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Europe as a source of biological control agents of exotic invasive weeds: status and implications

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This review catalogues the agent species which have been introduced directly from Europe into other continents for the biological control of weeds of European origin. 85 species belonging to 28 taxa have been used of which 53 became established. Diptera have the highest rate of establishment, followed by Coleoptera and Lepidoptera. 75% of the species released became established in the northern but only 55% in the southern hemisphere. 24% of failures in establishment are explained by climatic mismatching and predation but no reasons are given for 50% of all cases. Overall 12% of all agent species are considered effective control agents, and chrysomelids and curculionids are conspicuously more successful than other taxa.

Keywords: Europe, invasive weeds, biological control, coleoptera.

INTRODUCTION

Classical biological control of weeds is the deliberate use of specialized herbivores or pathogens to reduce and stabilize target plant density at sub-economic levels (e.g. SCHROEDER, 1992). Since 1928, Europe has been an important source of agents for the biological control of exotic invasive weeds of European origin in the northern and southern hemisphere, especially in the United States, Canada, Australia, and New Zealand. This review will focus on the releases of agents made in these four countries, since the number of biological control projects on European weeds in South Africa, Argentina, and Chile has been very limited. Several extensive reviews of the successes and failures in biological weed control projects worldwide have been published in the past few years (HOKKANEN, 1986; CRAWLEY, 1989a; JULIEN, 1989; LAWTON, 1990). They are all aiming to determine trends that might help raising success rates in future control attempts. The data for the present analysis is based on list A in the third edition of Julien's catalogue edited in 1992 which deals with exotic invertebrates and fungi that have been released up to the end of 1990 for biological control of weeds (JULIEN, 1992). A release (or introduction) in Julien's catalogue is defined as the year when the first release was carried out. Further releases are included only if the initial release failed or if material of subsequent releases was originating from a different source. Direct release means direct importation of agents from Europe into the country of introduction. Redistribution of agents from the first country of introduction into other areas is defined as indirect releases. Multiple direct releases means direct importation of agents from Europe into more than one country. Classical biological control of weeds is not a familiar topic in Europe, and no exotic herbivores have yet been introduced in Europe for biological control, with the exception of the chrysomelid *Zygogramma suturalis* FAB. against *Ambrosia artemisifolia* L. in the former USSR and Yugoslavia. This paper has two main purposes: 1) to review the important number

of European herbivores which have already been used in other continents against weeds of European origin; and 2) to try to draw some conclusions and find trends that might help selecting effective agents against temperate weeds in future projects.

THE ORIGIN OF WEEDS

The weed flora in North America and the Australian continent consists of a high number of European species which have been introduced either accidentally or deliberately during the past 200 years. Some 52% of the 516 weeds recorded in the inventory of Canadian weeds are of European and/or Eurasian origin (CROMPTON *et al.*, 1988), as are 71% of the 126 most common weed species in the same country, and only very few are native species (MULLIGAN, 1987) (Tab. 1). For obvious rea-

Tab. 1. Origin of weeds in Canada, Australia and State of Victoria

	No.weeds	Native	Origin of weeds (per cent)			
			Eurasia	America	Asia	Africa
Canada	516	40.3	52.3	3.9	2.7	0.4
Common weeds of Canada	126	2.4	71.4	24.6	1.6	0.0
Australia	637	6.9	39.1	25.6	7.2	18.2
State of Victoria	83	3.6	60.2	22.9	3.6	9.6

sons, Australian weeds are originating from various parts of the world. Only 7% of the 637 weed species recorded are native, and 39% are of European and/or Eurasian origin (SWARBRICK & SKARRATT, 1992). The percentage of European weeds reaches 60% in the State of Victoria, most of them being Mediterranean species (PARSONS, 1973). The large majority of the weed species concerned occur in non-crop land and thus are amenable to classical biological control. Up to the end of 1990, direct releases of biological control agents of European origin were made against 33 terrestrial weed species in 12 families (Tab. 2), of which some 50% are perennials species.

Tab. 2. Target weeds of European origin

Family	No. of species
Asteraceae	14 (42%)
Fabaceae	3
Boraginaceae	2
Euphorbiaceae	2
Polygonaceae	2
Rosaceae	2
Scrophulariaceae	2
Caryophyllaceae	2
Clusiaceae	1
Convolvulaceae	1
Labiatae	1
Zygophyllaceae	1
TOTAL	33

AGENT SPECIES ESTABLISHMENT AND SUCCESSFUL DIRECT RELEASES

Within 64 years, 71% of a total of 85 agent species which have been introduced directly from Europe into the United States, Canada, Australia, and New-Zealand became established (Tab. 3). These agent species correspond to 181 direct releases (Tab. 4). 29 of these are recent releases (usually made during the past 2-3

Tab. 3. Number of agent species established on weeds of European origin

	No. of species	Species establishment		
		yes	no	unknown
Coleoptera	35	22 (67%)*	11	2
Bruchidae	1		1	
Chrysomelidae	15	9 (64%)*	5	1
Curculionidae	16	10 (67%)*	5	1
Buprestidae	2	2		
Cerambycidae	1	1		
Diptera	20	14 (88%)*	2	4
Tephritidae	9	5	2	2
Cecidomyiidae	5	5		
Anthomyiidae	4	3		1
Syrphidae	1			1
Agromyzidae	1			1
Lepidoptera	21	10 (56%)*	8	3
Gelechiidae	1	1		
Cochylidae	2	2		
Tortricidae	2		1	1
Oecophoridae	1	1		
Noctuidae	3	1	2	
Sphingidae	1	1		
Lyonetiidae	1	1		
Pterolonchidae	1		1	
Geometridae	3	1	2	
Pyralidae	1		1	
Sesiidae	3		1	2
Arctiidae	1	1		
Gracillariidae	1	1		
Hemiptera				
Aphididae	1	1		
Thysanoptera				
Thripidae	1			1
Acari				
Eriophyidae	3	2	1	
Tetranychidae	1	1		
Fungi				
Uredinale	3	3		
TOTAL	85	53 (71%)*	22	10

* The percentage is calculated excluding the number of species of which the establishment is unknown.

years before the publication of the third edition of Julien's catalogue) and are still under evaluation. 64% of the remaining ones were successful and resulted in agent establishment. The rates of species establishment and successful releases were both higher for Diptera, followed by Coleoptera and Lepidoptera. Internally and externally feeding Lepidoptera have nearly the same rate of establishment in direct releases. This is in contradiction with the data obtained from a worldwide analysis (CRAWLEY, 1989a) which shows that external feeders, particularly Lepidoptera, have a poor rate of establishment. The rate of successful direct releases is significantly different between the northern hemisphere (68%; N = 107) and the southern hemisphere (44%; N=43) (Chi-square test; P=0.006). There is also a significant difference in species establishment between the northern and southern hemisphere, with 75% (N=77) and 55% (N=31) of species established, respectively (Chi-square test; P = 0.037) .

MULTIPLE DIRECT RELEASES

Greater difficulty to establish species of European origin in the southern hemisphere is also evident when considering species establishment after multiple direct releases. Because too few cases are documented, only Canada and the United States are being compared, as well as the northern and southern hemisphere, without further country-by-country comparison. 15 species succeeded both in Canada and the United States, and four failed. Most of the successfully released species were introduced in the same ecoregion, e.g. the prairies. The picture is different when comparing the northern and southern hemisphere. There have been seven multiple successes and one multiple failure – *Chrysolina varians* (SCHALLER) – but seven contrasting results: *Aphis chloris* KOCH succeeded in Australia but failed to establish in Canada; five species succeeded in the northern hemisphere, but failed in the southern hemisphere; finally, *Tyria jacobaea* (L.) established itself in the USA, Canada and New Zealand, but failed in Australia.

Tab. 4. Percentage of establishment after direct releases

	No. of releases	Establishment		
		yes	no	unknown
Coleoptera	86	46 (65%)*	25	15
Chrysomelidae	26	16 (62%)*	10	0
Curculionidae	36	24 (67%)*	12	0
Diptera	33	22 (79%)*	6	5
Lepidoptera	53	21 (48%)*	23	9
external feeders	27	12 (50%)*	12	3
internal feeders	26	9 (45%)*	11	6
Others	9	8 (89%)*	1	0
TOTAL	181	97 (64%)*	55	29

* The percentage is calculated excluding the number of releases of which the establishment is unknown.

INDIRECT RELEASES

60 cases of indirect releases are documented from countries where agents, directly released, became established. The rate of establishment is 73% and thus not much higher than that for direct releases. However, 91% of all the species involved succeeded at least once to become established after indirect introduction. Although 28 species have been involved in indirect introductions, almost half of the cases of establishment refer to only four species – *Rhinocyllus conicus* (FROELICH), *Longitarsus jacobaeae* (WATERHOUSE), *Chrysolina quadrigemina* (SUFFRIAN) and *Ch. hyperici* (FORSTER), – which also controlled their target weeds.

REASONS FOR ESTABLISHMENT FAILURES

Some 9% of the 55 failures in release establishment were due to host plant incompatibility and human activities. Failure due to host plant incompatibility has been avoided in the more recent programmes by testing the target plant compatibility of the agent. Some 15% of the failures are believed to have occurred due to the release of an inadequate number of agents. Here improvement is possible, but this may depend on the agent species concerned. Only one failure is explained by the fact that the laboratory-reared progeny released was weak and suffered from reduced genetic variability. It is quite probable that prolonged laboratory rearing before release is the reason for several unexplained failures in establishment. Some 24% of all failures are explained by climatic mismatching and predation. This applies to only less than 9% of the total number of releases, most of which are reported from Australia. No reasons for failures are given in over half of the cases. In some cases, failures may have been due to bad luck (chance events that killed the founder population) or bad management in other cases. Of the 22 species which completely failed to become established so far (Tab. 3) (note that the programme is continuing for at least seven of the species concerned), failures due to climatic mismatching or predation (most often both) are claimed for only 6 species, five of them in Australia and one in Canada. The higher rate of failure of the establishment in Australia is probably associated with the difficulty to switch the agent's life cycle to southern hemisphere conditions and necessary prolonged laboratory rearing. Altogether, Europe offers high chances for climatic matching in general, with probably a slight disadvantage for Australia, particularly in areas with prolonged drought.

SUCCESSFUL AGENTS

Among the 28 agent taxa of European origin which have been released in North America, Australia, and New-Zealand, clearly only chrysomelids, curculionids as well as a fungus can be associated with success, which means cases in which effective biological control of the target weed is claimed (Tab. 5). Of the 14 chrysomelid species used, five are effective control agents (Tab. 6). Another three *Aphthona* species show good promises to become effective control agents against *Euphorbia esula* L. All chrysomelid species recorded as failures simply did not become established, but all established species did provide or are close to providing effective control of their target weeds. Nearly all releases of successful chrysomelid species resulted in establishment, and more than two thirds achieved effective control of their target weeds. Four of the 16 curculionid species provide more or less good control of four of the 16 target weeds (Tab. 6). Although established on all five *Carduus* and three other thistle species, more or less good control

Tab. 5. Effects of agent taxonomy on levels of control

	Total No. of species	Control level
Coleoptera	35	
Bruchidae	1	
Chrysomelidae	15	***
Curculionidae	16	***
Buprestidae	2	
Cerambycidae	1	
Diptera	20	
Tephritidae	9	
Cecidomyiidae	5	*
Anthomyiidae	4	
Syrphidae	1	
Agromyzidae	1	
Lepidoptera	21	
Gelechiidae	1	
Cochylidae	2	*
Tortricidae	2	
Oecophoridae	1	
Noctuidae	3	
Sphingidae	1	
Lyonetiidae	1	
Pterolonchidae	1	
Geometridae	3	
Pyalidae	1	
Sesiidae	3	
Arctiidae	1	*
Gracillaridae	1	
Hemiptera		
Aphididae	1	
Thysanoptera		
Thripidae	1	
Acari		
Eriophyidae	3	*
Tetranychidae	1	
Fungi		
Uredinales	3	***

*** effective control

* complementary species or reduction of plant density observed, but no effective control claimed.

by *R. conicus* was only achieved for three of the *Carduus* species. As shown by ZWÖLFER & PREISS (1983), there are regional and local variations in host selection and adaptation by *R. conicus* which could explain the missing impact of the weevil on several thistle species on which *R. conicus* has become established. The effective fungus is a strain of *Puccinia chondrillina* BUBAK & SYDENHAM which con-

trolled the narrow-leaf form of *Chondrilla juncea* L. in Australia. A few other taxa are associated with success but only as complementary species or have caused a decline in weed density without achieving overall control. For example, in some sites in North America the cecidomyiid *Zeuxidiplosis giardi* (KIEFFER) is associated with control of *Hypericum perforatum* L., and a cochylid moth, *Agapeta zoegana* L., has caused a reduction in density of *Centaurea maculosa* LAMARCK rosettes without yet achieving overall control. Altogether, Diptera and Lepidoptera seem to be less effective control agents. Most Diptera feed in capitula, destroy seeds or feed on plant tissues within galls induced on leaves or vegetative buds. Tephritids, although usually having an important impact on plant performance, do not have any noticeable impact on plant density. In total, about 12% of all agent species released can be considered effective control agents, and 18% of the target weeds have been controlled, to a greater extent, across their geographical pest range.

COMPARISON WITH TROPICAL AND SUBTROPICAL WEEDS

Of the 60 weed species of non-European origin (including two representatives for the Cactaceae family), 16 (27%) were partially or completely controlled of which the most conspicuous successes involves aquatic weeds (e.g. *Salvinia molesta* D.S. MITCHELL and *Alternanthera philoxeroides* [MARTIUS] GRISEBACH). Considering only the 55 terrestrial weed species, the percentage of successful control drops to 22% and is similar to that attained for weed species of European origin (18%). From the 12 successes reported against terrestrial weeds, two are attributed exclusively to coleoptera, i.e. *Sida acuta* BURMAN f. and *T. cistoides*. Three other weeds were controlled by agents from various other taxa, including chrysomelids (i.e. *Parthenium hysterophorus* L., *Cordia curassavica* (JACQUIN) ROEMER & SCHULTES and *Lantana camara* L.). Thus, in successful control programmes of terrestrial weeds in subtropical and tropical areas, leaf beetles and weevils are so far not of such dominant importance as in temperate areas. A possible explanation for this discrepancy is that in temperate areas most species have only one generation per year, and the total feeding period of chrysomelids, curculionids and other coleoptera is longer than that of Lepidoptera and Diptera. In the subtropics and tropics, this relative advantage of coleoptera is counterbalanced by more or less continuous and overlapping breeding of species belonging to other taxa.

DISCUSSION

Several general characteristics of biocontrol agents and target plants have been associated with successes and failures in biological control (BURDON & MARSHALL, 1981; CRAWLEY, 1989a,b; JULIEN, 1989; LAWTON, 1990). Regarding insects, patterns of success are associated with high intrinsic rate of increase, low per-capita feeding rates associated with small individual body size, high voltinism or long-lived adults and a widespread distribution in their native land. This review on European insects tends to show that success in biological control of temperate weeds largely depends on the choice of the agent taxa. So far, chrysomelids and curculionids provided a greater number of effective control agents than any other taxa. The predominance of beetles among effective biocontrol agents was also shown on a worldwide basis (e.g. LAWTON, 1990). It is unclear to what extent the mode of feeding by the agent is a factor determining success. While no lepidopterous defoliators became effective agents acting on their own (e.g. MCEVOY *et al.*, 1989), both defoliators (*Chrysolina* spp.) and root feeders (*Longitarsus* and *Aphthona* spp.) in

Tab. 6. Establishment and effectiveness of Chrysomelidae and Curculionidae on weeds of European origin.

Weed species	Beetle species	Establishment	Effectiveness
	Chrysomelidae		
<i>Cirsium arvense</i>	<i>Altica carduorum</i>	no	
	<i>Lema cyanella</i>	no	
<i>Senecio jacobaeae</i>	<i>Longitarsus flavicornis</i>	yes	good
	<i>Longitarsus jacobaeae</i>	yes	good
<i>Heliotropium europaeum</i>	<i>Longitarsus albineus</i>	no	
<i>Hypericum perforatum</i>	<i>Chrysolina brunsvicensis</i>	no	
	<i>Ch. hyperici</i>	yes	good
	<i>Ch. quadrigemina</i>	yes	good
	<i>Ch. varians</i>	no	
<i>Euphorbia cyparissias</i>	<i>Aphthona cyparissiae</i>	yes	none
	<i>A. czwalinae</i>	no	
	<i>A. flava</i>	no	
	<i>A. nigriscutis</i>	yes	none
<i>E. esula</i>	<i>A. cyparissias</i>	yes	partial
	<i>A. czwalinae</i>	yes	?
	<i>A. flava</i>	yes	partial
	<i>A. nigriscutis</i>	yes	good
<i>Silene vulgaris</i>	<i>Cassida azurea</i>	?	
	Curculionidae		
<i>Carduus nutans</i>	<i>Rhinocyllus conicus</i>	yes	good
	<i>Trichosirocalus horridus</i>	yes	none
<i>C. acanthoides</i>	<i>R. conicus</i>	yes	partial
	<i>T. horridus</i>	yes	partial
<i>C. pycnocephalus</i>	<i>R. conicus</i>	yes	none
	<i>T. horridus</i>	yes	?
<i>C. tenuiflorus</i>	<i>R. conicus</i>	yes	none
	<i>T. horridus</i>	yes	?
<i>C. thoermeri</i>	<i>R. conicus</i>	yes	good
	<i>T. horridus</i>	yes	good
<i>Silybum marianum</i>	<i>R. conicus</i>	yes	none
<i>Cirsium vulgare</i>	<i>R. conicus</i>	?	
	<i>T. horridus</i>	yes	none
<i>Cirsium arvense</i>	<i>R. conicus</i>	yes	none
	<i>Ceutorhynchus litura</i>	yes	none
<i>Centaurea maculosa</i>	<i>Cyphocleonus achates</i>	yes	?
<i>C. solstitialis</i>	<i>Bangasternus orientalis</i>	yes	none
	<i>Eustenopus villosus</i>	?	
<i>Echium plantagineum</i>	<i>Ceutorhynchus larvatus</i>	?	
<i>Salvia aethiopis</i>	<i>Phrydiuchus spilmani</i>	no	
	<i>P. tau</i>	yes	partial
<i>Tribulus terrestris</i>	<i>Microlarinus lareynii</i>	yes	good
	<i>M. lypriformis</i>	yes	good
<i>Emex australis</i>	<i>Apion violaceum</i>	no	
<i>Cytisus scoparius</i>	<i>Apion fuscirostre</i>	yes	none
<i>Ulex europeus</i>	<i>Apion ulicis</i>	yes	none
	<i>A. scutellare</i>	?	
	<i>A. uliciperda</i> (?)	no	

the chrysomelid family are effective control agents. However, four of the five chrysomelid species which failed to become established are defoliators in the larval stage. Of the four successful curculionid species, two are feeding in capitula (*Rh. conicus* and *Microlarinus lareynii* (JACQUELIN DU VAL)) and two are mining the root crown of their host plants (*Trichosirocalus horridus* [PANZER] and *Microlarinus lypriformis* [WOLLASTON]). With the exception of the two above-mentioned weevils, it appears that pre-dispersal seed predators are not effective agents in general. Several tephritid and *Apion* species have failed to achieve control or stop the spread of their target weeds. However, there is a possibility that effectiveness will only be demonstrated after a few decades due to the importance of the seed bank of their target weed in the soil. Another explanation is that the recruitment of many weed species, in particular thistles species, is not seed-limited. The statement of HOKKANEN & PIMENTAL (1984), that agents closely associated with a target weed (old association) are generally less likely to exert a high degree of control than those less closely associated (new associations), is in most cases not confirmed by releases of agents originating from Europe. Both old and new associations resulted in effective biological control of target weeds. Examples for new associations are the chrysomelids controlling *E. esula* which are associated with several other spurge species in Europe, and the *Microlarinus* species collected from *T. terrestris* which controlled the tropical *T. cistoides*.

The major handicap of such a review analysis is that it is by no means easy to define success or failure in the classical biological control of weeds. Unfortunately, there is no absolute measure of success for a weed control project (CRAWLEY, 1989a). The status of control given by JULIEN (1992) is a brief precis of an exhaustive literature review and information obtained through personal communication. The successful establishment of an introduced agent is easier to define (i.e. the agent is present or not), although the number of years and releases may vary before this status is reached. Not all weeds are suitable targets for classical biological control. For the selection of target weeds, McCLAY (1989) proposes to consider the following: the geographical origin (exotic weeds are more suitable for classical biological control), relative abundance of the target weed in the native area and in the area of introduction, plant characteristics (reproduction mode, intraspecific variation), stability of the colonized habitat, degree of taxonomic isolation, economic aspects (cost/benefit ratio) as well as social and ecological aspects (weeds in recreation and conservation areas) and potential conflicts of interest. Based on the analysis presented, for weeds of European origin the presence of specialized chrysomelids and curculionids within the native distribution area of a target weed species would speak in favour of its selection for classical biological control. Whether success in biological control is associated with a number of agent characteristics, including agent taxonomy, obviously deserves much more attention. Although the chances of successful biological control of weed species which are not attacked by weevils and leaf beetles seem to be limited, the combined use of other taxa, like tephritids, gall-midges and root-boring moths, in an integrated and multiple stress approach, combined with increased competition by native flora, may still lead to successful control. This integrated approach still needs to be tested on a larger scale. So far, 33 invasive weed species of European origin have been biological control targets, about a dozen species are presently under investigation, and further species are considered to be potential targets in the future. There is a need for increased rates of agent establishment and for increased effectiveness in classical weed biological control. The provision is that potential target weeds and bio-

control agents are more carefully selected, release techniques refined and adapted to each specific target situation, and the attributes of control agents and their effect on the population density of target weeds in the area of release are monitored to provide feedback for the future selection of weed biocontrol agents.

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