



Prospects for biological control of *Ambrosia artemisiifolia* in Europe: learning from the past

E GERBER*, U SCHAFFNER*, A GASSMANN*, H L HINZ*, M SEIER† & H MÜLLER-SCHÄRER‡

*CABI Europe-Switzerland, Delémont, Switzerland, †CABI Europe-UK, Egham, Surrey, UK, and ‡Department of Biology, Unit of Ecology & Evolution, University of Fribourg, Fribourg, Switzerland

Received 18 November 2010

Revised version accepted 16 June 2011

Subject Editor: Paul Hatcher, Reading, UK

Summary

The recent invasion by *Ambrosia artemisiifolia* (common ragweed) has, like no other plant, raised the awareness of invasive plants in Europe. The main concerns regarding this plant are that it produces a large amount of highly allergenic pollen that causes high rates of sensitisation among humans, but also *A. artemisiifolia* is increasingly becoming a major weed in agriculture. Recently, chemical and mechanical control methods have been developed and partially implemented in Europe, but sustainable control strategies to mitigate its spread into areas not yet invaded and to reduce its abundance in badly infested areas are lacking. One management tool, not yet implemented in Europe but successfully applied in Australia, is biological control. Almost all natural enemies that have colonised *A. artemisiifolia* in Europe are polyphagous and cause little damage, rendering them unsuitable for a system

management approach. Two fungal pathogens have been reported to adversely impact *A. artemisiifolia* in the introduced range, but their biology makes them unsuitable for mass production and application as a mycoherbicide. In the native range of *A. artemisiifolia*, on the other hand, a number of herbivores and pathogens associated with this plant have a very narrow host range and reduce pollen and seed production, the stage most sensitive for long-term population management of this winter annual. We discuss and propose a prioritisation of these biological control candidates for a classical or inundative biological control approach against *A. artemisiifolia* in Europe, capitalising on past experiences from North America, Asia and Australia.

Keywords: common ragweed, non-native/exotic weed, biological control, integrated weed management, herbivory, fungi.

GERBER E, SCHAFFNER U, GASSMANN A, HINZ HL, SEIER M & MÜLLER-SCHÄRER H (2011). Prospects for biological control of *Ambrosia artemisiifolia* in Europe: learning from the past. *Weed Research* **51**, 559–573.

Introduction

In Europe, as in most other regions of the world, the number of alien plant species has increased considerably in the past 200 years as a result of increasing trade, tourism and disturbance (Pyšek *et al.*, 2009). However, in contrast to North America, South Africa, Australia or New Zealand, serious concern about the negative

economic or ecological effects of biotic invasions in Europe began to increase only recently (Hulme *et al.*, 2009). Because of this, regulation and management of exotic species in Europe is less advanced than elsewhere (Hulme *et al.*, 2009). Yet, Europe is also suffering from invasive species, and a crude estimate of monetary impact (costs of damage and control) suggests that this exceeds €12 billion annually (Kettunen *et al.*, 2009).

This is an underestimate, as potential economic and environmental impacts are unknown for most of the alien species found in Europe (Vilà *et al.*, 2010).

Like no other plant, *Ambrosia artemisiifolia* L. (common ragweed) has raised the awareness of invasive plants in Europe. First records of this plant species in western Europe date back to the mid-1800s and in eastern Europe to 1900, but it was only in the late 1920s that *A. artemisiifolia* became an increasing problem in Europe (Csontos *et al.*, 2010). The main concern regarding *A. artemisiifolia* is its large production of highly allergenic pollen that already causes rates of sensitisation among Europeans ranging from 15% (e.g. Germany, the Netherlands and Denmark) to 60% (Hungary: Rybnicek & Jäger, 2001; Tamarcaz *et al.*, 2005). This results in allergic rhinitis and severe asthma in over 20% of the population of affected areas (Kazinczi *et al.*, 2008).

The recent spread of *A. artemisiifolia* and the resulting increasing risk to human health and agriculture have resulted in a number of publications on the further invasion and potential danger of this invasive weed, its medical aspects, pollen monitoring across Europe and control methods at a local scale (Buttenschön *et al.*, 2009). In 2006, the national authorities in Hungary and Switzerland established a legal basis for mandatory control of *A. artemisiifolia*. Although chemical and mechanical control methods have been developed and partially implemented (Buttenschön *et al.*, 2009), sustainable control strategies to mitigate spread into areas not yet invaded and to reduce its abundance in badly infested areas are lacking in Europe. One management tool that has received little attention in Europe so far is biological control (cf. Müller-Schärer and Schaffner (2008), for a recent review on the various methods and strategies and Shaw *et al.* (2011) for control of *Fallopia japonica*). Based on a prioritisation scheme developed by Sheppard *et al.* (2006), *A. artemisiifolia* was identified as one of the 20 most promising species for classical biological control in Europe.

Ambrosia artemisiifolia also causes problems in the northern parts of North America, Australia and large parts of Asia, so there is a significant amount of information available on the biology of this plant and on the efficacy of various control measures. *Ambrosia artemisiifolia* has been subjected to classical biological control programmes in eastern Europe, Australia and eastern Asia with variable success (Julien & Griffiths, 1998; Zhou *et al.*, 2009). The information gathered in these biological control programmes may act as a basis on which to develop a biological control programme for Europe. Integration of biological control into existing short-term control measures may then lead to a sustainable management strategy of *A. artemisiifolia* and other *Ambrosia* species invasive in Europe.

This article outlines the present status, impact and management of *A. artemisiifolia* and other exotic *Ambrosia* species in Europe, reviews the available information on natural antagonists associated with *Ambrosia* species in Eurasia (their introduced range) and North and South America (their native range), summarises attempts to control *A. artemisiifolia* using biological control worldwide and explores prospects for its application in Europe, including a prioritisation of potential biological control organisms.

Taxonomy and distribution

Ambrosia species are annual or short-lived perennial plants in the family Asteraceae, placed in the tribe Heliantheae and subtribe Ambrosiinae. *Ambrosia* is said to contain between 21 (Sheppard *et al.*, 2006) and 41 species (Payne, 1966) worldwide. The genus is thought to have evolved in the Sonoran desert (south-western USA and adjacent Mexico) and subsequently radiated outwards, with species today mainly occurring in North and South America (Payne, 1966). The two species of main concern to Europe, *A. artemisiifolia* and *Ambrosia trifida* L., both apparently speciated after the genus had radiated, and neither species now occurs in the Sonoran desert (Payne, 1964). According to the Global Invasive Species Database, the native range of *A. artemisiifolia* includes Mexico, the United States and Canada (GISD, 2009).

Only one species of the genus, *Ambrosia maritima* L., is native in Europe, but it is restricted to the Mediterranean region (Greuter, 2006–2009). Payne (1966) suggested that *A. maritima* might be an ecological form of *A. artemisiifolia*, but its species status is now considered as accepted (Greuter, 2006–2009). Other genera within the subtribe Ambrosiinae include *Parthenium*, *Xanthium*, *Iva* and *Heptanthus*. With the exception of *Xanthium sibiricum* Patrin, a species native to Asia (GRIN, 2009), all other species from these genera are native only to North and/or South America (Bremer, 1994).

Several species have been accidentally introduced into Eurasia, four of which are naturalised in European countries (Table S1). *Ambrosia artemisiifolia* is the most important of the introduced *Ambrosia* species. This species has been recorded from almost all European countries (DAISIE, 2009; Table S1), but at variable densities. The regions most severely invaded in Europe are central (Hungary, Austria, Slovakia), eastern (Ukraine, European part of Russia), south-eastern (Romania, Croatia, Serbia) and southern Europe (southern France, Italy). In contrast, *A. artemisiifolia* is currently relatively rare in northern Europe (e.g. Ireland, Scotland, Norway and Sweden), but climate change is expected to facilitate the establishment of

ragweed as a self-propagating weed in these regions in the near future (Hyvönen *et al.*, 2011).

Based on molecular markers, populations in France have been found to have similar genetic variability as those in North America, but within-population variation was surprisingly higher in the introduced than in the native range (Genton *et al.*, 2005). Indeed, multiple sources of the French populations were diagnosed, but subsequent analyses showed that this was rather the result of introduction of seed mixtures containing different North American populations than due to multiple introductions (Genton *et al.*, 2005). The introduced range of two other species originating from North America, *A. trifida* and *Ambrosia psilostachya* DC, includes several European countries (EPPO, 2009; Table S1). A fourth species, *Ambrosia tenuifolia* Spreng., native to South America, is recorded from three European countries (Table S1). In addition to these four species, a single occurrence is reported for *Ambrosia acanthicarpa* Hook from the UK (GBIF, 2009).

Biology and dispersal

Ambrosia artemisiifolia is an annual pioneer species and flourishes in disturbed habitats, such as roadsides, waste places, construction sites, agricultural fields, disturbed or abandoned fields, waterways and urban areas (Fumanal *et al.*, 2008). This wind-pollinated monoecious plant has been assumed to be self-compatible and capable of selfing (Bassett & Crompton, 1975; Genton *et al.*, 2005), but more recent studies using allozyme markers demonstrated high outcrossing rates and strong self-incompatibility mechanisms (Friedman & Barrett, 2008). The plant overwinters as seed that germinates in spring. Plants are in the vegetative phase from May to August and bloom from August to October (Brandes & Nitzsche, 2007). Pollen production recorded for individual *A. artemisiifolia* plants collected in France ranged from 4 million to 10 billion grains and seed production from 346 to 6114 seeds per plant (Fumanal *et al.*, 2007a). *Ambrosia artemisiifolia* has a long-term persisting seedbank, with seeds remaining viable for more than 39 years (Bassett & Crompton, 1975).

Dispersal by seed occurs mostly by human activities through soil and seed transport (Bassett & Crompton, 1975). In addition, seeds can float and hydrochory appears to be an important dispersal mechanism along rivers, explaining the rapid colonisation of newly formed sand and gravel bars (Fumanal *et al.*, 2007b). *Ambrosia trifida* L. is also an annual weed, and its biology is similar to that of *A. artemisiifolia*, but it is more frost-resistant, develops faster and its mature seeds appear earlier (EPPO, 2009). *Ambrosia psilostachya* and *A. tenuifolia* Spreng. are perennial species. *Ambrosia*

psilostachya is considered to have less potential for establishment and spread in Europe, because it produces less seeds than the two annual exotic *Ambrosia* species (EPPO, 2009).

Impact and management

Impact on human health

Ambrosia species produce allergenic pollen, which can induce allergic disease, such as rhinitis, conjunctivitis and asthma, as well as contact dermatitis and urticaria (e.g. Tamarcaz *et al.*, 2005; Kazinczi *et al.*, 2008). A clear correlation was found between the amount of airborne pollen and the proportion of allergic response in the population (Jäger, 2000), with a threshold value of *c.* 10 pollen grains per m³ provoking allergic rhinitis in sensitive persons, compared with 50 grass pollen grains (Tamarcaz *et al.*, 2005). The medical costs of these allergies are already substantial in highly infested regions in Europe, such as in Hungary (110 million € per year; Kazinczi *et al.*, 2008) and Austria (88 million € per year; S. Jäger, HNO-Klinik, Med-UniWien, pers. comm.).

Besides financial losses because of expensive anti-allergy treatments, lost working time caused by debilitating allergic reactions constitutes an additional significant economic cost to society. In highly infested regions, *A. artemisiifolia* has rapidly become the main allergen, as it is in North America, where its pollen has been reported to account for 50–75% of pollen allergies (Frenz, 1999). Because of its late flowering, pollen affects allergic individuals at a time when many would normally be experiencing relief from their symptoms. *Ambrosia* species thus extend the ‘problem season’ of the pollen-allergic population. As a further consequence of its wide distribution and severe impact on human health, tourism can be affected if visitors avoid areas with high *Ambrosia* occurrence (e.g. the Dalmatian coast in Croatia).

Impact on agriculture

In Europe, *A. artemisiifolia* is mainly reported as a weed of spring-sown crops, causing significant yield losses, especially in sunflower, maize, sugar beet, soyabeans and cereal crops (Kazinczi *et al.*, 2008). Damage is especially high in crops with low canopy height, such as beets, which can have up to 70% yield loss (Buttenschön *et al.*, 2009). Because of its late emergence, *A. artemisiifolia* can also establish and reach high densities during intercrop periods in oilseed rape or cereal stubbles, as well as on fallow and set-aside land (Kazinczi *et al.*, 2008). In South Hungary and East Croatia, it is economically the most important weed in sunflower and soyabean, causing highest yield reductions and control costs

(Buttenschøn *et al.*, 2009). The species is particularly problematic for Hungary, where sunflower is a major crop plant, and where *A. artemisiifolia* was present on 5.4 million ha in 2003, of which 700 000 ha were heavily infested (Tóth *et al.*, 2004). Yield losses alone were estimated at €130 million per year for Hungary (Kémives *et al.*, 2006). Furthermore, herbicide use is greatly limited in sunflower because of its botanical similarity with the weed. The occurrence of *A. artemisiifolia* in sunflower crops further facilitates the dissemination of the plant throughout Europe, mainly as bird seed and crop seed. In addition, widespread herbicide resistance (e.g. Kazinczi *et al.*, 2008) and the ban or dose reduction of efficient herbicides greatly limit successful short-term management in crop fields.

Impact on biodiversity

As a pioneer species, *A. artemisiifolia* is a species primarily of secondary succession. It is generally dominant in undisturbed areas only in the first year of colonisation, but then, because of its late emergence, it is replaced by perennial species (Buttenschøn *et al.*, 2009). In early successional fields, dense layers of *A. artemisiifolia* in spring can temporarily reduce the number of native species, but this effect disappears again later in the season (Armesto & Pickett, 1985). In general, the habitat preference of *A. artemisiifolia* makes most habitats of high nature conservation value unsuitable for the species, but colonisation of dry and semi-dry grassland, open steppe vegetation, sand dunes and embankments along rivers has been reported (Brandes & Nitzsche, 2007).

Current management of Ambrosia species

Prevention of invasion is the most cost-effective measure against plant invaders. The alarming figures outlined earlier prompted some authorities to react quickly by establishing awareness-raising programmes and guidelines for prevention, early detection and rapid response (Buttenschøn *et al.*, 2009). This includes information and awareness campaigns, limiting unintentional spreading of *A. artemisiifolia* seeds and monitoring areas prone to invasions, such as along transport corridors.

However, the ability of *A. artemisiifolia* to grow side branches after partial control and its high multiplication rate renders control challenging. Herbicides and mechanical control (uprooting, cutting and ploughing) are best suited as local and short-term measures to eradicate initial and small populations and to mitigate further spread of established populations. Herbicide treatments in crops may be sufficient to prevent yield losses, but cannot prevent *A. artemisiifolia* populations

from flowering and setting seeds. In non-agricultural land, eradication of *A. artemisiifolia* using herbicides can be envisaged (Gauvrit & Chauvel, 2010), but often financial constraints and the need to protect the accompanying vegetation do not allow large-scale application of herbicides. Here, as well as in crops, the management of a competitive plant cover (the crop or the native vegetation) was found to reduce the biomass of *A. artemisiifolia* effectively, but again, seed set could not be prevented (Buttenschøn *et al.*, 2009).

Thus, effective short-term control measures that reduce the biomass of *A. artemisiifolia* are available for most crop species. However, flowering (including pollen production) and seed set and thus population propagation of *A. artemisiifolia* cannot be prevented at present. The large area already invaded by *A. artemisiifolia* in Europe and the fact that grassland communities, open habitats and riverbanks are increasingly invaded (DAISIE, 2009) will not only increase the impact on human health, but also on major crops across Europe, rendering this plant invader economically significant. Sustainable control strategies to mitigate its further spread into areas not yet invaded and to reduce its abundance in badly infested areas are therefore urgently needed in Europe. One alternative management option, already successfully implemented in several countries, is biological control.

Antagonists of *Ambrosia artemisiifolia*

To assess whether any natural enemies (herbivores or fungal pathogens) attacking *A. artemisiifolia* in its introduced range in Eurasia could be used in a system management approach in Europe or in an inundative approach using native antagonists, we conducted a literature survey using the 'CAB Abstracts' and 'scholar.google.com' databases in August 2009, using the search terms '*Ambrosia*' or 'ragweed', in combination with 'herbivore' or 'insect' or 'pathogen' or 'natural enem*' or 'biological control', with no restriction on publication year. From all retrieved papers, we also screened the reference lists for other suitable publications. A similar search was conducted for the native range to compile a comprehensive list of herbivores and pathogens associated with *A. artemisiifolia* and other *Ambrosia* species, as background data for a potential classical biological control approach or an inundative approach using exotic biological control agents.

Herbivores and pathogens associated with Ambrosia artemisiifolia in Eurasia

In total, the literature review revealed some 40 insect species (including two unidentified geometrids) associated

with *A. artemisiifolia* in Eurasia (Table S2). Most of these insect species are polyphagous, and they appear to cause only moderate damage to *A. artemisiifolia*. The only exception is the moth *Ostrinia orientalis* Mutuura & Munroe (Lepidoptera: Pyralidae), which was found to significantly reduce biomass and plant height of *A. artemisiifolia* in China (Wan *et al.*, 2003); however, this species is also recorded from *Xanthium sibiricum* and *Rumex* species (Polygonaceae) and hence has a relatively broad host range (Ishikawa *et al.*, 1999).

Of the 20 fungal pathogens found associated with *Ambrosia* species in Eurasia (Table S2), most have a wide host range and have little impact on the plant in the field (Kiss *et al.*, 2003). Outbreaks of disease epidemics caused by two biotrophic fungal pathogens, *Phyllachora ambrosiae* (Berk. & M.A. Curtis) Sacc. and *Plasmopara halstedii* (Farl.) Berl. & De Toni, did affect *A. artemisiifolia* in Hungary in 1999 and 2002 (Vajna *et al.*, 2000; Vajna, 2002), but not in other years (Kiss, 2007). A newly described species associated with *A. artemisiifolia* in Hungary, *Septoria epambrosiae* D.F. Farr (Farr & Castlebury, 2001), is also known from *A. trifida* in North America. In China, the damaging microcyclic rust *Puccinia xanthii* Schwein. has been recorded from *A. trifida* as *P. xanthii* f. sp. *ambrosiae-trifidae* Batra (Lu *et al.*, 2004), following Batra's initial classification of a host-specific *P. xanthii* accession from the same host plant in North America (Batra, 1981). This rust species is considered to comprise a number of host-specific rust populations adapted to specific Asteraceae hosts (Batra, 1981; Morin *et al.*, 1993; Kiss, 2007; Seier *et al.*, 2009).

Herbivores and pathogens associated with Ambrosia species in their native range

Compared with the low number of phytophagous organisms associated with *Ambrosia* species in their introduced range in Eurasia, numerous species are known from their native range. A combination of literature surveys, studies of museum collections and field surveys conducted from 1965 onwards has identified as many as 450 species of insects, mites and fungi associated with *Ambrosia* species in North and South America (Goeden & Andres, 1999). On individual *Ambrosia* species, as many as 113 (on *Ambrosia psilostachya*) and 88 (on *Ambrosia confertifolia* DC) insect species were recorded in Southern California alone (Goeden & Ricker, 1975, 1976). Many of these species also feed on other genera in the Asteraceae or other families. However, a combined literature and internet survey for species potentially specific at the subtribe level (i.e. associated with *Ambrosia* species and for which no other host plant record has been found outside of the

subtribe Ambrosiinae) revealed 109 specialist invertebrate (Table S3) and 19 specialist fungal species (Table S4). This amounts to c. 36% and 25% of the total number of invertebrates and fungal species recorded from the native range respectively. Within invertebrates, Lepidoptera (40 species) largely dominate, followed by Coleoptera (28 species), Diptera (19 species) and Hemiptera (18 species). In addition, four mite species have been recorded from members of the genus *Ambrosia*. The majority of herbivores with a known feeding niche are leaf feeders (50%), followed by stem miners (28%), seed feeders (12%) and flower or pollen feeders (9%).

Numerous fungal pathogens associated with *Ambrosia* species in the native range have a wide host range, either within the Asteraceae or across a number of different plant families. However, some fungal species are similarly restricted to the genus *Ambrosia*, e.g. *Septoria ambrosiicola* Speg. and *Passalora ambrosiae* (Chupp) Crous & U. Braun (synonym *Cercospora ambrosiae* Chupp; see Table S4). Other pathogen species such as the white blister 'rust', *Pustula tragopogonis* (Pers.) Thines [synonym *Albugo tragopogonis* (D.C.) Gray], and the true rust *P. xanthii* have been recorded from a number of different genera within the Asteraceae; however, *P. tragopogonis* and, as indicated earlier, *P. xanthii* have been shown to comprise different formae speciales with a highly restricted host range. The existence of formae speciales is also known for the powdery mildew species *Golovomyces cichoracearum* var. *chichoracearum* (DC.) V.P. Heluta (synonym *Erisyphe cichoracearum* DC.), and a restricted host range of accessions of this pathogen associated with *A. artemisiifolia* cannot be ruled out (Ellison & Barreto, 2003).

Biological control of *Ambrosia* species

Biological control of Ambrosia species in their native range

Ambrosia artemisiifolia and *A. trifida* are also noxious weeds in their native range, in particular in Canada (Cowbrough, 2006) and in the northern United States (USDA-NRCS, 2009), causing allergenic hay fever (Bassett & Crompton, 1975). As the highest densities of both species are found in the most densely populated part of Canada (southern Ontario and Quebec), the feasibility of the mycoherbicide approach, i.e. the periodic inundative application of high doses of indigenous pathogens over an entire weed population, was studied in both Canada and the USA. *Protomyces gravidus* Davis, which attacks *A. artemisiifolia*, *A. trifida*, *Xanthium strumarium* L. and members of the genus *Bidens* (tribe Coreopsideae, Asteraceae), was studied in

the USA (Cartwright & Templeton, 1988; Table S4). The species causes stem gall disease and killed plants when these were infected systemically. However, the low rate of infection and lack of virulence when applied as a mycoherbicide strongly limited the ability of this organism to control *A. artemisiifolia*. The project was therefore stopped.

A forma specialis of *P. tragopogonis* has been described from *A. artemisiifolia* in Canada (Hartmann & Watson, 1980; Appendix S1). Attack by *P. tragopogonis* can be very damaging and significantly reduces pollen and seed production if systemic infection is achieved (Hartmann & Watson, 1980), but difficulties in mass producing this white blister 'rust' have so far prevented the pathogen from being produced commercially (Teshler *et al.*, 2002).

A *Phoma* sp., recorded on *A. artemisiifolia* in North America, was considered as a potential mycoherbicide candidate (Brière *et al.*, 1995). A combination of this *Phoma* sp. and the leaf beetle *Ophraella communa* LeSage (Coleoptera: Chrysomelidae) had a synergistic effect and resulted in high plant mortality (Teshler *et al.*, 1996). Unfortunately, the culture of *Phoma* sp. lost its virulence and attempts to revive or re-isolate the species from natural sites failed (Teshler *et al.*, 2002). Two plurivorous pathogens, the soil-borne fungus *Rhizoctonia solani* J.G. Kuehn and the Gram-negative bacterium *Pseudomonas syringae* pv. *tagetis* (Hellmers) Young, Dye & Wilkie, have also been preliminarily evaluated as potential biocontrol agents for a crop management strategy against *Ambrosia grayi* (A. Nelson) Shinnery in the USA (Sheikh *et al.*, 2001). Under glasshouse conditions, *R. solani* was shown to cause significant disease in inoculated *A. grayi* plants seen as an increase in root necrosis and a reduction in plant emergence, as well as in fresh and dry leaf weight (Wheeler *et al.*, 1998). *Pseudomonas syringae* pv. *tagetis* proved to be pathogenic towards *A. grayi* causing systemic chlorosis in infected plants during glasshouse trials. Subsequent field trials conducted in Texas showed the bacterium to be effective against the weed at relatively low concentrations and following a single application (Sheikh *et al.*, 2001).

The beetles *Zygogramma suturalis* Fabricius (Table S3) and *Ophraella communa* LeSage are natural enemies of *A. artemisiifolia* in Canada and the United States and were studied as inundative biological control agents (Teshler *et al.*, 2002). The reduction or cessation of *Z. suturalis* oviposition on extensively damaged plants (as observed in the former USSR; Appendix S1) and pupation in soil are, however, an important limitation for the mass-rearing of this species (Teshler *et al.*, 2002). Under natural conditions, population densities and impact of *O. communa* in North America tend to be low, presumably because of strong attack by predators

and parasitoids by the end of summer (Teshler *et al.*, 2002). It was therefore suggested to use it in inundative biological control and to make releases of beetles early in the growing season (Teshler *et al.*, 1996).

Classical biological control of Ambrosia species worldwide

There is a long history of classical biological control attempts against exotic *Ambrosia*, mainly *A. artemisiifolia*, in different parts of the world, including eastern Europe (Russia, former Yugoslavia, Georgia, Ukraine), Australia and Asia (China and Kazakhstan). Classical biological control of *Ambrosia* species outside the native range started in the former Soviet Union in the 1960s, when more than 30 insect species from North America were introduced into quarantine (Goeden & Andres, 1999). In 1969, the release of the noctuid moth *Tarachidia candefacta* Huebner (Table S3) collected on *A. artemisiifolia* in Canada and California was the first intentional introduction of a natural enemy for the biological control of an invasive exotic plant into Europe (Kovalev, 1971). In 1972, a subspecies of *T. candefacta* collected on *A. psilostachya* (now *Ambrosia coronopifolia* Torr. & A. Gray) was also released (Kovalev, 1971; Julien & Griffiths, 1998), but so far, *T. candefacta* has been unsuccessful as a biological control agent (Appendix S1).

In 1978, the leaf beetle *Z. suturalis* (Table S3) was released and quickly established in the North Caucasus (Julien & Griffiths, 1998) and has since spread practically over the whole area heavily infested by *A. artemisiifolia* in Russia (Reznik *et al.*, 2007). In the same year, the species was also released in Kazakhstan, Georgia and Ukraine, but establishment is only confirmed in Kazakhstan (Julien & Griffiths, 1998). *Zygogramma suturalis* was further released in 1985 and again in 1990 in former Yugoslavia (now Croatia). At first, the results obtained with this beetle in Russia were very promising (Reznik, 1991). It reached densities as high as 5000 individuals per m² in a crop field in southern Russia and completely destroyed all of the *A. artemisiifolia*, thereby increasing crop yield by two- to threefold (Goeden & Andres, 1999). Further investigations have, however, shown that *Z. suturalis* is not able to control the weed sufficiently (Reznik, 1991; Reznik *et al.*, 2007; Appendix S1).

Between 1980 and 1984, three biological control agents from México were introduced into Australia for the biological control of *Parthenium hysterophorus* L., a species closely related to the genus *Ambrosia*: the leaf-feeding chrysomelid beetle *Zygogramma bicolorata* Pallister, the sap-sucking bug *Stobaera concinna* (Stål) and the tip-galling moth *Epiblema strenuana* Walker

(Table S3; McFadyen & Weggler-Beaton, 2000). All three insects also attack *A. artemisiifolia*, and in particular, *E. strenuana* is reported to reduce the size, abundance and pollen production of the weed. In 1990, *Z. suturalis* was introduced into Australia from the USA to increase *A. artemisiifolia* control, but the species failed to establish (Julien & Griffiths, 1998). Presently, *A. artemisiifolia* is considered under good control in south-eastern Queensland and northern New South Wales (Palmer *et al.*, 2010). From an economic point of view (Page & Lacey, 2006), biological control of *A. artemisiifolia* is regarded as an outstanding success in Australia (Palmer *et al.*, 2010).

Releases of *Z. suturalis* in China in 1985, both from Canada and from the former Soviet Union, resulted in establishment in some locations, but failed in others (Wan *et al.*, 1995). The seed-feeding fly *Euaresta bella* (Loew) was introduced into China in the late 1980s, but as in Russia, this fly failed to establish (Zhou *et al.*, 2009). In 1991, *E. strenuana* was introduced from Australia into China where additional host specificity tests were conducted (Wan *et al.*, 1995). In contrast to results from tests conducted in Australia (McFadyen, 1992), *E. strenuana* was able to complete its development on a local sunflower variety tested (Wan *et al.*, 1995), but the risk of *E. strenuana* causing economic damage to sunflowers was considered to be low (Appendix S1).

In addition to the deliberate releases of these biological control agents, the North American leaf beetle *O. communa* was accidentally introduced into Japan in the late 1990s (Yamanaka *et al.*, 2007 and references therein). In 2001, it was also found in Jiangsu province in China (Zhang *et al.*, 2005), from where good control of *A. artemisiifolia* populations is reported (Zhou *et al.*, 2009). Recently, a mass-rearing programme was established with *O. communa* in China with the aim to use this agent for inundative application in severely invaded habitats (Zhou *et al.*, 2009).

Biological control options for Europe: learning from the past

While both the inundative and the system management approach are primarily aimed at crop weeds, the classical approach has traditionally and most successfully been used against invasive plants spreading over large areas of natural and semi-natural habitats, extensively managed agro-ecosystems or aquatic ecosystems (environmental weeds; Müller-Schärer & Schaffner, 2008). As outlined earlier, with the possible exception of distinct virulent strains of *Puccinia xanthii* as well as the two pathogens *Phyllachora ambrosiae* and *Plasmopara halstedii*, no natural enemy recorded on *A. artemisiifolia* and other exotic *Ambrosia* species in Eurasia so far appears to be

sufficiently specific and/or damaging, particularly with regard to long-term and sustainable control. The apparent lack of a regular re-occurrence of epiphytotics by *P. ambrosiae* and *P. halstedii* (Kiss, 2007) raises the question whether they could be facilitated through artificial inundative application of these two fungal pathogens. However, neither of these fungi can be cultured *in vitro*; thus, their biology makes them presently unsuitable for mass production and application as a mycoherbicide. This renders a system management approach or an inundative application of European antagonists to control *A. artemisiifolia* in Europe unlikely and leaves either classical biological control or an inundative application of exotic organisms for managing *A. artemisiifolia* in Europe by biological means.

When developing a biological control approach as part of an integrated management programme against *A. artemisiifolia* in Europe, priority should be given to organisms with a narrow host range and that have the potential to either negatively impact the population growth rate of ragweed or to reduce ragweed biomass quickly. In terms of host specificity, one of the most critical issues is the close relatedness of the target to the commercially important sunflower, *Helianthus annuus*. As sunflower varieties might differ in their susceptibility to biological control candidates (Morin *et al.*, 1993), several varieties need to be included in biosafety studies, especially those that occur in the regions where *A. artemisiifolia* is abundant and biological control agents are planned to be released. Only one plant species of the subtribe Ambrosiinae is considered native to Europe, *A. maritima*, which is furthermore restricted to the Mediterranean. Such a low number of very closely related native species increases the chance of finding 'safe' biological control agents (Pemberton, 2000). On the other hand, because of the observed high within-population variation of *A. artemisiifolia* found in France (Genton *et al.*, 2005), biological control agents should also be not too (genotype or host strain) specific to account for genetic differences among populations and to control all individuals in a population.

In terms of impact, flower-, pollen- and seed-feeding organisms or those that contribute to a reduction in seed output should be considered first when applying the classical biological control approach. This is because pollen production is the prime factor causing the high impact on human health and a reduction in seed output is likely to translate into reduced population densities and dispersal of annuals (Ramula *et al.*, 2008). On the other hand, natural enemies that quickly reduce the biomass are expected to be especially suited for an inundative application to reduce crop losses because of competition (Müller-Schärer *et al.*, 2000; Harrison *et al.*, 2001). There is generally a lack of information on

whether ragweed specialists are able to reduce biomass of *A. artemisiifolia* quickly, but indirect evidence may come from congeners that are known to damage their host plants. Building on the information compiled earlier, we propose an outline to tackle biological control of *A. artemisiifolia* in Europe, involving both pathogens and insects and different biological control strategies for different habitats. Our prioritisation of potential biological control candidates for *A. artemisiifolia* is based on evidence of their narrow host range, their feeding niche and control efficacy, availability and suitability to rear, and past experience. This allowed us to identify 23 potential agents, seven of which were given first priority (Table 1 and Fig. 1).

Redistribute insects already established as biological control agents in eastern Europe

The moth *Tarachidia candefacta* is well established in Russia but so far is considered an ineffective agent. Predation of the exposed larvae (Goeden & Andres, 1999) and unsuitable climatic conditions (Poltavsky & Artokhin, 2006) have been stated as potential reasons for its failure. While in the past, strong frosts might have limited population growth, Poltavsky and Artokhin (2006) observed increased numbers in Rostov-on-Don from 2003 onwards after a series of mild winters. Based on the criteria listed above, we give this species first priority for further studies (Table 1, Fig. 1). Prior to considering *T. candefacta* or any other insect tested in Russia for further relocation or for release in Europe, additional host specificity tests need to be conducted, in particular with native plant species in the family Asteraceae. At the time when these insects were released in Russia, the main emphasis of host specificity tests was placed on crop plants, assuring that the species would not attack cultivated species.

Re-evaluate insect species tested and released in Russia that failed to establish

Three insect species, i.e. *Euaresta bella*, *Trigonorhinus tomentosus* (Say) and *Zygogramma disrupta* Rogers, were found to be sufficiently specific in host specificity tests conducted in Russia and were released, but did not establish (Julien & Griffiths, 1998). Additional releases of these insects should be attempted, in particular to establish *Trigonorhinus tomentosus* and *E. bella*, as these species occupy feeding niches exploited neither by native herbivores nor by the two established biological control agents *T. candefacta* and *Z. suturalis* in Russia. Larvae of *E. bella* develop in seeds, thereby directly reducing seed output. *Trigonorhinus tomentosus* feeds as adult and larva on pollen and could directly contribute to reduce

pollen load in the air. The third species, *Z. disrupta*, occupies a similar feeding niche as *Z. suturalis*. Additional efforts to establish this species could be considered, in case *Z. disrupta* does not display oviposition inhibition on damaged *A. artemisiifolia* as seen for *Z. suturalis*. We rank all these three species as first-priority control agents (Table 1, Fig. 1).

Reconsider species that have been studied but, for different reasons, were never released

Zygogramma tortuosa Rogers, originally recorded from *Ambrosia eriocentra* Gray, was introduced for testing in quarantine in Russia, but was rejected because adults also fed on sunflower (reviewed in Goeden & Ricker, 1979). Goeden and Ricker (1979) found, however, that *Z. tortuosa* did not feed and females did not oviposit on sunflower in open field tests. Furthermore, first instar larvae transferred onto sunflowers were not able to complete their development. *Zygogramma tortuosa* might therefore be reconsidered as a biological control agent, in particular if it does not show a similar oviposition inhibition on damaged *A. artemisiifolia* as *Z. suturalis*. Of the three *Zygogramma* species listed in Table 1, we consider *Z. disrupta* as the most promising biological control candidate and give *Z. tortuosa* second priority.

Three cecidomyid flies, *Contarinia partheniicola* Cockerell and *Rhopalomyia ambrosiae* Gagné and the stem-mining *Neolasioptera ambrosiae* Felt (Table S3), are likely to be host specific and have therefore been proposed as potential biological control agents against *A. artemisiifolia* (Gagné, 1975). Another gall midge, *Asphondylia ambrosiae* Gagné, was originally considered for field release in Australia, but as its larvae feed on symbiotic fungi, a release of *Asphondylia ambrosiae* would require the simultaneous importation of the fungi, which makes the use of this cecidomyiid fly as a biological control agent rather unlikely (Goeden & Palmer, 1995). *Neolasioptera* larvae may also rely on symbiotic fungi, but *C. partheniicola* and *Rhopalomyia ambrosiae* are not considered to live in symbiosis with fungi (Skuhravá, pers. com.). However, these appear to be difficult to collect; despite repeated, intensive surveys in Texas and Florida, *Rhopalomyia ambrosiae* could not be relocated and only small numbers of *C. partheniicola* were found (Goeden & Palmer, 1995). Nevertheless, these Dipteran species may have some potential as biological control agents against *A. artemisiifolia* in Europe (Table 1).

Assessment of additional phytophagous organisms recorded on Ambrosia species in the native range

The list of organisms recorded from *Ambrosia* species in their native range is long, and several species appear to

Table 1 Host range, prioritisation and management approach for proposed biological control candidates against *Ambrosia artemisiifolia* in Europe (see text for details)

Taxon	Host range*			Priority for Europe	Management approach
	Field observations	Experimental studies	Biosafety/feasibility		
Insecta					
Coleoptera					
<i>Ophraella slobodkini</i>	AMBEL	AMBEL, Ivafr		1	Classical/ inundative?
<i>Smicronyx perpusillus</i>	AMBEL	?		1	Classical
<i>Smicronyx tessellatus</i>	AMBEL, <i>Ambrosia</i>	?	Attack of <i>Ambrosia maritima</i> ?	2	Classical
<i>Trigonorhinus tomentosus</i> †	Ambca, FRSCO, Ambce, AMBDU, AMBER	AMBEL‡	Attack of <i>A. maritima</i> ? Establishment?	1	Classical
<i>Zygogramma bicolorata</i> §	AMBEL, <i>Parthenium</i>	?	Attack of <i>A. maritima</i> ?	2	Classical
<i>Zygogramma disrupta</i> †	AMBEL	AMBEL‡	Establishment?	1	Classical
<i>Zygogramma tortuosa</i> †	AMBER	<i>Ambrosia</i>	Attack of <i>A. maritima</i> ?	2	Classical
Diptera					
<i>Callachna gibba</i>	AMBEL, AMBPS	?	Attack of <i>A. maritima</i> ?	2	Classical
<i>Contarinia partheniicola</i>	Ambca, FRSCO, AMBDU, AMBER, AMBPS, Parin	?	Rare in native range?	2	Classical
<i>Euaesta bella</i> †	AMBEL	AMBEL‡	Establishment?	1	Classical
<i>Euaesta toba</i>	AMBEL, AMBCU, AMBTE	?	Attack of <i>A. maritima</i> ?	2	Classical
<i>Rhopalomyia ambrosiae</i>	AMBEL, AMBPS	?	Rare in native range?	2	Classical
Hemiptera					
<i>Stobaera concinna</i> §	AMBEL, <i>Parthenium</i>	?	Attack of <i>A. maritima</i> ?	2	Classical
Lepidoptera					
<i>Adania ambrosiae</i>	FRSAC, AMBEL, Ambca, AMBER, AMBPS	?	Attack of <i>A. maritima</i> ?	2	Classical
<i>Bucculatrix agnella</i>	AMBEL	?	Attack of <i>A. maritima</i> ?	2	Classical
<i>Schinia rivulosa</i>	AMBEL, AMBPS, <i>Ambrosia</i>	?	Attack of <i>A. maritima</i> ?	2	Classical
<i>Tarachidia candefacta</i> †	AMBEL, FRSCO, AMBPS	AMBEL¶	Attack of <i>A. maritima</i> ?	1	Classical
<i>Tischeria ambrosiae</i> ella	AMBEL, AMBTE	?	Attack of <i>A. maritima</i> ?	2	Classical
Fungi					
Ascomycota					
Dothideomycetes					
Capnodiales					
Mycosphaerellaceae					
<i>Septoria ambrosiicola</i> Speg.	<i>Ambrosia</i>		Attack of <i>A. maritima</i> ?	2	Classical/ inundative?
<i>Septoria epambrosiae</i> D.F. Farr	<i>Ambrosia</i>		Attack of <i>A. maritima</i> ?	2	Classical/ inundative?
<i>Passalora ambrosiae</i> (Chupp) Crous & U. Braun	<i>Ambrosia</i>		Attack of <i>A. maritima</i> ?	2	Classical
<i>Passalora trifidae</i> (Chupp) U. Braun & Crous	<i>Ambrosia</i>		Attack of <i>A. maritima</i> ?	2	Classical
Basidiomycota					
Pucciniomycetes					
Pucciniales					
Pucciniaceae					
<i>Puccinia xanthii</i> Schwein.				1	Classical

*Plant species: Eppo (Bayer) codes used when available (codes in capitals; see <http://eppt.eppo.org/index.php>); (*A.* = *Ambrosia*) FRSAC: *A. acanthicarpa*; AMBEL: *A. artemisiifolia*; Ambca: *A. chamissonis*; FRSCO: *A. confertiflora*; Ambce: *A. chenopodiifolia*; AMBCU: *A. cumanensis*; AMBDU: *A. dumosa*; AMBDE: *A. deltoideae*; AMBER: *A. eriocentra*; AMBPS: *A. psilostachya* (now *A. coronopifolia*); AMBTE: *A. tenuifolia*; Ivafr: *Iva frutescens*; Parin: *Parthenium incanum*.

†Tested as classical biological control agent against *A. artemisiifolia*.

§Released as classical biological control agent against *Parthenium hysterophorus*.

‡According to tests conducted in Russia but no access to data.

¶According to tests conducted in Russia (Kovalev, 1971).

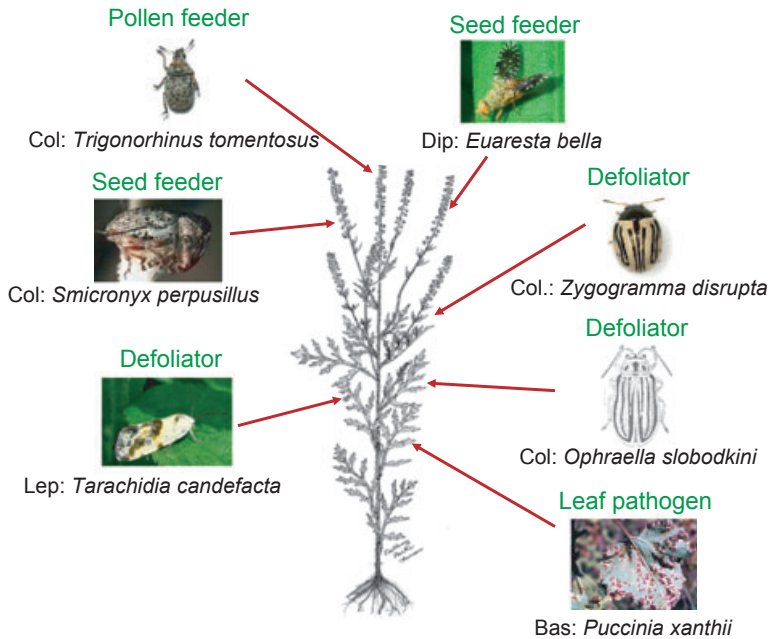


Fig. 1 Most promising candidate species for biological control of *Ambrosia artemisiifolia* in Europe and their feeding niche. Col., Coleoptera; Dip., Diptera; Lep., Lepidoptera; Bas., Basidiomycota.

have a narrow host range and are potentially of interest for biological control (Tables S3 and S4). However, Goeden and Palmer (1995) cautioned that the knowledge of the host range information on insects associated with Ambrosiinae might not prove to be reliable. Based on our prioritisation criteria given earlier, we propose several species associated with *A. artemisiifolia* in its native range to be considered as potential biocontrol agents for *A. artemisiifolia* (Table 1, Fig. 1) or potentially any of the other invasive *Ambrosia* species in Europe (Table S1).

Evaluation of invertebrates

The high number of species in the Curculionidae genus *Smicronyx* and the Lepidoptera genera *Schinia*, *Bucculatrix* and *Epiblema* recorded from *Ambrosia* species (Table S3) may indicate that speciation has occurred within the Ambrosiinae and consequently, narrow host associations can be expected. Furthermore, species in the genera *Epiblema* and *Smicronyx* have been reported to be successful biological control agents against *Parthenium hysterophorus* (McFadyen & Weggler-Beaton, 2000), indicating their potential as biological control agents for *Ambrosia* species. Of particular interest is the seed-feeding weevil, *Smicronyx perpusillus* Casey, which is only reported from *A. artemisiifolia* and to which we therefore give first priority (Table 1, Fig. 1).

Two additional species with a presumably narrow host range are the moth *Bucculatrix agnella* Clemens and the leaf beetle *Ophraella slobodkini* Futuyama, both of which feed on leaves. A closely related species of *Bucculatrix agnella*, *Bucculatrix parthenica* Bradley, was found to be specific enough to be released in

Australia for the biological control of *P. hysterophorus* (McFadyen, 1992). *Ophraella slobodkini* is described only from *A. artemisiifolia*, but could also be reared on the closely related *Iva frutescens* L. in the laboratory (Futuyama, 1991). Larval survival was, however, lower and development time longer than on *A. artemisiifolia*, suggesting that this species is indeed more specific than *O. communis* that was accidentally introduced to China and Japan (Appendix S1). Provided *O. slobodkini* is as damaging as its congener, it might contribute to the control of *A. artemisiifolia* in Europe, using either the classical or the inundative approach (as with *O. communis* in China). We therefore give this species first priority. Previous experiences in biological control of *A. artemisiifolia* indicate that defoliators can be effective in controlling plant populations in the invaded range (Appendix S1).

In addition to these three species that seem to feed exclusively on *A. artemisiifolia* under field conditions, several other insect species are reported from *A. artemisiifolia* and also from other *Ambrosia* species in their native range (Table 1). These species could possibly be considered as biological control agents against *A. artemisiifolia* in Europe, if the risk of non-target attack on *A. maritima*, the only native congeneric species in Europe, turns out to be minimal. Moreover, several insect and mite species listed in Table S3, including the eriophyid mite *Eriophyes boycei* Keifer, which was also considered as a potential agent of *A. artemisiifolia* in the former Soviet Union but did not survive the transport (Goeden *et al.*, 1974), have been recorded on other *Ambrosia* species, but not on *A. artemisiifolia* under field conditions. Some of these

herbivores may also have potential as biological control agents against *A. artemisiifolia*, provided that this plant species belongs to their fundamental host range.

Evaluation of fungal pathogens

The potential of pathogens to impact adversely on *A. artemisiifolia* and its pollen production was documented during naturally occurring epiphytotics of *Phyllachora ambrosiae* and *P. halstedii* observed in Hungary in 1999 and 2002 (Vajna *et al.*, 2000; Vajna, 2002; Kiss *et al.*, 2003).

Among the range of fungal pathogens known to attack *Ambrosia* species in their native range (see Table S4), the highly damaging rust fungus *P. xanthii* is the most promising candidate for biological control of *A. artemisiifolia*. The rust completes its life cycle on one of the host species, and while recorded from numerous genera of the Asteraceae (Hennen *et al.*, 2005), individual rust populations or accessions within *P. xanthii* have shown a high degree of host specialisation. For example, an accession of *P. xanthii* collected on *A. trifida* in North America showed high specificity to its original host, but failed to infect *A. artemisiifolia* and *X. strumarium*; this accession was therefore named *P. xanthii* f. sp. *ambrosiae-trifidae* (Batra, 1981). Similarly, accessions of the rust originating from *Xanthium* species were shown to be non-infectious to *A. artemisiifolia* (Morin *et al.*, 1993; Kiss, 2007). Accessions of *P. xanthii* from *A. artemisiifolia* collected in Texas (USA) in 1989 showed evidence of an equally high host specialisation; they proved to be highly pathogenic to an *A. artemisiifolia* biotype from Australia during initial evaluations, while failing to infect *P. hysterophorus* and *Xanthium* species (H.C. Evans, pers. comm.). The significant impact *P. xanthii* can have on its hosts has been documented in China when a sudden outbreak of *P. xanthii* f. sp. *ambrosiae-trifidae* on *A. trifida* caused serious die-back of infected plants in 2003 (Lu *et al.*, 2004). In Australia, a strain of *P. xanthii* successfully controlled a number of highly invasive *Xanthium* species of the Noogoora burr complex (Morin *et al.*, 1996). Based on the documented host specificity of individual *P. xanthii* accessions and their damaging impact, we give this rust first priority. Doubts have been cast on the potential of *P. xanthii* as a biocontrol agent for *A. artemisiifolia*, based on a lack of disease incidence following unsuccessful attempts to collect the rust on this host in North America in 2002 and 2003. However, these latest surveys included neither the region in Texas, where the most recent collections of this rust strain were made, nor the majority of other sites where previous herbarium material had been collected (Kiss, 2007).

The documented host range of *S. ambrosiicola* and *S. epambrosiae*, as well as of *P. ambrosiae* (synonym

Cercospora ambrosiae) and *Passalora trifidae* (Chupp) U. Braun & Crous (synonym *Cercospora trifidae* Chupp 1949), is restricted to the genus *Ambrosia* (Table S4). These fungal pathogens could be considered for biological control, if the risk of damage to *A. maritima*, the only European native congeneric species, was assessed as minimal. Based on this uncertainty, as well as a lack of data about the impact of the two *Septoria* and *Passalora* species on their *Ambrosia* hosts in the native range, we give them second priority. However, *Septoria* as well as *Cercospora* species have previously been evaluated and used against a number of invasive weed species and, in the case of *Septoria passiflorae*, applied inundatively to control banana poka vine, *Passiflora tripartita* var. *tripartita*, in Hawaii (Julien & Griffiths, 1998).

New surveys in source regions matching specific European conditions

We expect that further explorations of the natural enemy complexes associated with *A. artemisiifolia* or closely related species will reveal new candidate species, or biotypes of known species (Tables S3 and S4), for the biological control of *A. artemisiifolia* in Europe.

Most biological control agents for *A. artemisiifolia* and *A. trifida* have so far been collected in the eastern United States and Canada, where both ragweed species occur. However, the genus *Ambrosia* covers a much larger geographical area, including different climatic zones. Targeting regions with climatic conditions comparable to those in the invaded range in Europe increases the chances that biological control agents will establish and persist. The richest source of natural enemies is probably the Sonoran desert region (i.e. in the south-western United States and northern México), the centre of origin and diversification of the genus *Ambrosia* (Harris & Piper, 1970). Surveys for phytophagous or pathogenic organisms in the Sonoran Desert have so far mainly been restricted to the state of California, and large areas remain unexplored (Goeden & Palmer, 1995). Natural enemies from the Sonoran desert itself might well be pre-adapted to warmer climates in Mediterranean Europe, e.g. the Rhone Valley, Northern Italy and some parts of the Balkans. These organisms are, however, unlikely to become adapted to more temperate or continental areas, except if they are collected at high elevations. The most likely regions to harbour cold-adapted specialised herbivore species are the mountains of México adjacent to the Sonoran desert (Harris & Piper, 1970) and/or areas at higher elevation in the northern part of México (Bohar & Vajna, 1996). Because of their eco-geographical separation from the southern parts of the United States through the Sonoran

desert, different organisms are likely to have evolved in these mountain ranges.

Early on in the history of biological control of *Ambrosia* species, mountain regions of South America were also highlighted as a potential source for climatically adapted phytophagous species for Canada and Europe (Harris & Piper, 1970). These regions are likely to have different natural enemy complexes because they are isolated from the Mexican mountain range by a tropical region. The presence of several *Ambrosia* species in mountain regions of South America originates from an early phylogenetic invasion, indicating that the genus might have been present there long enough to acquire specialist phytophages originating from the local fauna (Harris & Piper, 1970). Despite these recommendations by Harris and Piper (1970), few surveys have been conducted and little information is available on species associated with *Ambrosia* in South America. In 1975–1976, McFadyen (1976) conducted limited surveys on insects associated with *A. tenuifolia* (later attributed to *Ambrosia elatior*, an accepted synonym of *A. artemisiifolia*) in northern Argentina and reported several potentially specific insect species from this area. Besides an undescribed *Liothrips* species (Appendix S1), two stem-mining beetles (Curculionidae and Cerambycidae) were sent to a quarantine facility in Canada, but the species entered diapause from which they failed to emerge and no host specificity tests could be conducted (Maw, 1981). The weevil *Conotrachelus albocinereus* Fiedler (Coleoptera, Curculionidae), which was collected from *A. elatior* in Argentina, was released in Australia as a biological control agent of *Parthenium hysterophorus* and has proven to be highly damaging to this weed (R. McFadyen, pers. comm.). Recent collections in warm temperate, mountainous areas of southern Brazil have revealed new pathogen records on *A. artemisiifolia* (H.C. Evans, pers. comm.), confirming the recommendations made by Harris and Piper (1970).

Outlook

Reduction of the abundance and the spread of ragweed in Europe can only be achieved by reducing flowering, seed set and dispersal (both naturally and by human activities) at the local and regional scale. However, to mitigate crop losses because of competition with ragweed, ragweed biomass needs to be reduced quickly. Thus, with regard to biological control interventions, we see the need for a strategy with two approaches. First, a classical approach is needed for the widespread and highly infested non-crop areas, such as grassland, wasteland, roadsides and riverbanks, using mainly agents that reduce flowering, pollen production and seed set. A number of herbivores and pathogens associated

with *A. artemisiifolia* in its native range are likely to have a very narrow host range that is restricted either to the target species itself or to a few species within the genus *Ambrosia*. Altogether, we identified 18 insect and 5 fungal pathogens to be promising candidates for a classical biological control approach, and of these, we prioritised six insect and one fungal pathogen species (Table 1, Fig. 1). Second, an inundative approach will be necessary for crop fields that suffer from ragweed infestations. Candidate biological control agents for mass-rearing and repeated releases against ragweed in Europe are the defoliator *O. slobodkini* or the fungus *S. epambrosiae* (Table 1). A combination of biological agents with other weed management tools will probably be needed to produce acceptable levels of overall weed control in crops (Müller-Schärer *et al.*, 2000).

Acknowledgements

We thank Paul Hatcher and two anonymous reviewers for comments on an earlier version of this manuscript. The study was partially funded by the National Centre of Competence in Research (NCCR) Plant Survival, the research programme of the Swiss National Science Foundation and the University of Fribourg (Pôle de Recherche). We also thank Monica Miller (*Tarachidia candefacta*), Dan Bahauddin (*Smicronyx*), Margarether Brummermann (*Trigonorhinus tomentosus*), Thomas Whelan (<http://www.whelanphoto.com>; *Euaresta bella*), Mike Quinn (TexasEnto.net; *Zygogramma disrupta*) and Doug Futuyama (*Ophraella slobodkini*) for allowing us to use their photographs or hand-drawings.

References

- ARMESTO JJ & PICKETT STA (1985) Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* **66**, 230–240.
- BASSETT IJ & CROMPTON CW (1975) The biology of Canadian weeds 11. *Ambrosia artemisiifolia* L. and *A. psilostachya* DC. *Canadian Journal of Plant Science* **55**, 463–476.
- BATRA SWT (1981) *Puccinia xanthii* forma specialis *ambrosia-trifidae*, a microcyclic rust for the biological control of giant ragweed, *Ambrosia trifida* (Compositae). *Mycopathologia* **73**, 61–64.
- BOHAR G & VAJNA L (1996) Occurrence of some pathogenic fungi of common ragweed (*Ambrosia artemisiifolia* var. *elatior*) in Hungary. *Novenyvedelem* **32**, 527–528 (in Hungarian).
- BRANDES D & NITZSCHE J (2007) Ecology, distribution and phytosociology of *Ambrosia artemisiifolia* L. in Central Europe. *Tuexenia* **27**, 167–194.
- BREMER K (1994) *Asteraceae: Cladistics and Classification*. Timber Press, Portland, OR, USA.
- BRIÈRE SC, WATSON AK, PAULITZ TC & HALLETT SG (1995) First report of a *Phoma* sp. on common ragweed in North America. *Plant Disease* **79**, 968.

- BUTTENSCHÖN RM, WALDISPÜHL S & BOHREN C (2009) Guidelines for management of common ragweed, *Ambrosia artemisiifolia*. Available at: <http://www.EUPHRESKO.org> (last accessed 18 October 2010).
- CARTWRIGHT RD & TEMPLETON GE (1988) Biological limitations of *Protomyces gravidus* as a mycoherbicide for giant ragweed, *Ambrosia trifida*. *Plant Disease* **72**, 580–582.
- COWBROUGH M (2006) Noxious weeds in Ontario. Ragweeds. Available at: http://www.omafra.gov.on.ca/english/crops/facts/info_ragweed.htm (last accessed 11 November 2009).
- CSONTOS P, VITALOS M, BARINA Z & KISS L (2010) Early distribution and spread of *Ambrosia artemisiifolia* in Central and Eastern Europe. *Botanica Helvetica* **120**, 75–78.
- DAISIE (2009) *Handbook of Alien Species in Europe*. Springer, Dordrecht, the Netherlands.
- ELLISON CA & BARRETO RW (2003) Prospects for the management of invasive alien weeds using co-evolved fungal pathogens: a Latin American perspective. *Biological Invasions* **6**, 23–45.
- EPPO (2009) European and Mediterranean Plant Protection Organization. *Ambrosia psilostachya*, *Ambrosia trifida*. Available at: http://www.eppo.org/QUARANTINE/ias_plants.htm (last accessed 10 March 2011).
- FARR DF & CASTLEBURY LA (2001) *Septoria epambrosiae* sp. nov. on *Ambrosia artemisiifolia* (common ragweed). *Sydowia* **53**, 81–92.
- FRENZ DA (1999) Comparing pollen and spore counts collected with the rotorod sampler and Burkard spore trap. *Annals of Allergy, Asthma & Immunology* **83**, 341–349.
- FRIEDMAN J & BARRETT SCH (2008) High outcrossing in the annual colonizing species *Ambrosia artemisiifolia* (Asteraceae). *Annals of Botany* **101**, 1303–1309.
- FUMANAL B, CHAUVEL B & BRETAGNOLLE F (2007a) Estimation of pollen and seed production of common ragweed in France. *Annals of Agricultural and Environmental Medicine* **14**, 233–236.
- FUMANAL B, CHAUVEL B, SABATIER A & BRETAGNOLLE F (2007b) Variability and cryptic heteromorphism of *Ambrosia artemisiifolia* seeds: what consequences for its invasion in France? *Annals of Botany* **100**, 305–313.
- FUMANAL B, GIROD C, FRIED G, BRETAGNOLLE F & CHAUVEL B (2008) Can the large ecological amplitude of *Ambrosia artemisiifolia* explain its invasive success in France? *Weed Research* **48**, 349–359.
- FUTUYMA DJ (1991) A new species of *Ophraella* Wilcox (Coleoptera: Chrysomelidae) from the southeastern United States. *Journal of the New York Entomological Society* **99**, 643–653.
- GAGNÉ RJ (1975) The gall midges of ragweed, *Ambrosia*, with descriptions of two new species (Diptera: Cecidomyiidae). *Proceedings of the Entomological Society of Washington* **77**, 50–55.
- GAUVRIT C & CHAUVEL B (2010) Sensitivity of *Ambrosia artemisiifolia* to glufosinate and glyphosate at various developmental stages. *Weed Research* **50**, 503–510.
- GBIF (2009) Global Biodiversity Information Facility: *Ambrosia acanthicarpa*. Available at: <http://data.gbif.org/> (last accessed 10 November 2009).
- GENTON BJ, SHYKOFF JA & GIRAUD T (2005) High genetic diversity in French invasive populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of introduction. *Molecular Ecology* **14**, 4275–4285.
- GISD (2009) Global Invasive Species Database: *Ambrosia artemisiifolia*. Available at: <http://www.issg.org/database/species/distribution.asp?si=1125&fr=1&sts=sss&lang=EN> (last accessed 10 November 2009).
- GOEDEN RD & ANDRES LA (1999) Three recent successes outside of North America. In: *Handbook of Biological Control* (ed. TW FISHER), 884–885. Academic Press, San Diego, CA, USA.
- GOEDEN RD & PALMER WA (1995) Lessons learned from studies of the insects associated with Ambrosiinae in North America in relation to the biological control of weedy members of this group. In: *Eighth International Symposium on Biological Control of Weeds, Canterbury, New Zealand* (ed. RR SCOTT), 565–573. CSIRO, Melbourne, Australia.
- GOEDEN RD & RICKER DW (1975) The phytophagous insect fauna of the ragweed, *Ambrosia confertiflora*, in Southern California. *Environmental Entomology* **4**, 301–306.
- GOEDEN RD & RICKER DW (1976) The phytophagous insect fauna of the ragweed, *Ambrosia psilostachya*, in Southern California. *Environmental Entomology* **5**, 1169–1177.
- GOEDEN RD & RICKER DW (1979) Life history of *Zygogramma tortuosa* Rogers on the ragweed, *Ambrosia eriocentra* (Gray) Payne, in southern California (Coleoptera: Chrysomelidae). *Pan-Pacific Entomologist* **55**, 261–266.
- GOEDEN RD, KOVALEV OV & RICKER DW (1974) Arthropods exported from California to the U.S.S.R. for ragweed control. *Weed Science* **22**, 156–158.
- GREUTER W (2006–2009) Compositae (pro parte majore). In: *Compositae. Euro + Med Plantbase – The Information Resource for Euro-Mediterranean Plant Diversity* (eds W GREUTER & E VON RAAB-STRAUBE). Available at: <http://www.emplantbase.org/home.html> (last accessed 19 May 2011).
- GRIN (2009) USDA ARS National Genetic Resources Program. Germplasm Resources Information Network – (GRIN). *Xanthium sibiricum*. Available at: http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl?Xanthium%20sibiricum National Germplasm Resources Laboratory, Beltsville, Maryland (last accessed 10 November 2009).
- HARRIS P & PIPER GL (1970) Ragweed (*Ambrosia* spp.: Compositae): its North American insects and the possibilities for its biological control. *Commonwealth Institute of Biological Control Technical Bulletin* **13**, 117–140.
- HARRISON SK, REGNIER EE, SCHMOLL JT & WEBB JE (2001) Competition and fecundity of giant ragweed in corn. *Weed Science* **49**, 224–229.
- HARTMANN H & WATSON AK (1980) Damage to common ragweed (*Ambrosia artemisiifolia*) caused by the white rust fungus (*Albugo tragopogi*). *Weed Science* **28**, 632–635.
- HENNEN JF, FIGUEIREDO MB, DE CARVALHO JR AA & HENNEN PG (2005) Catalogue of the species of plant rust fungi (Uredinales) of Brazil. Available at: http://www.jbrj.gov.br/publica/uredinales/Brazil_Catalogue1dreviado.pdf (last accessed 11 February 2011).
- HULME PE, PYŠEK P, NENTWIG W & VILA M (2009) Will threat of biological invasions unite the European Union? *Science* **324**, 40–41.

- HYVÖNEN T, GLEMNITZ M, RADICS L & HOFFMANN J (2011) Impact of climate and land use type on the distribution of Finnish casual arable weeds in Europe. *Weed Research* **51**, 201–208.
- ISHIKAWA Y, TAKANASHI T, KIM C, HOSHIZAKI S, TATSUKI S & HUANG Y (1999) *Ostrinia* spp. in Japan: their host plants and sex pheromones. In: *Proceedings of the 10th International Symposium on Insect–Plant Relationships* (ed. J HARDIE), 237–244. Kluwer Academic Publisher, Dordrecht, the Netherlands.
- JÄGER S (2000) Ragweed (*Ambrosia*) sensitisation rates correlate with the amount of inhaled airborne pollen. A 14-year study in Vienna, Austria. *Aerobiologia* **16**, 149–153.
- JULIEN MH & GRIFFITHS MW (1998) *Biological Control of Weeds – A Catalogue of Agents and Their Target Weeds*, 4th edn. CABI Publishing, Wallingford, UK.
- KAZINCZI G, BÉRES I, PATHY Z & NOVÁK R (2008) Common ragweed (*Ambrosia artemisiifolia* L.): a review with special regards to the results in Hungary: II. Importance and harmful effect, allergy, habitat, allelopathy and beneficial characteristics. *Herbologia* **9**, 93–118.
- KÉMIVES T, BÉRES I, REISINGER P *et al.* (2006) New strategy of the integrated protection against common ragweed (*Ambrosia artemisiifolia* L.). *Hungarian Weed Research and Technology* **6**, 5–50.
- KETTUNEN M, GENOVESI P, GOLLASCH S *et al.* (2009) *Technical Support to EU Strategy on Invasive Species (IAS): Assessment of the Impacts of IAS in Europe and the EU*. Final module report for the European Commission. Institute for European Environmental Policy, Brussels.
- KISS L (2007) Why is biocontrol of common ragweed, the most allergenic weed in Eastern Europe, still only a hope? In: *Biological Control: A Global Perspective* (eds C VINCENT, M GOETTEL & G LAZAROVITS), 80–91. CABI, Wallingford, UK.
- KISS L, VAJNA L, BOHAR G *et al.* (2003) *Phyllachora* epidemic on common ragweed (*Ambrosia artemisiifolia*): a unique natural control phenomenon in Hungary in 1999. In: *Workshop on Biocontrol of Weeds with Pathogens, Lincoln, New Zealand* (eds G BOURDOT & S LAMOUREAUX), 17–18. AgResearch, Lincoln, New Zealand.
- KOVALEV OV (1971) Phytophages of ragweeds (*Ambrosia* L.) in North America and their application in biological control in the USSR. *Zoologicheskii Zhurnal* **50**, 199–209 (in Russian).
- LU G-Z, YANG H, SUN X-D, YANG R-X & ZHAO Z-H (2004) *Puccinia xanthii* f. sp. *ambrosiae-trifidae*, a newly recorded rust taxon on *Ambrosia* in China. *Mycosystema* **23**, 310–311.
- MAW MG (1981) *Ambrosia artemisiifolia* L., common ragweed (Compositae). In: *Biological Control Programmes Against Insects and Weeds in Canada 1869–1980* (ed. MA HULME), 111–112. Commonwealth Agricultural Bureaux (CAB), Slough, UK.
- McFADYEN R (1976) *Report on a Survey of Insects Attacking Ambrosia tenuifolia* in Tucuman, Argentina. Unpublished report. Commonwealth Institute of Biological Control, West Indian Station, Curepe, Trinidad.
- McFADYEN R (1992) Biological control against *Parthenium* weed in Australia. *Crop Protection* **11**, 400–407.
- McFADYEN R & WEGGLER-BEATON K (2000) The biology and host specificity of *Lyothrips* sp. (Thysanoptera: Phlaeothripidae), an agent rejected for biocontrol of annual ragweed. *Biological Control* **19**, 105–111.
- MORIN L, AULD BA & BROWN J (1993) Host range of *Puccinia xanthii* and postpenetration development on *Xanthium occidentale*. *Canadian Journal of Botany* **71**, 959–965.
- MORIN L, AULD BA & SMITH HE (1996) Rust epidemics, climate and control of *Xanthium occidentale*. In: *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds VC MORAN & JH HOFFMANN), 385–391. Stellenbosch, South Africa, University of Cape Town, South Africa.
- MÜLLER-SCHÄRER H & SCHAFFNER U (2008) Classical biological control: exploiting enemy escape to manage plant invasions. *Biological Invasions* **10**, 859–874.
- MÜLLER-SCHÄRER H, SCHEEPENS PC & GREAVES MP (2000) Biological control of weeds in European crops: recent achievements and future work. *Weed Research* **40**, 83–98.
- PAGE AR & LACEY KL (2006) *Economic Impact Assessment of Australian Weed Biological Control: Report to the CRC for Australian Weed Management. Technical Series 10*. CRC for Australian Weed Management, Adelaide, Australia.
- PALMER WA, HEARD T & SHEPPARD AW (2010) A review of Australian classical biological control of weeds programs and research activities over the past 12 years. *Biological Control* **52**, 271–287.
- PAYNE WW (1964) A re-evaluation of the genus *Ambrosia* (Compositae). *Journal of the Arnold Arboretum* **54**, 401–438.
- PAYNE WW (1966) Notes on the ragweeds of South America with the description of two new species: *Ambrosia pannosa* and *A. parvifolia* (Compositae). *Brittonia* **18**, 28–37.
- PEMBERTON RW (2000) Predictable risk to native plants in weed biological control. *Oecologia* **125**, 489–494.
- POLTAVSKY AN & ARTOKHIN KS (2006) *Trachidia candefacta* (Lepidoptera: Noctuidae) in the south of European Russia. *Phegea* **34**, 41–44.
- PYŠEK P, LAMBDON PW, ARIANOUTSOU M, KÜHN I, PINO J & WINTER M (2009) Chapter 4 – Alien vascular plants of Europe. In: *Handbook of Alien Species in Europe* (eds DAISIE), 43–61. Springer, Dordrecht, the Netherlands.
- RAMULA S, KNIGHT TM, BURNS JH & BUCKLEY YM (2008) General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *Journal of Applied Ecology* **45**, 1124–1133.
- REZNIK SY (1991) The effects of feeding damage in ragweed *Ambrosia artemisiifolia* (Asteraceae) on populations of *Zygogramma suturalis* (Coleoptera, Chrysomelidae). *Oecologia* **88**, 204–210.
- REZNIK SY, SPASSKAYA IA, DOLGOVSKAYA MY, VOLKOVITSH MG & ZAITZEV VF (2007) The ragweed leaf beetle *Zygogramma suturalis* F. (Coleoptera: Chrysomelidae) in Russia: current distribution, abundance and implication for biological control of common ragweed, *Ambrosia artemisiifolia* L. In: *XII International Symposium on Biological Control of Weeds, La Grande Motte, France* (eds MH JULIEN, R SFORZA, MC BON, HC EVANS, PE HATCHER, HE HINZ & BG RECTOR), 614–619. CAB International, Wallingford, UK.
- RYBNICEK O & JÄGER S (2001) *Ambrosia* (Ragweed) in Europe. *ACI International* **13**, 60–66.
- SEIER MK, MORIN L, VAN DER MERWE M, EVANS HC & ROMERO A (2009) Are the microcyclic rust species *Puccinia*

- melampodii* and *Puccinia xanthii* conspecific? *Mycological Research* **113**, 1271–1282.
- SHAW RH, TANNER R, DJEDDOUR D & CORTAT G (2011) Classical biological control of *Fallopia japonica* – lessons for Europe. *Weed Research*, **51**, doi: 10.1111/j.1365-3180.2011.00880.x.
- SHEIKH T, WHEELER TA, DOTRAY PA & ZAK JC (2001) Biological control of woolly bursage (*Ambrosia grayi*) with *Pseudomonas syringae* p.v. *tagetis*. *Weed Technology* **15**, 375–381.
- SHEPPARD AW, SHAW RH & SFORZA R (2006) Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations and other barriers to adoption. *Weed Research* **46**, 93–117.
- TARAMARCAZ P, LAMBELET C, CLOT B, KEIMER C & HAUSER C (2005) Progression and risk of ragweed allergy in Geneva: will Switzerland resist this invasion? *Swiss Medical Weekly* **135**, 538–548.
- TESHLER MP, BRIÈRE SC, STEWART RK, WATSON AK & HALLETT SG (1996) Life table and feeding ability of *Ophraella communa* (Coleoptera: Chrysomelidae) a potential biocontrol agent for *Ambrosia artemisiifolia*. In: *IX International Symposium on Biological Control of Weeds, Stellenbosch, South Africa* (eds VC MORAN & JH HOFFMANN), 420. University of Cape Town, Cape Town, South Africa.
- TESHLER MP, DITOMMASO A, GAGNON JA & WATSON AK (2002) *Ambrosia artemisiifolia* L., common ragweed (Asteraceae). In: *Biological Control Programmes in Canada* (ed. JT HUBER), 290–294. CABI Publishing, New York, USA.
- TÓTH Á, HOFFMANNÉ PZS & SZENTÉY L (2004) *A parlagfő* (*Ambrosia elatior*) *helyzet 2003-ban, Magyarországon. A levegi pollenzám csökkentésének nehézségei*. Növényvédelmi Tudományos Napok, Budapest, Öszefoglalók, 69.
- USDA-NRCS (2009) The PLANTS Database. *Ambrosia artemisiifolia*. Available at: <http://plants.usda.gov>, National Plant Data Center, Baton Rouge, LA 70874-4490 USA (last accessed 10 November 2009).
- VAJNA L (2002) Downy mildew epidemic on common ragweed in Hungary caused by *Plasmopara halstedii*. *Plant Pathology* **51**, 809.
- VAJNA L, BOHAR G & KISS L (2000) First report of *Phyllachora ambrosiae* in Europe causing epidemics on common ragweed. *Plant Disease* **84**, 489.
- VILÀ M, BASNOU C, PYŠEK P *et al.* (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* **8**, 135–144.
- WAN F-H, WANG R & DING J (1995) Biological control of *Ambrosia artemisiifolia* with introduced insect agents, *Zygogramma suturalis* and *Epiblema strenuana*, in China. In: *Eighth International Symposium on Biological Control of Weeds, Canterbury, New Zealand* (ed. RR SCOTT), 193–200. DSIR/CSIRO, Melbourne, Australia.
- WAN F-H, MA J, GUO J-Y & YOU L-S (2003) Integrated control effects of *Epiblema strenuana* (Lepidoptera: Tortricidae) and *Ostrinia orientalis* (Lepidoptera: Pyralidae) against ragweed, *Ambrosia artemisiifolia* (Compositae). *Acta Entomologica Sinica* **46**, 473–478.
- WHEELER TA, DOTRAY P & WINCHESTER J (1998) Root rot by *Rhizoctonia solani* on *Ambrosia grayi* in Texas. *Plant Disease* **82**, 959.
- YAMANAKA T, TANAKA K, OTUKA A & BJORNSTAD ON (2007) Detecting spatial interactions in the ragweed (*Ambrosia artemisiifolia* L.) and the ragweed beetle (*Ophraella communa* LeSage) populations. *Ecological Research* **22**, 185–196.
- ZHANG L-J, YANG X-K, LI W-Z & CUI J-Z (2005) A new record of *Ophraella communa* of mainland China. *Chinese Bulletin of Entomology* **42**, 227–228.
- ZHOU Z-S, GUO J-Y, CHEN H-S & WAN F-H (2009) Effect of humidity on the development and fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae). *BioControl* **55**, 313–319.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Distribution (outside their North or South American native range) of the four main *Ambrosia* species recorded in Europe. Data source GISD (2009) and EPPO (2011) for *A. artemisiifolia*, EPPO (2011) for *A. psilostachya* and *A. trifida*, and Behçet (2004) and DAISIE (2009) for *A. tenuifolia*.

Table S2 Herbivores and pathogens recorded on *Ambrosia artemisiifolia* in the introduced range in Eurasia.

Table S3 Selected attributes of phytophagous organisms recorded exclusively from *Ambrosia* spp. (and some closely related species within the subtribe Ambrosiinae) in North America. Organisms not identified to the species level are not considered in the list.

Table S4 Fungi recorded exclusively from *Ambrosia* spp. (and some closely related species within the subtribe Ambrosiinae) in North America. Country names given in brackets are likely to indicate records from the introduced range of a fungus.

Appendix S1 Biology and host range data of herbivores previously considered for classical biological control against *Ambrosia artemisiifolia*.

Data S1 List of references quoted in the supporting information.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.