Meigen (1972) (Dip.: Tephritidae) and *Metzneria paucipunctella* Zeller (1973) (Lep. Gelechiidae), followed by *Sphenoptera jugoslavica* Obenb. (1976) (Col.: Buprestidae), a root-mining species (Table 2).

When it became apparent that seed-head-infesting insects had only a limited potential for reducing weed density (Harris, P., 1992, pers. comm.), a detailed investigation of the complex of rosette- and root-feeders was initiated in 1978 by the International Institute of Biological Control (IIBC). Between 1979 and 1983, this investigation was carried out at 37 sites in eastern Austria, Hungary, Bulgaria, Rumania and Switzerland.[35,38,39] As a result, an additional four root-feeding species were selected for release in North America: *Agapeta zoegana* L. (released 1982) (Lep.: Cochylidae), *Pelochrista medullana* Zeller (1982) (Lep.: Tortricidae), *Pterolonche inspersa* Stgr. (1986) (Lep.: Pterolonchidae) (studied by the United States Department of Agriculture, USDA) and *Cyphocleonus achates* (Fahr.) (1987) (Col.: Curculionidae) (Table 2).

In 1991, introductions were made of three additional seed-feeding control agents, two tephritid flies, *Terellia virens* Loew. and *Chaetorellia acrolophi* White, and the weevil *Larinus minutus* Gyll., all of which were studied by the IIBC and first released in Canada in 1992 (Groppe, K., 1992, pers. comm.).

4.1.2 The North American side: establishment, spread and present status of the control agents

The biological control programme against the two knapweeds began in Canada in 1970 (British Columbia) and in the USA (Montana, Oregon) in 1973, with the introduction of the European seed-head fly *U. affinis*. Until the early 1980s this fly was the only biocontrol agent established throughout the Pacific Northwest.[40] The combined attack of *U. affinis* and *U. quadrifasciata* reduced seed production by up to 80–95%, but did not influence knapweed density, because a sufficiently large number of seeds remained for replacement.[40] The situation did not change with the establishment of *S. jugoslavica*, although, at high densities, the beetles reduce survival of seedlings and rosettes, delay reproduction and eventually reduce seed output. Under favourable conditions, the beetle can contribute to a significant reduction in knapweed population growth[41] but, unfortunately, great fluctuations in beetle populations result in only isolated effects on knapweed populations.[41] Of the four root-feeders introduced after 1982, currently only *A. zoegana* is thoroughly established in British Columbia and Montana, with high rates of rosette attack at a few sites and first signs of reduction in knapweed densities (Harris, P., 1992 and Story, J., 1992, pers. comm.). Hence, only a decade ago, new and very promising agents have been introduced, and their population increase, redistribution and spread has only occurred in the past few years (Table 2). Detailed analyses of the impact and joint occurrence of the agents have recently been reviewed by Müller,[35] Story,[40] and Harris.[42]

If all agents listed in Table 2 were released, a total of 11 and 10 insect control agents will have been introduced against spotted and diffuse knapweed, respectively. The pool of suitable biological control agents for spotted and diffuse knapweed is practically exhausted. Therefore, it is

TABLE 2
Release, Establishment and Present Status of Biological Control Agents Introduced for Spotted and Diffuse Knapweed in North America

Biological control agent	*Main host*[a]	*European studies*[b]	*First release Canada*	*First release USA*	*Establishment, effect and present status*
Widely established insects					
Urophora affinis Frfld. (seed-head gall fly)	S/D	IIBC	1970	1973	Well established on both plants throughout the Pacific Northwest, causing seed reductions in the range of 50 to 95%; *U. quadrifasciata* disperses faster, but *U. affinis* is the more consistent colonizer and the dominant species, where the two flies coexist
Urophora quadrifasciata Meig. (seed-head gall fly)	S/D	IIBC	1972	1980 (spread from (B.C.)[c]	
Metzneria paucipunctella Zell. (seed-head moth)	S	IIBC	1973	1980 (spread from B.C.)	Now widely distributed; although up to 63% of the flies are destroyed, seed production is further reduced when the moth is present
Sphenoptera jugoslavica Obenb. (root-gall beetle)	D	IIBC	1976	1980 (coll. in B.C.)	1991: redistributed to 5500 sites in B.C., with establ. rate of 55–96%; locally, 55% of plants attacked, resulting in decline of rosette density
Locally established agents					
Agapeta zoegana L. (root moth)	S	IIBC	1982	1984	B.C.: 200 release sites with establ. rate of 48–60%; local attack rates of 85%; Montana: establ. at 14 sites in 1991 (suited especially for moister sites)
Pelochrista medullana Zell. (root moth)	S/D	IIBC	1982	1984	Small population establ. in B.C., but no establ. in the USA; due to difficulties in locating the moth in Europe, new intr. only in 1991
Pterolonche inspersa Stgr. (root moth)	S/D	USDA/ IIBC	1986	1986	Small cage population in B.C., but yet no establ. population in the USA, especially suited for dry sites
Cyphocleonus achates (Fahr.) (root weevil)	S	IIBC	1987	1988	B.C.: small establ. cage population, of which 1000 adults were redistr. in 1991; Montana: well establ. at 2 sites, 1400 adults redistr. in 1991
Puccinia centaureae var. *diffusae*	S	By accident	1988 (found in B.C.)	.	Pustules are also found on safflower, but risk to safflower production is assumed to be minimal
Newly introduced agents					
Larinus minutus Gyll. (seed-head weevil)	D	IIBC/ USDA	1991	1991	Feeds on soft developing seeds
Terellia virens Loew. (seed-head fly)	S	IIBC	1992	1992	Feeds on soft developing seeds
Chaetorellia acrolophi White (seed-head fly)	S	IIBC	1992	1992	Feeds in the ovaries
Agents recommended for introduction					
Larinus obtusus (seed-head weevil)	S/D	IIBC	1993	1993	Feeds on soft developing seeds
Bangasternus fausti (seed-head weevil)	D	USDA	not to be released	1992	May affect performance of *U. affinis*
Aceria centaureae (leaf-gall mite)	D	USDA		1993	Blister galls on areal parts of rosettes and bolting plants, causing death to small rosettes or reduced plant growth and seed prod.
Promising agents yet to be screened					
Isoculus minutus (seed-head gall wasp)	S/D	USDA?			Last promising agent to be screened

[a] S, spotted knapweed; D, diffuse knapweed.
[b] IIBC, International Institute of Biological Control, Switzerland; USDA, United States Department of Agriculture.
[c] B.C., British Columbia, Canada.

not planned to investigate additional potential insect control agents.

In the early 1980s, research was begun at Montana State University with *Sclerotina sclerotiorum* de Bary as a possible mycoherbicide for knapweed control. *S. sclerotiorum* is a well-known plant pathogen with a very broad host range, which includes major crops,[43] and was detected on the two knapweeds in the early 1970s.[44] Through mutation under ultra-violet light, constraints could be placed successfully on this fungus for (a) exotic food requirements, and (b) for a limited ability to spread and survive.[45] Further laboratory studies are needed, however, before field application can be considered (Sànds, D., 1992,. pers. comm.).

5 DO INSECTS SOLVE THE PROBLEM?

According to Harris,[42] the objective of the knapweed control programme is to achieve < 5% knapweed cover on rangeland, which is the situation in the assumed area of origin of the two weeds, the former USSR. At the present time, this level of infestation has clearly not been reached. Moreover, overall knapweed density has increased in the Pacific Northwest during the past decade (see above).

Much of the knapweeds' success in North America has been due to the lack of stress-causing natural enemies which has enabled the plants to out-compete other vegetation. The spread was further enhanced by prolific seed production and selective overgrazing. Clearly, the biological control project against knapweeds has been initiated simply because all other means of weed control have failed (see above). According to biological control theory, these two weeds have attributes of plants difficult to control biologically, particularly spotted knapweed with its perennial growth form and its high potential for regrowth.

Initial funding, and hence effort involved, was very restricted during the first phase of the project. After struggling for nearly 20 years, only recently has the stage been reached where the 'total package' of biological control agents—proposed by Harris and Cranston in 1979[21] for effective biological control—is being implemented. In other words, a spectacular impact can hardly be expected at the present time, since biological control can only now be fully implemented.

To reach a break-through in knapweed control, it is now generally agreed, that besides containment and efforts in propagation and redistribution of biocontrol agents, particularly of the root-feeders, special emphasis should now be given to grazing regimes and programmes for reseeding of forage species to increase grass competition and cover bare ground patches, after knapweed populations have been depressed.[20,43] This strategy is briefly described below.

6 THE FUTURE STRATEGY

6.1 Public awareness, containment and redistribution of agents

Weeds respect no boundaries. Maintaining a high level of public awareness and communication is most important for successful knapweed control.[46] Emphasis should be placed particularly on protecting as yet uninfested grassland, as prevention is the cheapest control method. Public educational programmes are well established in Montana and British Columbia and contribute largely to successful containment programmes.[23] With regard to biological control, main efforts are currently being placed on extending propagation facilities and coordinating redistribution programmes. As outlined above, biological control can be expected to be successful only if a set of agents is well established at high population densities over large areas. At present, Agriculture Canada, British Columbia Ministry of Forests, British Columbia Ministry of Agriculture, Montana Department of Natural Resources, USDA-CSRS (Cooperative State Research Service), USDA-ARS, USDA-APHIS, and various universities are all involved in the knapweed project. Four agencies are currently redistributing knapweed insect biocontrol agents in Montana. Coordination, especially with range management and spraying programmes, demands, however, great efforts of all agencies involved (Story, J., 1992, pers. comm).

6.2 The cumulative stress approach in biological weed control

The question of whether the introduction of a single species of natural enemy or a range of control agents is likely to provide better weed control has been debated recently for the knapweed programme by Harris[47] and Myers.[48] Harris introduced the cumulative stress model to biological control of weeds, the hypothesis being that damage to the weed increases with the number of organisms attacking it.[27] Myers' suggestion is to try new agent species until a successful one is found. This will then largely displace the previous ones and mainly contribute to an eventual control success. No case is known, however, where the release of multiple species has ever led to the replacement of an economically effective species by one which is economically less effective, and hence, reduced the effectiveness of a biological control programme.[49,50]

6.2.1 Exploiting feeding niches within plant organs

Harris[5,6,42] applied the cumulative stress approach to knapweed capitula. During the first phase of the project, mainly flower-head-infesting insects were selected as control agents due to their ready availability, ease of handling and apparent reduction of the prolific seed production of the two knapweeds. Flower-heads are highly structured mini-ecosystems, disposing of a variety of niches, differing both in space (tissue structure) and time (developmental stage). The feeding strategy, coexistence and impact of insects in spotted knapweed capitula has been analysed in detail recently by Harris.[6] When all available control agents are established, most of these niches will be occupied by control agents (Table 3). Field studies carried out in Montana have already shown that the combined presence of the two fly species, *U. affinis* and *U. quadrifasciata*, and the moth *M. paucipunctella* significantly reduced seed production in attacked seed heads below the level caused by the two fly species alone.[51]

The tap-roots of the two knapweeds also consist of specific tissue structures (food niches) which are exploited by a different set of insect herbivores.[35,39] After successful establishment of the root-feeding agents released so far in North America, most of these niches will also be occupied (Table 3). Investigations to study interactions

TABLE 3
Feeding Strategies of Knapweed Biological Control Agents (Adapted from Harris[12])

Developmental stage	*Main host*[a]	*Gall former*	*Main host*[a]	*Non-gall former*
Capitulum-Feeders				
Immature bud		Woody gall		Receptacle feeder
	S/D	*Urophora affinis* Frfld.	S/D	*Bangasternus fausti*
Floret growth		Ovary gall		Ovule feeder
	S/D	*Urophora quadrifasciata* Meig.	S	*Chaetorellia acrolophi* White
Achene growth		Achene gall		Soft achene feeder
	S/D	*Isoculus minutus*	D	*Larinus minutus* Gyll.
			S	*Terellia virens* Loew.
			S/D	*Larinus obtusus*
Ripe achene		Not applicable		Achene feeder-predator
			S	*Metz. paucipunctella* Zell.
Root-Feeders				
Rosette plants/		Central meristem	S/D	Central meristem
Bolting plants	S	*Cyphocleonus achates* (Fahr.)		*Pterolonche inspersa* Stgr.
	D	*Sphenoptera jugoslavica* Obenb.		
Rosette plants/		Root-cortex		Root-cortex
Bolting plants		Not applicable	S	*Agapeta zoegana* L.
			D	*Pelochrista medullana* Zell.

[a] S, spotted knapweed; D, diffuse knapweed.

between root-feeding species on spotted knapweed and their impact on plant performance demonstrated that joint occurrence of the root-weevil *C. achates* and the root-moth *A. zoegana* on a single plant further reduced seed output below the level achieved by either of the agents alone.[52]

6.2.2 *Seed-feeders versus root-feeders*

Herbivores associated with different plant tissues and attacking different phenological stages of the host plant may exert greatly different effects on plant performance and on the subsequent population development.[53,54]

Seed production has been used as a measure to monitor the impact of the seed-feeders established so far. At a site in British Columbia, seed production of spotted knapweed has steadily declined from 40000 seeds m^{-2} in 1974 to 108 in the dry summer of 1987, 1600 in 1988, 7200 in 1989 and 3303 in 1990.[5] This is slightly over the threshold of 1500 seeds m^{-2} suggested by Roze,[55] needed for population maintenance. Similarly, total seed production of diffuse knapweed has declined from about 33000 seeds m^{-2} in 1978 to 2038 in 1987, 598 in 1988, 478 in 1989 and 1240 in 1990,[42] which is also suggested to be slightly above the replacement level.[41]

Reductions in seed output, however, will only lead to reduced weed density if seedling recruitment is seed-limited. Populations of both knapweeds were found to be regulated by density-dependent seedling mortality.[55,56] Powell[57] recently developed a population model for diffuse knapweed, based on functional forms of density-dependent birth and death rates. The model indicates that the population dynamics are well buffered from reductions in seed output and predicts an equilibrium density of approximately 70 rosette plants m^{-2}. Rosette mortality, on the other hand, was found to be only weakly density-dependent. This suggests that biological control agents that kill rosettes would be most effective, since little compensation would occur following increased rosette mortality. Experimental removal of rosette plants, however, did not confirm this prediction, as rosette removal in spring significantly increased seedling survival during the summer.[58] Moreover, reduced rosette density produced larger rosettes with increased fecundity (density-dependent fecundity).[55,56] It is important to keep in mind that all these studies had to be conducted at sites where biological control agents are currently established, which is generally in pure, or nearly pure, knapweed stands. However, the effect of the control agents, especially of the root-feeders, is greatly influenced by the presence of competing vegetation (see Section 6.2.4).

6.2.3 *Maximizing resource utilization of the knapweed populations*

Analyses of field surveys in Europe on the phytophagous insects infesting the flower heads of spotted and diffuse knapweed, showed a positive correlation between the infestation rate (percentage of infested flower heads) and the number of species present in a sample (population).[59] A similar positive correlation for root-feeding insects was found for the more stable and predictable habitats (such as those in the infested areas in North America), but not for disturbed, ephemeral sites, which are most numerous within the European areas surveyed.[35]

Hence, by gradually filling the feeding niches of these knapweeds, an increased overall resource utilization due to species-specific preferences for habitats and oviposition sites can be expected. From this point of view, the introduction of as many additional species as possible can be recommended. However, the number of control species co-existing at a site, the outcome of herbivore–species interactions and their joint effect on plant performance are difficult to predict and may vary from site to site.[35]

6.2.4 *Combining herbivory with plant competition to reduce weed densities*

By comparing data on the percentage of alien plant species in different terrestrial habitats in Britain, Crawley[50] found the average degree of plant cover to be best correlated with high invasibility in plant communities. Low plant cover, however, is typical for over-grazed range in North America and explains much of the weed problem in these habitats.[18]

Herbivores, even in relatively low densities, may be responsible for the outcome of competitive species interactions by tipping the balance in favour of the non-palatable species.[53,60] Biological control agents may act in this way when knapweed invades natural communities, or when management practices are applied that increase the competitive status of neighbouring plant species, such as reseeding of forage grass, special grazing regimes or herbicide treatments.[20]

There is general agreement that, in parallel to establishment and redistribution programmes of the agents, emphasis should now be placed on pasture management practices that increase grass competition without decreasing the effect of the biological control agents.[20,23,42,46]

According to Lacey,[23] a major change in management philosophy has occurred since 1978, when most research scientists reported minimal forage value for these knapweeds. The concept of using grazing animals (cattle and sheep) to manage large-scale infestations has been implemented on farms in Montana and Washington, with encouraging results.[61]

In 1979, Berube and Myers[62] re-examined diffuse knapweed plots in the dry interior of British Columbia, which were treated with picloram eleven years previously and then reseeded with either crested wheat-grass (*Agropyron cristatum* Gaertn.) or Russian wild rye (*Elymus junceus* Fisch.), to assess the potential of these grass species in suppressing invasions of diffuse knapweed. They found a high knapweed density in the non-seeded plots, moderate densities in Russian wild rye plots, and a very low density in crested wheat-grass plots. However, diffuse knapweed re-invaded a similar experimental area in a higher rainfall area of British Columbia. These findings, together with their results of watering experiments indicate that the same cultural practice will have different effects on knapweed populations under different climatic conditions. Recent experiments in British Columbia and Oregon to study the potential of reseeding forage species to compete with diffuse knapweed were also encouraging, but further showed the importance of selecting forage species best adapted to specific site conditions.[63]

We have recently carried out field and pot experiments to study single and joint effects of knapweed density, grass competition and root herbivory by the moth *A. zoegana* and the weevil *C. achates* on survival, resource allocation and seed output of spotted knapweed. Interspecific competition with *Festuca pratensis* Huds. was shown to have a predominant effect on both survival and seed output, and further increased the effect achieved by the root herbivores. The combined effect of competition and herbivory on plant survival was additive, but was less than might be expected from an additive model for seed output. Nevertheless, the combined effect of the two herbivores and competition with grass reduced seed output to less than 10% of that in 'unstressed' plants.[64–66] Under the generally poor soil conditions of the infested areas in North America, the main effect of most of the newly established root-feeders on knapweed density is, therefore, expected to be through reduced rosette survival. Infested plants die relatively late in the growing season and will be replaced mainly by grass, if present.[52] Hence, establishment of a competitive grass cover is most effective for both the reduction of knapweed density and the long term stabilization of its population by refilling the empty niches, once the knapweed population has declined. In other words, if land management practices are not changed, openings created in the plant community due to successful reduction in knapweed density will simply be filled by other, and possibly more serious, weed species.

6.2.5 *A complex problem needs a complex solution: integrating biological control into range management*

As has been outlined above, the success of knapweeds in North America has been favoured by a set of factors, including favourable plant attributes (high potential for regrowth, high seed output), lack of indigenous antagonists, selective overgrazing and human activities (transport, seeding by bee-keepers!). We believe that a multi-pronged strategy will be the only solution for knapweed control (Table 4). This will need a combination of proper grazing management, reasonable use of herbicides, effective biological control agents and increased public awareness and responsibility, as has also been suggested by Cranston,[46,47] Lacey[23] and Harris.[42]

Classical biological control and herbicide application are generally believed to be mutually exclusive. Phenoxy-herbicides, such as 2,4-D, however, have even been shown to stimulate the effect of certain insects, as protein synthesis, and hence, availability of nitrogen to the insect,

TABLE 4
Integrating Biological Weed Control into Rangeland Management: a Cumulative Stress Approach for Knapweed Control in North America (Steps Illustrate Increasing Stress, but Do Not Indicate Temporal Sequence)

Increasing stress on knapweeds	*Methods*	*Effect on knapweeds*
Occupying sensitive[a] feeding-niches of plant organs	Introduction and establishment of a set of control agents	Reduction of biomass and seed output
Occupying sensitive[b] plant organs and phenostages	Introduction and establishment of a set of control agents	Optimizing herbivore stress on knapweed performance (fitness)
Maximizing resource utilization in the knapweed population	Propagation and redistribution of all introduced control agents	Optimizing herbivore stress on the knapweed population
Combining herbivory with grass competition	Reseeding of selected forage grass species and selective grazing regimes	Intensifies biocontrol effect and refills openings in the vegetation, leading to local population decrease
Application of techniques for integrated rangeland management	Legislation (e.g. transport), judicious herbicide use and public awareness programmes	Reduction of further spread and large-scale decrease in knapweed density

[a] Sensitive to reduction in biomass and/or seed output.
[b] Sensitive to population change of knapweeds (cf. text).

is generally increased after application (see Ref. 6 and references therein).

In fact, Story *et al.*[68] found that it is possible to combine the two flies, *U. affinis* and *U. quadrifasciata* with applications of 2,4-D for control of spotted knapweed, provided that the herbicide is applied during the rosette stage in spring. Application at the flower-bud or flowering stage, however, was detrimental to *U. affinis*, and also not effective against spotted knapweed and cannot, therefore, be recommended. Interactions between grazing and biological weed control remain to be studied.

7 WHAT DID WE LEARN?

7.1.1 Biological control is partly political, as public agreement and funding have first to be conveyed before a scientific project can be started

Biological control (especially the classical approach) is akin to provision of a public facility. As only a small fraction of its economic benefits can generally be recouped by the providers (those who introduce and/or release the agents), public funding is needed, at least at the beginning of a project.

7.1.2 Basic studies on agent-plant interactions will result in fewer species introductions and more efficient species will be released first

The limited available knowledge of knapweed population ecology available suggests that, with little investment in experiments to detect the phenostage most sensitive to population change, root-feeders should have been proposed as the prime candidates for introductions. Furthermore, according to Harris,[42] only three of the seven niches presently occupied in the knapweed capitula account for most of the damage. Currently, each agent costs around $400000 to screen for release in North America.[42] In addition, the concern that introduced biological control agents may compromise the survival of endangered, native species has become more important in recent years, despite the excellent safety record of biological control. Hence, both from an economic and ecological point of view, only the most promising agents should be screened and introduced. In addition, at the beginning of a new project we strongly recommend studies on the weed's population ecology, in particular the identification of transitions in the life cycle to which population growth is most sensitive in the area of introduction.[35] Detailed field surveys and preliminary screenings in the area of origin of the weed can then be directed to such phenostage-specific organisms.

7.1.3 Base-line data are needed prior to the introduction of control agents

Because of resource limitations, a formal knapweed survey has not been accomplished in North America prior to agent introductions. The lack of such basic data at the starting point makes it difficult to monitor programme impact and greatly accounts for the paucity of quantitative data in biological weed control.

7.1.4 Propagation techniques and field nurseries should be set up as early as possible

The two knapweed species have a rather scattered distribution in their area of origin and only localized high-density populations occur.[36,39] The same holds true for the associated herbivores. For instance, inability to locate populations of the root moth *P. medullana* has prevented subsequent introductions, after a small population was established in Montana in 1984, and then died out. Tremendous progress in the knapweed project has been achieved during the past five years after establishment of propagation facilities and implementation of coordinated redistribution programmes. There is general agreement now that such propagation facilities should be installed in the area of introduction as early as possible.

7.1.5 Release of agents offers unique possibilities for ecological experiments

Release attempts represent some of the biggest and best field experiments ever carried out in ecology.[54] Special attention should, therefore, be given to hypothesis testing by releasing variable numbers, and different agent and genotype assemblages under various ecoclimatic conditions. Careful follow-up studies will be of primary importance for further development of risk assessment in future biological control projects and hopefully, will also render biological control more efficient.

7.1.6 The public needs to be involved in the decision about biological control

Classical biological control is done by government in the public interest regardless of property ownership; there may, therefore, be conflicts of interest such as beekeepers wanting to retain the knapweeds that rangers want to eliminate. In recent decades such conflicts have increasingly reached the legal and political arena. We strongly suggest that public responses need to be invited on proposed biological control programmes in order to reach a decision which is of common interest. The preparation of an FAO Code of Conduct for the Introduction of Biological Control Agents is at present under way.

7.1.7 Biocontrol projects need to be managed by an interdisciplinary consortium

Biological control projects require long-term research and should not be regarded as quick and cheap. A complete biological control programme is likely to require approximately 20 scientist years,[69] but concerted efforts will allow the completion of programmes within a reasonable time. Although those affected by weed problems know that they have a problem, they are hardly supportive for studies which quantify the problem in order to justify investment in biological control. Government departments that are concerned about the weed problem may be best placed to fund initial investigations, including studies on weed population ecology, as well as overseas exploration and preliminary screenings for host specificity. Harris,[42] in reviewing the knapweed projects, stated that the formation of a consortium of federal departments, provinces/states, universities and user groups is best suited to optimize funding, project management and political aspects, such as conflict of interest. By covering the different objectives of researchers, governments and users, a biological control project can be well designed and carried out.

7.1.8 Biocontrol has a great future

Biological control offers an environmentally friendly weed-control strategy, has an excellent track record for safety and can result in permanent ecological management of weed populations. We are convinced that biological control has reached an exciting stage where it may undergo major and rapid development; it will be the only practical solution for an increasing number of problems. Apart from providing a good tool for solving certain weed problems in an environmentally safe manner, successful biological weed control will also reduce the rate of herbicide application and the problems associated with it so that interest in biological control will increase because of increasing public concern about the large-scale application of herbicides and its potential environmental impacts.

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REFERENCES

1. Julien, M. H., *Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds*, 3rd edn. CAB International, Wallingford, 1992, 186 pp.
2. Jeffrey, D., *Kew Bull.*. **22** (1967) 107–40.
3. Dittrich, M., In *The Biology and Chemistry of the Compositae*, ed. V. H. Heywood, J. B. Harborne & B. L. Turner. Academic Press, London, 1977, pp. 999–1015.
4. Crawley, M. J., *Biocontr. News Inform.*, **10** (1989) 213–23.
5. Harris, P., *Canad. Entomol.*, **123** (1991) 827–49.
6. Harris, P., In *Proc. VII. Int. Symp. Biol. Contr. Weeds* (Rome), ed. E. S. Delfosse. 1st Sper. Patol. Veg. (MPAF), 1989, 37–45.
7. Myers, J. H., In *Proc. VIII. Int. Symp. Biol. Contr. Weeds* (Canterbury, New Zealand, 1992), ed. E. S. Delfosse & R. R. Scott. Melbourne, 1992, in press.
8. McEvoy, P. B., In *Proc. VI. Int. Symp. Biol. Contr. Weeds* (Vancouver, 1984), ed. E. S. Delfosse. Agriculture Canada, Ottawa, 1985, 57–64.
9. Crawley, M. J., *Phil. Trans. Royal Soc. London*, **B 330** (1990) 125–40.
10. Moran, V. C., In *Proc. VI. Int. Symp. Biol. Contr. Weeds* (Vancouver 1984), ed. E. S. Delfosse. Canadian Government Publishing Centre, Supply and Services Canada, Ottawa, 1985, 65–8.
11. Julien, M. H., Kerr, J. D. & Chan, R. R., *Protection Ecol.*, **7** (1984) 3–25.
12. Julien, M. H., *Biocontr. News Inform.*, **10** (1989) 299–306.
13. Hokkanen, H. & Pimentel. D., *Canad. Entomol.*, **116** (1984) 1109–21.

14. Watson, A. K., In *Proc. 1st Int. Weed Contr. Con.* (Melbourne, 1992), **1**, 64–73.
15. Groh, H., *2nd Annual Rep. of the Canadian Dept of Agric.*, 1943, p. 74.
16. Groh, H., *Sci. in Agric.*, **21** (1940) 36–43.
17. Harris, P. & Myers, J. H., In *Biological Contr. Progr. against Insects and Weeds in Canada*, ed. CAB International, Wallingford, 1984, pp. 127–37.
18. Watson, A. K. & Renney, A. J., *Canad. J. Plant. Sci.*, **54** (1974) 681–701.
19. Müller, H., In *Proc. VII. Int. Symp. Biol. Contr. Weeds* (Rome, 1988), ed. E. S. Delfosse. 1st Sper. Patol. Veg. (MPAF), 1990, pp. 181–90.
20. Müller, H. & Schroeder, D., In *Proc. Knapweed Symposium*. Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 151–62.
21. Harris, P. & Cranston, R., *Canad. J. Plant Sci.*, **B 59** (1979) 375–82.
22. Fay, P. K. & Lacey, J. R., *Knapweed Symposium*. (Bozeman, Montana), Montana State University, 1989.
23. Lacey, C., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 1–6.
24. Ali, S. In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 105–6.
25. Fay, P. K., *Knapweed Symposium*. (Bozeman, Montana), Montana State University, 1989, 235–6.
26. Fay, P. K., Davis, E. S., Chicoine, T. B. & Lacey, C. A., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 43–6.
27. McKone, M. B., Lacey, C. A. & Bedunah, D., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 83–7.
28. Durgan, B. R., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 119–25.
29. Fagerlie, D., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 220–1.
30. Lownds, N. K., Sterling, T. M. & Fuerst, E. P., *Plant Physiology* (Suppl.), **96** (1991) 78.
31. Stierle, A. C., Cardellina II, J. H. & Strobel, G. A., In *Proc. Natl Acad. Sci. USA*, **85** (1988) 8008–11.
32. Cuda, J. P., Sindelar, B. W. & Cardellina II, J. H., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 197–203.
33. Story, J. M., Boggs, K. W., Good, W. R. & Nowierski, R. M., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 172–4a.
34. Zwölfer, H., *Commonw. Inst. Biol. Contr. Tech. Bull.*, **6** (1965) 81–154.
35. Müller, H., *Oecologia*, **78** (1989) 41–52.
36. Schroeder, D., In *Proc. VI. Int. Symp. Biol. Contr. Weeds* (Vancouver), ed. E. S. Delfosse. Agriculture Canada, Ottawa, 1985, pp. 103–9.
37. Harris, P., *Zeit. Ang. Entomol.*, **90** (1980) 190–210.
38. Müller, H., Schroeder, D. & Gassmann, A., *Canad. Entomol.*, **120** (1988) 109–24.
39. Müller, H., Stinson, C. S. A., Marquardt, K. & Schroeder, D., *J. Appl. Entomol.*, **107** (1989) 83–98.
40. Story, J. M., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 37–42.
41. Powell, R. D. & Myers, J. H., *J. Appl. Entomol.*, **106** (1988) 25–45.
42. Harris, P., In *Range Weeds Revisited*, ed. B. R. Roche & C. T. Roche. Washington State University, Pullmann, WA, 1990, pp. 61–8.
43. Purdy, L. H., *Phytopathology*, **69** (1979) 875–80.
44. Watson, A. K., Copeman, R. J. & Renney, A. J., *Canad. J. Bot.*, **52** (1974) 2639–40.
45. Ford, E. J., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 182–9.
46. Cranston, R., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 7–9.
47. Harris, P., In *Proc. VI. Int. Symp. Biol. Contr. Weeds* (Vancouver, 1984), ed. E. S. Delfosse. Agriculture Canada, Ottawa, 1985, 13–26.
48. Myers, J. H., In *Proc. VI. Int. Symp. Biol. Contr. Weeds* (Vancouver, 1984), ed. E. S. Delfosse. Agriculture Canada, Ottawa, 1985, 77–82.
49. Cock, M. J. W., *Biocon. News Inform.* CAB International, Wallingford, 1986, **7(1)**, 7–16.
50. Crawley, M. J., *Trends Ecol. Evol.*, **2** (1987) 167–8.
51. Story, J. M., Boggs, K. W., Good, W. R., Harris, P. & Nowierski, R. M., *Canad. Entomol.*, **123** (1991) 1001–7.
52. Müller-Schärer, H., *J. Appl. Ecol.*, **28** (1991) 759–76.
53. Crawley, M. J., *Herbivory*. Blackwell Publications, Oxford, 1983, p. 437.
54. Crawley, M. J., *A. Rev. Entomol.*, **34** (1989) 531–64.
55. Roze, L. D., PhD thesis, University of British Columbia, Vancouver, BC, 1974, p. 208.
56. Myers, J. H., Risley, C. & Eng, R., In *Proc. VII. Int. Symp. Biol. Contr. Weeds* (Rome), ed. E. S. Delfosse. 1st Sper. Patol. Veg. (MPAF), 1989, 65–71.
57. Powell, R. D., *J. Ecol.*, **78** (1990) 374–88.
58. Myers, J. H., Risley, C. & Eng, R., In *Proc. VIII. Int. Symp. Biol. Contr. Weeds* (Rome 1988), ed. E. S. Delfosse. 1990, 67–74.
59. Zwölfer, H., In *Proc. VI. Int. Symp. Biol. Contr. Weeds* (Vancouver), ed. E. S. Delfosse. Agriculture Canada, Ottowa, 1985, 407–16.
60. Whittaker, J. B., In *Population Dynamics*, ed. R. M. Anderson, B. D. Turner & L. R. Turner. Blackwell Scientific Publications, Oxford, 1979, pp. 202–22.
61. Robertson, K., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., 1989, 33–6.
62. Berube, D. E. & Myers, J. H., *J. Range Manage.*, **35** (1982) 459–61.
63. *Knapweed Newsletter*, ed. B. F. Roché. Washington Interagency Knapweed Committee, **2** (1988) 3.
64. Müller-Schärer, H. & Steinger, T., In *Proc. VII. Int. Symp. Insect–Plant Relationship* (Budapest), ed. A. Szentesi. Akadémiai Kiadó, Budapest, 1990, 215–24.
65. Müller-Schärer, H., In *Populationsbiologie der Pflanzen*, ed. B. Schmid & J. Stöcklin. J. Birkhäuser Verlag, Basel, **17** (1991) 281–97.
66. Steinger, T. & Müller, H., *Oecologia*, **91** (1992) 141–9.
67. Cranston, R., In *Proc. Knapweed Symposium*, Plant and Soil Dept and Coop. Ext. Serv. Montana State Univ. Bull., **1315**, 1984, 4–7.
68. Story, J. M., Boggs, K. W. & Good, W. R., *Environ. Entomol.*, **17** (1988) 911–14.
69. Harris, P., *Weed. Sci.*, **27** (1979) 242–50.