

Review

Classical biological control of weeds with Curculionidae

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Abstract

The intentional use of insects to control weeds has been in practice for more than 150 years. Historically, species from the orders Lepidoptera and Coleoptera have shown the greatest success. Among the Coleoptera, the weevils (family Curculionidae) have played an integral role in the suppression of more than 50% of targeted weed programmes in various regions of the world. Notable successes using Curculionidae are in the control of waterhyacinth, Australian *Acacia* spp. and several thistle species. Published records indicate that of the 67 weed species targeted for control with Curculionidae worldwide, most are terrestrial-herbaceous weeds (65.7%). Curculionidae used for most of the targeted terrestrial-herbaceous ($n=44$) and aquatic/semi-aquatic weeds ($n=6$) are in North America, while the majority of the terrestrial-arborescent weeds ($n=17$) are in Africa. Of the 75 species of Curculionidae used to control these weeds worldwide, 34 are in North America. Success, as defined by the establishment of a biological control agent that has a detrimental impact on the target weed, is dependent on the number of programmes implemented and the resources for follow-through. This review provides insight into the successful establishment of some selected weevil species and their impact on their target weeds.

Keywords: Curculionidae, Classical biological control of weeds, Terrestrial-herbaceous weeds, Aquatic/semi-aquatic weeds, Terrestrial-arborescent weeds

Introduction

Species representing several specific insect orders constitute the vast majority of beneficial organisms used in classical biological control programmes. Hymenopterans have been widely used in the biological control of arthropods, while coleopterans have been prominent in the biological control of weeds [1–3]. Many species of moths (Lepidoptera) and beetles (Coleoptera) are known to be destructive plant pests and thus it is not surprising that members of these two orders are generally more efficacious weed biological control agents than representatives from other orders [4]. Effective biological control agents are necessarily well synchronized with the target plant, as they have evolved in a close relationship and, in many cases, close association with the weed limits herbivory to one or few plant species. Several species of

beetles in the family Curculionidae have played a vital role in the suppression of invasive weeds throughout the world [1, 2, 5].

The philosophical differences on what constitutes a 'weed' are worth reviewing. Zimdahl [6] considered various definitions of weeds such as (i) plants whose virtues have yet to be discovered; (ii) plants growing where they are not wanted or plants out of place; (iii) pioneer species adapted to grow in disturbed habitats; and (iv) plants that are unusually persistent and pernicious, interfering with the growth of more desirable plants. All of these definitions have merit, but for this review we define a weed as an alien plant species that is non-native to the ecosystem under consideration and whose introduction causes or is likely to cause economic and/or environmental harm, and/or harm to human health [7]. An exotic plant species often becomes a weed because major suppressing factors,

such as insect herbivores and plant pathogens, do not accompany the weed upon their introduction into a new, non-native habitat. In the absence of suppressing agents, weeds out-compete native vegetation and exceed population densities that would otherwise have been suppressed in their native range. Van Driesche *et al.* [4] summarized the various mechanisms and hypotheses by which weeds can become invasive in their introduced habitats.

A common long-term tactic for dealing with weed invasions is the intentional deployment of insect herbivores; although use of plant pathogens is increasing in importance for invasive weed suppression. Classical biological control of weeds (CBCW) for long-term weed suppression [5, 8] is a multi-step process and generally involves taxonomic identification of the suspected weed, environmental and economic cost-benefit analysis, foreign exploration to locate, identify and import potential insect control agents from their place of origin, quarantine testing to evaluate host specificity, rearing and/or mass production of the agent, assessment of the best methodology for release if approved by the US Department of Agriculture Animal and Plant Health Inspection Service Plant Protection and Quarantine (USDA-APHIS-PPQ) for field release (in the USA) and post-release evaluations [3]. Although the initial investment in a classical biological control programme is expensive, the monetary gain after programme implementation is greater [5, 9].

The first unintentional use of CBCW was in 1795 when India mistakenly imported *Dactylopius ceylonicus* (Green) as *Dactylopius cacti* (Hemiptera: Dactylopiidae), the cochineal insect of commerce, from Brazil. It became established and was used to control *Opuntia vulgaris* Miller [10–12]. However, the first intentional introduction occurred in 1865 when *D. ceylonicus* was imported into Ceylon from India for *O. vulgaris* control [10, 11]. This accomplishment towards the advancement of CBCW is relatively unknown to most novices in the field of weed biological control. Absence of awareness of the control of *O. vulgaris* in India is partially attributable to the major success and widely publicized impact of *Cactoblastis cactorum* (Berg.) (Lepidoptera: Pyralidae) on *Opuntia* spp. in Australia during the 1920s [13, 14], and *Agasicles hygrophila* Seiman & Vogt (Coleoptera: Chrysomelidae) on *Alternanthera philoxeroides* (Martius) Grisebach in the USA during the 1960s [15, 16].

In this review, we define success as *any* agent that establishes on the target weed, and the absence of the establishment is considered a failure. We use this definition because some releases are too new to evaluate success and it is not the goal of this review to evaluate success. Furthermore, success cannot be estimated across regions because of disproportionate programme implementation. Success is also dependent on the number of programmes implemented and the resources for follow-through. Denoth *et al.* [17] have discussed inconsistencies in definitions of success in biological control.

Of the 996 citations reported by Julien and Griffiths [1], 514 (51.6%) involved Coleoptera and 281 (28.2%) cited

Curculionidae. Thus, Curculionidae made up more than half of the Coleoptera used in biological control of weeds. Of the 75 species of curculionids used to control 67 target weed species, 49 (65.3%) successfully established.

The earliest reported use of a weevil for CBCW was in 1925. Purple nutsedge, *Cyperus rotundus* L., was the target weed and the weevil *Athesapecta cyperi* Marshall was the agent selected for its control on the island of Oahu [18]. However, despite its spread to neighbouring islands, the weevil did not control the weed [19]. In 1948, *Metamasius [Cactophagus] spinolae* (Gyllenhal) was released in Africa to suppress *Opuntia ficus-indica* (L.) Miller, but control was limited to a few release sites [20–22]. Reportedly, the most successful use of a curculionid species for CBCW in the USA occurred in the late 1960s when *Rhinocyllus conicus* (Frölich) was imported from Canada, the progeny of individuals originally obtained in France for control of musk thistle, *Carduus nutans* L. [23–25]. It should be noted that *R. conicus* has non-target impacts but the impact to non-target species often is considered relatively negligible [25, 26] compared with the benefits realized throughout its release. However, several reports indicate detrimental impacts of the weevil to non-target species [27–30]. Generally, the overall programme is considered a success resulting in greater than 80% reduction of *C. nutans* in areas of North America [31–34], but its success remains under debate [27–30].

Coleoptera is a large order that consists of a diverse assemblage of species that occur throughout the world. Within the order, the family Curculionidae represents more than 60 000 species [35], many of which are significant plant pests, while others are significant weed control agents. Members of this family are the most abundant and most common of the snout beetles. There is wide variation in size, shape and length of the snout in this group and the family is divided into a number of subfamilies. Our objective is to consider the whole family, which has representatives adapting to plants growing in various habitats. The larvae of many species feed internally and develop in fruits, roots, or as seed pod borers, and being protected from their own natural enemies, have coevolved and adapted well to their host plants. Other attributes that make them successful as biological control agents are high fecundity, ability to disperse and ease of handling. Based on personal experience, we have found that curculionids provided with moisture generally can survive for a week to 10 days without food. This is especially important during shipment between countries, where delays are common.

The aim of this review is not to recapitulate the history of CBCW, but to summarize the major advances made in CBCW with respect to Curculionidae in major weed habitats throughout the world and to emphasize the contribution of some species within the family. Although documentation exists that encompasses all insects implemented for CBCW [1], we believe that a better understanding of CBCW can be gained by

Table 1 Target plant species (67) worldwide, grouped by habitat, using Curculionidae as biological control agents

Habitat type	Number of plants species targeted worldwide	% of species	Number of <i>Curculionidae</i> spp. used as biological control agents
Terrestrial-herbaceous	44	65.7	47
Terrestrial-arborescent	17	25.3	18
Aquatic or semi-aquatic	6	9.0	10
Total	67	100	75

highlighting the achievements of a specific insect family. Provided with the previous background and literature, we will focus on selected examples of Curculionidae successfully used as biological control agents to provide a greater understanding, appreciation and contribution of these organisms towards classical biological weed control. We will use examples of specific and widely used genera and/or species adapted to specific plant habitats to facilitate these objectives.

Overview

Worldwide, the 67 plant species targeted for biological control using 75 species of Curculionidae can be partitioned into three major habitat types: aquatic/semi-aquatic (6 spp.), terrestrial-arborescent (17 spp.) and terrestrial-herbaceous (44 spp.) (Table 1). Terrestrial herbaceous weed targets are the most numerous representing 14 plant families (Table 2). Of these, 17 species (38.6%) are members of the Asteraceae and occur across all habitat types [1, 36, 37]. This review is an overview of CBCW in these habitats with emphasis on important curculionid genera.

Terrestrial-Herbaceous Weeds

Terrestrial-herbaceous weeds are plants that occur on land, are more succulent than terrestrial-arborescent plants, and generally will not persist in environments inundated with water or dense overstorey vegetation. North America has the greatest number of exotic terrestrial-herbaceous weeds (44 spp.) targeted for biological control using curculionid species (Table 2). Three genera: *Larinus* (5 spp.), *Ceutorhynchus* (4 spp.) and *Smicronyx* (4 spp.) [1, 36–45] are often used in various continents/countries of the world.

Terrestrial-Arborescent Weeds

Terrestrial-arborescent weeds (tree species) represent the second most abundant group targeted for CBCW,

with 18 curculionid agents being used in this habitat type (Table 3). Most efforts to control such weeds have occurred in Africa (78%, $n=18$). By far the most invasive genus in this category is *Acacia* (Mimosaceae). *Acacia* represents 41% of all the terrestrial-arborescent weeds targeted for biological control; agents currently include five species of weevils in the genus *Melanterius*. Additional terrestrial-arborescent weeds targeted for control in Africa are plume albizia [*Paraserianthes lophantha* (Willdenow) Nielsen] (Mimosaceae), Scots pine (*Pinus* sp.) (Pinaceae), earleaf nightshade [*Solanum mauritanum* Scop., *Chromolaena odorata* (L.) King & H. Rob.] (Solanaceae) and 2 *Hakea* spp. (pincushion tree, Proteaceae). Australia targeted two terrestrial-arborescent weeds for control: catclaw mimosa (*Mimosa pigra* L.) (Mimosaceae) and eastern baccharis (*Baccharis halimifolia* L.) (Asteraceae). North America has thus far targeted only one, the paperbark tree [*Melaleuca quinquenervia* (Cav.) S. F. Blake] (Myrtaceae) [1, 36, 37, 46]. A new programme has recently been initiated on a second species, tree-of-heaven [*Ailanthus altissima* (Mill.) Swingle] (Simaroubaceae) with *Eucryptorrhynchus brandti* (Harold) and is undergoing host specificity testing in the eastern USA [47].

Aquatic/Semi-Aquatic Weeds

Aquatic/semi-aquatic plants grow in or in close association with a water body. Relatively few plants (6 spp.) in this group have been targeted for control with Curculionidae (Table 1); although some highly invasive weeds are present in this group. Water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach, has invaded all major regions of the world except for New Zealand. Similarly, *Salvinia molesta* D.S. Mitchell and water lettuce (*Pistia stratiotes* L.) are problem weeds in Australia, Asia, Africa and North America. Most attempts at biological control of exotic aquatic/semi-aquatic weeds have occurred in these four continents (Table 4). New Zealand has not documented any aquatic/semi-aquatic weed invasions, where curculionids are used as biological control agents. In contrast, North America has implemented 9 of the 10 weevil species used for control of various weeds invading this habitat type, with significant efforts made to release *Hylobius transversovittatus* Goeze and *Nanophyes marmoratus* Goeze for control of the semi-aquatic weed purple loosestrife, *Lythrum salicaria* L. There have not been any reports of new aquatic weed invasions where curculionids have been used as control agents since the invasion of *L. salicaria* and *S. molesta* in North America. Africa represents a second continent actively using curculionids (6 spp.) for aquatic/semi-aquatic weed control. The use of *Stenopelmus rufinus* Gyllenhal to control the invasion of water fern, *Azolla filiculoides* Lam., is unique to Africa [1, 36, 37].

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Table 2 Curculionidae (47 species) used for classical biological control of terrestrial-herbaceous weeds in various regions of the world¹

Region/Country (No. of species)	Biological control agent		Target weed		
	Genus	Species	Family	Genus	Species
North America (n=24)	<i>Bangasternus</i>	<i>fausti</i> (Reitter) ²	Asteraceae	<i>Centaurea</i>	<i>diffusa</i> <i>maculosa</i> <i>virgata</i>
	<i>Cyphocleonus</i>	<i>orientalis</i> Capiomont ²	Asteraceae	<i>Centaurea</i>	<i>solstitialis</i> <i>maculosa</i> <i>virgata</i>
		<i>achates</i> (Fahraeus) ²	Asteraceae		<i>solstitialis</i> <i>maculosa</i> <i>virgata</i>
	<i>Larinus</i>	<i>minutus</i> Gyllenhal ²	Asteraceae	<i>Centaurea</i>	<i>solstitialis</i> <i>maculosa</i> <i>virgata</i>
		<i>obtusus</i> Gyllenhal ²	Asteraceae		<i>solstitialis</i> <i>solstitialis</i>
		<i>curtus</i> Hochhut ²	Asteraceae		<i>solstitialis</i> <i>solstitialis</i>
		<i>filiformis</i> Petri	Asteraceae		<i>solstitialis</i> <i>solstitialis</i>
	<i>Lixus</i>	<i>scolopax</i> Boheman	Asteraceae	<i>Centaurea</i>	<i>solstitialis</i> <i>solstitialis</i>
	<i>Eustenopus</i>	<i>villosus</i> (Boheman) ²	Asteraceae	<i>Centaurea</i>	<i>solstitialis</i> <i>solstitialis</i>
	<i>Ceutorhynchus</i>	<i>litura</i> (Fabricius) ²	Asteraceae	<i>Cirsium</i>	<i>arvense</i> <i>arvense</i>
	<i>Rhinocyllus</i>	<i>conicus</i> Frölich ²	Asteraceae	<i>Cirsium</i>	<i>arvense</i> <i>nutans</i>
			Asteraceae	<i>Carduus</i>	<i>acanthoides</i> <i>pycnocephalus</i> <i>macrocephalus</i> <i>tenuiflorus</i> <i>acanthium</i> <i>marianum</i>
	<i>Trichosirocalus</i>	<i>horridus</i> (Panzer) ²	Asteraceae	<i>Onopordum</i> <i>Silybum</i> <i>Cirsium</i> <i>Carduus</i>	<i>vulgare</i> <i>nutans</i> <i>acanthoides</i> <i>pycnocephalus</i> <i>macrocephalus</i> <i>acanthium</i> <i>cistoides</i>
			Asteraceae	<i>Onopordum</i> <i>Tribulus</i>	<i>terrestris</i> <i>cistoides</i> <i>terrestris</i> <i>genistifolia</i> <i>vulgaris</i> <i>dalmatica</i> <i>aethiopsis</i> <i>aethiopsis</i>
<i>Microlarinus</i>	<i>lareynii</i> (Jacquelin du Val) ²	Zygophyllaceae	<i>Onopordum</i> <i>Tribulus</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>	
	<i>lypriformis</i> (Wollaston) ²	Zygophyllaceae		<i>grandis</i> <i>perfoliata</i> <i>officinale</i> <i>rotundus</i> <i>ficus-indica</i> <i>punicea</i> <i>punicea</i> <i>marianum</i> <i>hermontheca</i> <i>rotundus</i> <i>cistoides</i>	
<i>Mecinus</i>	<i>janthinus</i> Germar ²	Scrophulariaceae	<i>Linaria</i>	<i>genistifolia</i> <i>vulgaris</i> <i>dalmatica</i> <i>aethiopsis</i> <i>aethiopsis</i>	
<i>Phrydiuchus</i>	<i>spilmani</i> Warner ² <i>tau</i> Warner ²	Lamiaceae	<i>Salvia</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>	
<i>Microplontus</i>	<i>edentulus</i> (Schultze) ²	Asteraceae	<i>Matricaria</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>	
<i>Gymnetron</i>	<i>linariae</i> (Panzer) ² <i>tetrum</i> (Fabricius) ²	Scrophulariaceae	<i>Linaria</i> <i>Verbascum</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>	
<i>Acythopeus</i>	<i>coccinae</i> O'Brien and Pakaluk ² <i>burkhartorum</i> O'Brien ²	Cucurbitaceae	<i>Coccinia</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>	
Africa (n=6)	<i>Rhinoncomimus</i>	<i>latipes</i> Korotyayev ²	Polygonaceae	<i>Persicaria</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Mogulones</i>	<i>cruciger</i> (Herbst) ²	Boraginaceae	<i>Cnyoglossum</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Athesapeuta</i>	<i>cyperi</i> Marshall	Cyperaceae	<i>Cyperus</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Metamasius</i>	<i>spinolae</i> (Gyllenhal) ²	Cactaceae	<i>Opuntia</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Neodiplogrammus</i>	<i>quadrivittatus</i> (Oliver) ²	Fabaceae	<i>Sesbania</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Rhyssomatus</i>	<i>marginatus</i> (Oliver) ²	Fabaceae	<i>Sesbania</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
Asia (n=6)	<i>Rhinocyllus</i>	<i>conicus</i> Frölich ²	Asteraceae	<i>Silybum</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Smicronyx</i>	<i>albovariegatus</i> Faust	Scrophulariaceae	<i>Striga</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Athesapeuta</i>	<i>cyperi</i> Marshall	Cyperaceae	<i>Cyperus</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Microlarinus</i>	<i>lareynii</i> (Jacquelin du Val) ² <i>lypriformis</i> (Wollaston) ²	Zygophyllaceae	<i>Tribulus</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Acythopeus</i>	<i>coccinae</i> O'Brien and Pakaluk <i>burkhartorum</i> O'Brien	Cucurbitaceae	<i>Coccinia</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>
	<i>Smicronyx</i>	<i>roridus</i> Pallas	Cuscutaceae	<i>Cuscuta</i>	<i>perforata</i> <i>genistifolia</i> <i>thapsus</i> <i>blattaria</i> <i>grandis</i>

Table 2 (Cont.)

Region/Country (No. of species)	Biological control agent		Target weed		
	Genus	Species	Family	Genus	Species
Australia (n=13)	<i>Eriocereophaga</i>	<i>humeridens</i> O'Brien ²	Cactaceae	<i>Harrisia</i>	<i>martinii</i>
	<i>Eutinobothrus</i>	<i>pilosellus</i> (Boheman) ²	Malvaceae	<i>Sida</i>	<i>acuta</i> <i>rhubifolia</i>
	<i>Larinus</i>	<i>latus</i> (Herbst) ²	Asteraceae	<i>Onopordum</i>	<i>illyricum</i>
	<i>Lixus</i>	<i>cardui</i> Olivier ²	Asteraceae	<i>Onopordum</i>	<i>illyricum</i>
		<i>cribricollis</i> Boheman	Polygonaceae	<i>Emex</i>	<i>australis</i>
	<i>Mogulones</i>	<i>geographicus</i> (Goeze) ²	Boraginaceae	<i>Echium</i>	<i>plantaginum</i>
	<i>Rhinocyllus</i>	<i>conicus</i> Frölich ²	Asteraceae	<i>Carduus</i>	<i>nutans</i>
				<i>Cirsium</i>	<i>vulgare</i>
				<i>Silybum</i>	<i>marianum</i>
		<i>tenuipes</i> (Fairmaire)	Crassulaceae	<i>Bryophyllum</i>	<i>delagoense</i>
		<i>lutulentus</i> Dietz ²	Asteraceae	<i>Parthenium</i>	<i>hysterophorus</i>
		<i>briesei</i> Alonso-Zarazaga & Sánchez-Ruiz ²	Asteraceae	<i>Onopordum</i>	<i>illyricum</i>
	South America (n=4)	<i>Rhinocyllus</i>	<i>horridus</i> (Panzer) ² <i>mortadelo</i> Alonso-Zarazaga & Sánchez-Ruiz ²	Asteraceae	<i>Carduus</i>
<i>Trichosirocalus</i>		<i>conicus</i> Frölich ²	Asteraceae	<i>Carduus</i>	<i>acanthoides</i>
<i>Neodiplogrammus</i>		<i>horridus</i> (Panzer)	Asteraceae	<i>Sesbania</i>	<i>exaltata</i>
<i>Trichapion</i>		<i>quadrivittatus</i> Fahraeus ²	Fabaceae		
Caribbean (n=5)		<i>lativentre</i> (Beguin-Billecocq) ²	Fabaceae	<i>Sesbania</i>	<i>drummondii</i>
	<i>Athesapeuta</i>	<i>cyperi</i> Marshall	Cyperaceae	<i>Cyperus</i>	<i>rotundus</i>
	<i>Microlarinus</i>	<i>lareynii</i> (Jacquelin du Val)	Zygophyllaceae	<i>Tribulus</i>	<i>cistoides</i>
New Zealand (n=5)		<i>lypriformis</i> (Wollaston)			<i>cistoides</i>
		<i>roridus</i> Pallas	Cuscutaceae	<i>Cuscuta</i>	<i>americana</i>
	<i>Ceutorhynchus</i>	<i>rufovittatus</i> Anderson	Asteraceae	<i>Cirsium</i>	<i>arvense</i>
	<i>Rhinocyllus</i>	<i>litura</i> (Fabricius)	Asteraceae	<i>Carduus</i>	<i>acanthoides</i> <i>nutans</i> <i>pycnocephalus</i> <i>tenuiflorus</i>
		<i>conicus</i> Frölich ²			<i>nutans</i> <i>pycnocephalus</i> <i>tenuiflorus</i>
		<i>horridus</i> (Panzer) ²	Asteraceae	<i>Carduus</i>	<i>palustre</i> <i>vulgare</i> <i>davidii</i>
	<i>japonicus</i> Wingelmüller	Buddlejaceae	<i>Buddleja</i>		
	<i>erro</i> (Pascoe)				

¹Information was obtained from [1, 36–45].

²Established.

Role of Biological Control in the Management of Major Weeds by Habitat Type

Terrestrial-Herbaceous Weeds: The Thistle Complex

North America

Thistles are the most widely distributed terrestrial-herbaceous weeds to be targeted worldwide for control with Curculionidae [1, 36, 37]. Weeds from the genera *Carduus*, *Cirsium* and *Silybum* are native to Europe and Eurasia [1]. One or more species in these genera have become invasive in North America, Africa, Australia,

South America and/or New Zealand [1, 36, 37]. *R. conicus* Frölich and *Trichosirocalus horridus* (Panzer) have been used around the world for control of *Carduus*, *Cirsium* and *Silybum* species. Initial releases of *R. conicus* and *T. horridus* in North America were originally exported via France and Italy, respectively [1]. The first release of *R. conicus* in 1968 was for control of the spiny plumeless thistle, *Carduus acanthoides* L., and the musk or nodding thistle, *C. nutans* L. Although *R. conicus* reduced seed production, it was eventually determined that *C. acanthoides* was not the preferred host of this weevil [18, 24, 25]. Subsequent releases in North America provided variable control of

Table 3 Curculionidae (18 species) used for classical biological control of terrestrial-arborescent weeds in various regions of the world¹

Region/Country (No. of species)	Biological control agent		Target weed		
	Genus	Species	Family	Genus	Species
North America (n=1)	<i>Oxyops</i>	<i>vitiosa</i> Pascoe ²	Myrtaceae	<i>Melaleuca</i>	<i>quinquenervia</i>
Africa (n=14)	<i>Anthonomus</i>	<i>morticinus</i> Clark <i>santacruzii</i> Hustache	Solanaceae	<i>Solanum</i>	<i>mauritianum</i>
	<i>Conotrachelus</i>	<i>squalidus</i> Boheman ² Sp.	Solanaceae	<i>Solanum</i>	<i>mauritianum</i>
	<i>Lixus</i>	<i>aemulus</i> Petri ²	Asteraceae	<i>Chromolaena</i>	<i>odorata</i>
	<i>Cydmaea</i>	<i>binotata</i> Lea ²	Asteraceae	<i>Chromolaena</i>	<i>odorata</i>
	<i>Dicomada</i>	<i>rufa</i> Blackburn	Proteaceae	<i>Hakea</i>	<i>sericea</i>
	<i>Erytenna</i>	<i>consputa</i> Pascoe ²	Proteaceae	<i>Hakea</i>	<i>gibbosa</i> <i>sericea</i>
	<i>Melanterius</i>	<i>acaciae</i> Lea ² <i>compactus</i> Lea ² <i>maculatus</i> Lea ²	Mimosaceae	<i>Acacia</i>	<i>melanoxyton</i> <i>saligna</i> <i>mearnsii</i> <i>dealbata</i> <i>decurrens</i> <i>longifolia</i> <i>cyclops</i> <i>lophantha</i> spp.
		<i>ventralis</i> Lea ² <i>servulus</i> Pascoe ²		<i>Paraserianthes</i>	<i>lophantha</i> spp.
Australia (n=3)	<i>Pissodes</i>	<i>validirostris</i> (Sahlberg)	Pinaceae	<i>Pinus</i>	
	<i>Chalcodermus</i>	<i>serripes</i> Fahraeus ²	Mimosaceae	<i>Mimosa</i>	<i>pigra</i>
	<i>Sibinia</i>	<i>fastigiata</i> Clark ²	Mimosaceae	<i>Mimosa</i>	<i>pigra</i>
	<i>Helipodus</i>	<i>intricatus</i> (Boheman) ²	Asteraceae	<i>Baccharis</i>	<i>halimifolia</i>

¹Information was obtained from [1, 36, 37, 46, 47].²Established.**Table 4** Curculionidae (10 species) used for classical biological control of aquatic/semi-aquatic weeds in various regions/countries of the world¹

Region/Country (No. of species)	Biological control agent		Target weed		
	Genus	Species	Family	Genus	Species
North America (n=9)	<i>Bagous</i>	<i>affinis</i> Hustache ² <i>hydrillae</i> O'Brien ²	Hydrocharitaceae	<i>Hydrilla</i>	<i>verticillata</i>
	<i>Cyrtobagous</i>	<i>salviniae</i> Calder and Sands ² <i>singularis</i> Hustache ²	Salviniaceae	<i>Salvinia</i>	<i>molesta</i>
	<i>Hylobius</i>	<i>transversovittatus</i> Goeze ²	Lythraceae	<i>Lythrum</i>	<i>salicaria</i>
	<i>Nanophyes</i>	<i>marmoratus</i> Goeze			
	<i>Neochetina</i>	<i>bruchi</i> Hustache ² <i>eichhorniae</i> Warner ²	Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>
Africa (n=6)	<i>Neohydronomous</i>	<i>affinis</i> Hustache ²	Araceae	<i>Pistia</i>	<i>stratiotes</i>
	<i>Cyrtobagous</i>	<i>salviniae</i> Calder and Sands ² <i>singularis</i> Hustache ²	Salviniaceae	<i>Salvinia</i>	<i>molesta</i>
	<i>Neochetina</i>	<i>bruchi</i> Hustache ² <i>eichhorniae</i> Warner ²	Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>
	<i>Neohydronomous</i>	<i>affinis</i> Hustache ²	Araceae	<i>Pistia</i>	<i>stratiotes</i>
Asia (n=5)	<i>Stenopelmus</i>	<i>rufinusus</i> Gyllenhal ²	Azollaceae	<i>Azolla</i>	<i>filiculoides</i>
	<i>Cyrtobagous</i>	<i>salviniae</i> Calder and Sands ² <i>singularis</i> Hustache ²	Salviniaceae	<i>Salvinia</i>	<i>molesta</i>
	<i>Neochetina</i>	<i>bruchi</i> Hustache ² <i>eichhorniae</i> Warner ²	Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>
Australia (n=4)	<i>Neohydronomous</i>	<i>affinis</i> Hustache ²	Araceae	<i>Pistia</i>	<i>stratiotes</i>
	<i>Cyrtobagous</i>	<i>salviniae</i> Calder and Sands ²	Salviniaceae	<i>Salvinia</i>	<i>molesta</i>
	<i>Neochetina</i>	<i>bruchi</i> Hustache ² <i>eichhorniae</i> Warner ²	Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>
	<i>Neohydronomous</i>	<i>affinis</i> Hustache ²	Araceae	<i>Pistia</i>	<i>stratiotes</i>
South America (n=2)	<i>Neochetina</i>	<i>bruchi</i> Hustache ² <i>eichhorniae</i> Warner ²	Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>
Caribbean (n=1)	<i>Neochetina</i>	<i>bruchi</i> Hustache ²	Pontederiaceae	<i>Eichhornia</i>	<i>crassipes</i>

¹Information was obtained from [1, 36, 37].²Established.

C. acanthoides in the West, but oviposition of the agent was not synchronized with thistle flowering in the East [1, 18, 24, 25, 48]. The impact of *R. conicus* on *C. nutans* was highly successful, reducing plant density by as much as 99% in some pasture areas of eastern North America [25, 32, 33]. *R. conicus* was also released in 1969 for control of the milk thistle, *Silybum marianum* (L.) Gaertner, but it did not establish on this target weed [1]. *T. horridus* was released in 1974 for additional control of *C. acanthoides* and provided significant reduction in plant density on some sites in eastern North America [18, 24, 25]. *T. horridus* also provided good control of *C. nutans*, especially in pasture systems [25]. As pointed out earlier, non-target impacts of *R. conicus* [27–30] have raised the question as to whether it would receive approval for release based on present-day criteria.

Africa

Attempts were also made in Africa in 1985 to use *R. conicus* to control *S. marianum*; however, the weevil did not successfully establish because host plants were destroyed with herbicides soon after the insects were released [1]. The literature does not indicate any subsequent release of *R. conicus* or any other curculionid species for thistle control in this region of the world.

Australia

Efforts to control *C. nutans*, *Cirsium vulgare* and *S. marianum* in Australia with *R. conicus* were initiated in 1988 and continued into 1989 with releases of strains of weevils obtained in France and Italy. Early season damage to *C. nutans* seed heads was reported to exceed 70%. However, as in North America, asynchrony of oviposition with host plant phenology has limited late-season control because the majority of seed heads are produced after cessation of oviposition by the weevil. *R. conicus* failed to establish in Australia on *C. vulgare* and *S. marianum*. In 1993, *T. horridus* was released to increase herbivore stress on *C. nutans* populations. *T. horridus* proved to be more successful than *R. conicus* in Australia, killing and reducing rosette growth of surviving plants by 50%, and impeding reproductive potential by as much as 67% [1].

South America

South America initiated control of *C. acanthoides* and *C. nutans* in 1981 with *R. conicus*. Although the weevil established, its impact remains largely undocumented. In 1983, *T. horridus* obtained from Virginia was also released for control of the same thistle species but failed to establish [1].

Caribbean

Very little information exists on the five agents released (Table 2) for biological weed control in the Caribbean.

New Zealand

In 1973 and 1979, New Zealand released *R. conicus* and *T. horridus*, for control of *Carduus* and *Cirsium* species, respectively [1]. Subsequent to their release, destruction of seed has been recorded to be as high as 50%. However, the amount of control attributable to *T. horridus* is questionable [49–52].

Terrestrial-Arborescent Weeds: Mimosaceae Species in Africa

Africa is at the forefront of classical biological control of terrestrial-arborescent weed species with Curculionidae. The primary target weeds in this continent are species in Mimosaceae. Because biological control programmes targeting trees or shrubs in Australia (2 spp.) and North America (1 sp.) are far fewer than in Africa (14), our discussion will focus on African Mimosaceae [1, 36, 37].

Of 18 weevil species used worldwide, 14 were released for control of this group of weeds in Africa. Because all eight Mimosaceae species in Africa targeted for control with curculionids are native to various areas of Australia, the classical biological control agents used in Africa are from the genus *Melanterius* obtained from Australia. Releases made to control 7 *Acacia* species and *P. lophantha* were initiated in 1985 and are ongoing [1, 52, 54]. *Acacia* and *Paraserianthes* spp. are economically important trees in Africa, but they can be highly invasive outside of non-cultivated areas [55]. The five *Melanterius* spp. used for control of these invasive weed trees have similar life history characteristics in that seed feeding, ovipositional and larval development characteristics are nearly identical. Impact of these agents on their various hosts is difficult to distinguish at the species level because of their similarities, and is therefore often evaluated at the genus level. The most studied species-specific impact is of *Melanterius servulus* Pascoe on *Acacia cyclops* A. Cunn. ex G. Don [54].

M. servulus was imported from Australia for control of *A. cyclops* in 1994. After 5 years, 95% seed damage was reported. Although this programme is considered a success, additional agents are needed because sustained reduction in weed density requires more than 99% seed mortality [54].

Aquatic/Semi-Aquatic Weeds: *E. crassipes* (Martius) Solms-Laubach

North America

Waterhyacinth, *E. crassipes*, native to South America is the most widely distributed, actively targeted and invasive aquatic weed worldwide [5, 8, 56, 57]. Economically, and in practice, the suppression of waterhyacinth is considered one of the most successful examples of CBCW in the world [58, 59].

In North America, waterhyacinth infestations are mostly limited to the southern USA, but the weed can survive as far north as New York [57]. Waterhyacinth was originally introduced into Louisiana from South America's Amazon Basin in 1884 and quickly spread to Florida in 1890 [5, 57]. By the 1950s, waterhyacinth occupied approximately 51 000 ha of Florida's water bodies [57]. In 1972 and 1974, *Neochetina eichhornia* Warner and *Neochetina bruchi* Hustache, respectively, were imported from Argentina for waterhyacinth control [1]. Although both species have established throughout the range of the weed, there is some confusion in the literature as to the extent of control attributable to the agents [60, 61]. Generally, suppression has been attributed to *N. eichhornia* and/or a synergistic interaction of weevil feeding damage and infection by the native fungus *Cercospora piaropi* Tharp [62]. Waterhyacinth populations have been reduced by more than 30% in the Gulf Coast states, but some of this is because of growth inhibition subsequent to winter or herbicidal diebacks [5, 8].

Africa

Although waterhyacinth was introduced into several areas of Africa in the late 1800s, invasions were more commonly reported in the 1980s [63]. It is a severe pest in Africa, covering as much as 12 000 ha on Lake Victoria alone [57]. There have been several releases of *N. eichhornia* and *N. bruchi* in various locations throughout Africa since 1972. Most of these releases were made from insects obtained from North American field releases [1]. Both agent species have had variable impacts on the weed throughout its distribution. In Zimbabwe, waterhyacinth control has been reported to be as high as 85%. While these species have been highly successful in some areas of Africa, variable impact is suspected to be because of their poor adaptation to nutrient-enriched conditions and/or climate variations across the distribution of the weed [56, 57, 64–71].

Asia

Waterhyacinth made its way into several Asian countries by the 1900s, where it quickly spread and severely impeded sustainability of rice fields, waterways and aquaculture. Releases of *N. eichhornia* and *N. bruchi* were initiated in 1979 and 1984, respectively, again with insects obtained from North American release sites [1]. Control of waterhyacinth has been highly successful with reduction of the weed exceeding 40% within two and one-half years in some regions [1, 72, 73].

Australia

Waterhyacinth was introduced into Brisbane, Sydney and Grafton, Australia in the 1890s and quickly spread to all mainland states and territories (66). Classical biological control of waterhyacinth in Australia was initiated in 1975 with *N. eichhornia* obtained also from North American

release sites [1]. *N. eichhornia* successfully controlled waterhyacinth in many areas of Australia, but as in many other regions of the world, sustained impact was limited in cool weather climates [74, 75] and in areas where pesticide use continues [75]. *N. bruchi* was also released in 1990 with North-America-sourced insects [1], and is typically the more predominant of the two species, comprising as much as 80% of the weevil population at some sites [1]. Australia's Commonwealth Scientific and Industrial Research Organisation [76] estimated that using both weevils reduced waterhyacinth populations by 74% within 5 years.

Caribbean

N. bruchi was released in 1995 with insects obtained from North America to control waterhyacinth in the Caribbean. It has become established in this region but little information exists on its distribution or impact on the weed [1].

Summary

CBCW is well documented in the literature. Of the 996 citations in [1], 514 involved Coleoptera (51.6%) and 281 (28.2%) cited Curculionidae. The invaluable contribution of Curculionidae towards invasive weed control with minimal non-target impacts is evident despite the challenges posed by these invasive weeds. Several notable successes using curculionid agents are apparent in the control of Waterhyacinth (aquatic/semi-aquatic), *Acacia* spp. (terrestrial-arborescent) and thistle species (terrestrial-herbaceous). Of these three habitat groups, terrestrial-herbaceous weeds are by far the most numerous plant pests in the world. Within these major weed categories, North America has used more biological control agents in the family Curculionidae for weed suppression than any other continent.

Success in weed control with curculionid agents in many cases involves multiple species introductions; for example, most successful cases discussed require the release of one or more weevil species. Our review also indicates that the establishment of single weevil species release is high in terrestrial-arborescent weeds. Multiple species releases are more common in aquatic/semi-aquatic and terrestrial-herbaceous habitats. Success is often directly related to the resource available for implementation of programmes; as the numbers of programmes increase within a region or continent, more knowledge is gained to assist successful implementation of the programme in other areas. North America has documented the greatest success using curculionid species in aquatic/semi-aquatic and terrestrial-herbaceous habitats than any other region/country of the world, but Africa has had the greatest success in terrestrial-arborescent habitats.

Conclusions

This review documents the important role of Curculionidae in biological weed control. It is likely that species in this family will continue to make great contributions in the future. CBCW is a viable option for weed control because of its sustainability. As herbicide plant resistance increases with herbicide use and discoveries of new herbicide modes of action decrease, demand for sound biological control of weeds programmes will likely increase in the future. Pressure on practitioners of biological control of weeds to find safe and effective agents expeditiously also will increase across the globe. Non-target impact is one critical issue that needs more attention and more thorough evaluation.

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