

Biological Flora of the British Isles: *Ambrosia artemisiifolia*

Franz Essl^{1,2†}, Krisztina Biró³, Dietmar Brandes⁴, Olivier Broennimann⁵, James M. Bullock⁶, Daniel S. Chapman⁷, Bruno Chauvel⁸, Stefan Dullinger^{1,9}, Boris Fumanal^{10,11}, Antoine Guisan^{5,12}, Gerhard Karrer¹³, Gabriella Kazinczi¹⁴, Christoph Kueffer¹⁵, Beryl Laitung¹⁶, Claude Lavoie¹⁷, Michael Leitner¹⁸, Thomas Mang¹, Dietmar Moser¹, Heinz Müller-Schärer¹⁹, Blaise Petitpierre⁵, Robert Richter²⁰, Urs Schaffner²¹, Matt Smith²², Uwe Starfinger²³, Robert Vautard²⁴, Gero Vogl²⁰, Moritz von der Lippe²⁵ and Swen Follak²⁶

¹Department of Botany and Biodiversity Research, Division of Conservation, Vegetation and Landscape Ecology, University of Vienna, Rennweg 14, 1030 Vienna, Austria; ²Centre for Invasion Biology, Stellenbosch University, Private Bag, Matieland, 7602 South Africa; ³Georgikon Faculty, Institute for Plant Protection, University of Pannonia, Deák F.str. 16, 8361 Keszthely, Hungary; ⁴Institute for Plant Biology, Technical University Braunschweig, Mendelsohnstraße 4, 38106 Braunschweig, Germany; ⁵Department of Ecology & Evolution, University of Lausanne, Biophore, 1015 Lausanne, Switzerland; ⁶NERC Centre for Ecology & Hydrology, Benson Lane, Wallingford, Oxfordshire OX10 8BB, UK; ⁷NERC Centre for Ecology & Hydrology, Bush Estate, Edinburgh EH26 0QB, UK; ⁸INRA, UMR1347, Agroécologie, 21000 Dijon, France; ⁹Vienna Institute for Nature Conservation & Analyses, Giessergasse 6/7, 1090 Vienna, Austria; ¹⁰Université Blaise-Pascal, UMR547 PIAF, BP 10448, Clermont Université, 63000 Clermont-Ferrand, France; ¹¹INRA, UMR547 PIAF, 63100 Clermont-Ferrand, France; ¹²Institute of Earth Surface Dynamics, University of Lausanne, Geopolis, 1015 Lausanne, Switzerland; ¹³Institute of Botany, University of Natural Resources and Life Sciences Vienna, Gregor Mendel Street 33, 1180 Vienna, Austria; ¹⁴Department of Plant Production and Plant Protection, Institute of Plant Science, Faculty of Agricultural and Environmental Sciences, Kaposvár University, Guba S. str. 40, 7400 Kaposvár, Hungary; ¹⁵Institute of Integrative Biology, ETH Zürich, Universitätsstrasse 16, 8092 Zürich, Switzerland; ¹⁶Université de Bourgogne, UMR 1347, Agroécologie, AgroSup/INRA/uB, 17 rue Sully, 21065 Dijon Cedex, France; ¹⁷Ecole supérieure d'aménagement du territoire et de développement régional, Université Laval, Québec City, QC G1V 0A6, Canada; ¹⁸Heinz Maier-Leibnitz-Zentrum, Technische Universität, München, Lichtenbergstraße 1, 85747 Garching, Germany; ¹⁹Department of Biology, Unit Ecology & Evolution, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland; ²⁰Faculty of Physics, University Vienna, Boltzmanngasse 5, 1090 Vienna, Austria; ²¹CABI Switzerland, Chemin des Grillons 1, 2800 Delémont, Switzerland; ²²Laboratory of Aeropalynology, Faculty of Biology, Adam Mickiewicz University, Poznań, Poland; ²³Julius Kühn Institute, Federal Research Centre for Cultivated Plants, Institute for National and International Plant Health, Messeweg 11/12, 38104 Braunschweig, Germany; ²⁴Laboratoire des Sciences du Climat et de l'Environnement, IPSL, CEA/CNRS/UVSQ, 91191 Gif sur Yvette Cedex, France; ²⁵Institute of Ecology, Technical University of Berlin, Rothenburgstrasse 12, 12165 Berlin, Germany; and ²⁶Austrian Agency for Health and Food Safety, Institute for Sustainable Plant Production, Spargelfeldstraße 191, 1220 Vienna, Austria

Summary

1. This account presents information on all aspects of the biology of *Ambrosia artemisiifolia* L. (Common ragweed) that are relevant to understanding its ecology. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, and history, conservation, impacts and management.

*Nomenclature of vascular plants follows Stace (2010) and, for non-British species, *Flora Europaea*.

†Correspondence author. E-mail: franz.essl@univie.ac.at

2. *Ambrosia artemisiifolia* is a monoecious, wind-pollinated, annual herb native to North America whose height varies from 10 cm to 2.5 m, according to environmental conditions. It has erect, branched stems and pinnately lobed leaves. Spike-like racemes of male capitula composed of staminate (male) florets terminate the stems, while cyme-like clusters of pistillate (female) florets are arranged in groups in the axils of main and lateral stem leaves.

3. Seeds require prolonged chilling to break dormancy. Following seedling emergence in spring, the rate of vegetative growth depends on temperature, but development occurs over a wide thermal range. In temperate European climates, male and female flowers are produced from summer to early autumn (July to October).

4. *Ambrosia artemisiifolia* is sensitive to freezing. Late spring frosts kill seedlings and the first autumn frosts terminate the growing season. It has a preference for dry soils of intermediate to rich nutrient level.

5. *Ambrosia artemisiifolia* was introduced into Europe with seed imports from North America in the 19th century. Since World War II, it has become widespread in temperate regions of Europe and is now abundant in open, disturbed habitats as a ruderal and agricultural weed.

6. Recently, the North American ragweed leaf beetle (*Ophraella communa*) has been detected in southern Switzerland and northern Italy. This species appears to have the capacity to substantially reduce growth and seed production of *A. artemisiifolia*.

7. In heavily infested regions of Europe, *A. artemisiifolia* causes substantial crop-yield losses and its copious, highly allergenic pollen creates considerable public health problems. There is a consensus among models that climate change will allow its northward and uphill spread in Europe.

Key-words: agriculture, biogeography, climate change, ecophysiology, geographical and altitudinal distribution, germination, health, modelling, parasites and diseases, reproductive biology

Ambrosia artemisiifolia wird sich in Mitteleuropa wohl nie in gefahrdrohender Weise vermehren' [*Ambrosia artemisiifolia* will never become dangerously abundant in Central Europe']. (P. Ascherson 1874)

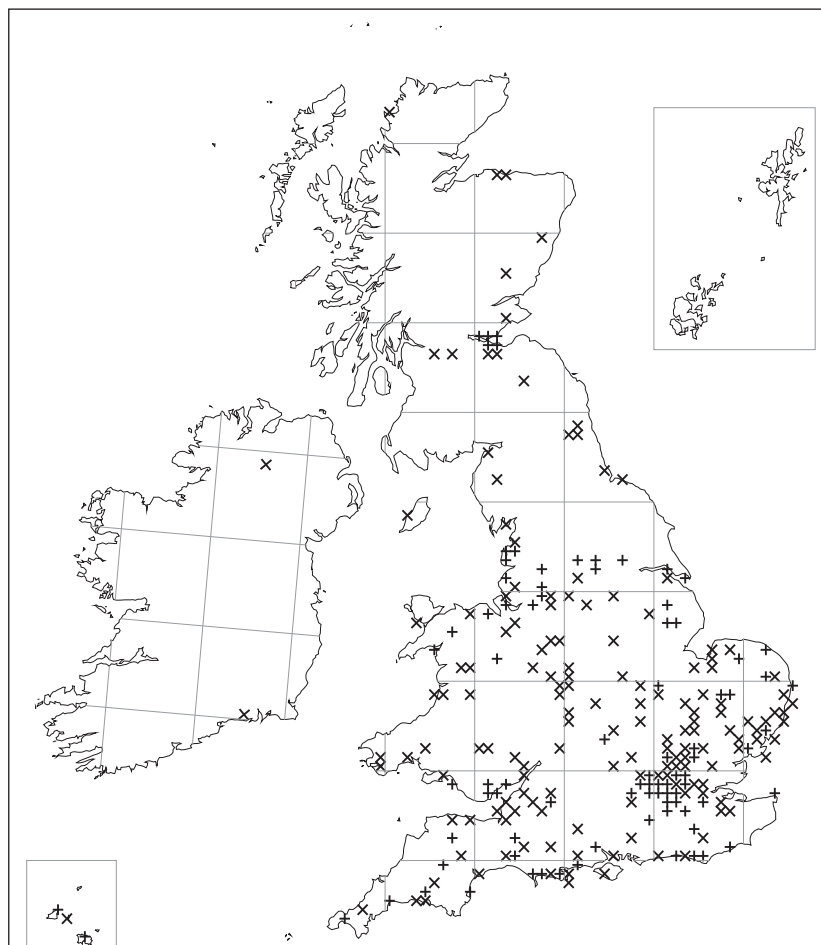
Ragweed. Asteraceae, tribe Heliantheae. *Ambrosia artemisiifolia* L. is a wind-pollinated, monoecious annual herb, which germinates in the spring and sets fruit in the autumn. Plants to 2.5 m tall; stems hairy, erect, bluntly four-angled, ridged and leafy, with several branches; leaves mostly opposite, alternate above, deltate to lanceolata or elliptic in outline, 25–55(90) × 20–30(50) mm, deeply pinnatifid, bases cuneate, margins entire or toothed; abaxial faces sparsely finely hairy or with stiff slender bristles (strigillose), adaxial faces strigillose, both gland-dotted. Inflorescences of two kinds: male capitula short stalked in dense, elongating spike-like ebracteate racemes and female capitula in axillary clusters immediately below the male. Male flowers with cream, yellowish or pale green corolla in drooping short-stalked (2–5 mm) capitula; involucre campanulate or turbinate, 2–3 mm in diameter, glabrous, hispid or finely hairy, florets 12–20, anthers free. Female flowers without corolla or pappus, capitula erect in 2–5 groups, surrounded by small bracts; involucre cupule-like with 5–8 small bristle-like spines (each 3–5 mm) each with single flower. Seeds c. 3–4 mm × 1.8–2.5 mm enclosed in woody achenes. Fruit yellowish to reddish-brown, ± ovoid, each achene adnate to its involucre forming a hairy syconium with (4)5–7(8) longitudinal ridges ending in spiny

projections. Male flowers produce copious amounts of wind-dispersed pollen.

The genus *Ambrosia* contains at least 40 species, with numerous intraspecific taxa. Its centre of diversity comprises the south-western USA and adjacent northern Mexico (FNA Editorial Committee 2006). Only *A. maritima* L. is native to the Old World (Mediterranean region and tropical Africa), whereas two others native to North America (*A. psilostachya*, *A. trifida*) are established in Europe (Rich 1994; Fumanal 2007; Follak *et al.* 2013). European populations have been distinguished from *A. artemisiifolia* s. str. as a distinct species (*A. elatior* L.; see Tropicos 2014). However, genetic studies (Genton *et al.* 2005; Gaudeul *et al.* 2011) confirm their conspecific status. Although the native range of *A. artemisiifolia* is restricted to North America, it has colonized temperate regions of the world, including the British Isles and continental Europe, where it has greatly increased in range and abundance since the mid-20th century.

In the British Isles, *Ambrosia artemisiifolia* is primarily an alien invasive plant of open, ruderal habitats; in both its native and continental European ranges, it is an important weed of agricultural crops. In addition to its economic impact on crop yields (Reinhardt *et al.* 2003; Sheppard, Shaw & Sforza 2006), the strongly allergenic pollen of common ragweed causes considerable public health problems in Central and East Europe, and these are becoming increasingly apparent in southern parts of the British Isles.

Fig. 1. The distribution of *Ambrosia artemisiifolia* in the British Isles. Each dot represents at least one record in a 10 km square of the National Grid. (+) non-native 1970 onwards; (x) non-native pre-1970. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology, mainly from records collected by members of the Botanical Society of the British Isles, using Dr A. Morton's DMAP software.



I. Geographical and altitudinal distribution

In Britain, *Ambrosia artemisiifolia* has scattered occurrences but is expanding its distribution, whereas it is rare in Ireland (Lockton & Crocker 2014; Fig. 1). Most records have been made in southern England, in particular in urban areas (e.g. London).

Since the mid-19th century, and especially in recent decades, *A. artemisiifolia* has invaded several temperate regions of the world including Europe, China (where it is widespread; Duan & Chen 2000; European and Mediterranean Plant Protection Organization (EPPO) 2013), Japan (widespread; Nakayama 1998; Watanabe *et al.* 2002; European and Mediterranean Plant Protection Organization (EPPO) 2013), South Korea (European and Mediterranean Plant Protection Organization (EPPO) 2013), South Africa (established; L. Henderson unpubl. data), Australia (Lazarides, Cowley & Hohnen 1997) and New Zealand (Webb 1987; European and Mediterranean Plant Protection Organization (EPPO) 2013). In the Americas, the species has spread to Argentina (Anton & Zuloaga 2014), Chile (established; N. Fuentes unpubl. data), the Bahamas and the island of Hispaniola (Acevedo-Rodríguez & Strong 2007), Brazil (Mondin & Nakajima 2014) and possibly Paraguay and Uruguay, but there are few details on the distribution and invasion status of the species in Central and South America.

In Europe, *Ambrosia artemisiifolia* has greatly increased in range and abundance since the mid-20th century (e.g. Song & Prots 1998; Chauvel *et al.* 2006; Kiss & Beres 2006; Brandes & Nitzsche 2007; Tokarska-Gudzik *et al.* 2011; Bullock *et al.* 2012). Currently, the species is most widespread in southern parts of Eastern and Central Europe (Fig. 2), with the largest populations in the Pannonian Plains of Hungary, Croatia and Serbia (Kazinczi *et al.* 2008a). Further east, *A. artemisiifolia* is also widespread in Ukraine (Song & Prots 1998) and Russia (CABI 2014). In Russia, it had invaded an area of more than 50 000 km² by the end of the 20th century and it was still spreading at the very beginning of the 21st century (Moskalenko 2001).

Other invasion hotspots are southern and central France, in particular the Rhône valley (Chauvel *et al.* 2006), and the Po plains of northern Italy. *Ambrosia artemisiifolia* is patchily distributed in the northern regions of Central, Western and Eastern Europe, and most populations are small and often ephemeral. It is largely absent from Mediterranean Europe and in the far north of Europe. Bullock *et al.* (2012) collated records as far north as Scandinavia, but it is unclear to what extent these are naturalized populations or transient and repeated colonizations (Chapman *et al.* 2014).

Ambrosia artemisiifolia is native and widespread in the United States and southern Canada. However, due to historical range expansion within North America following colonization by settlers, the extent of common ragweed's native range is

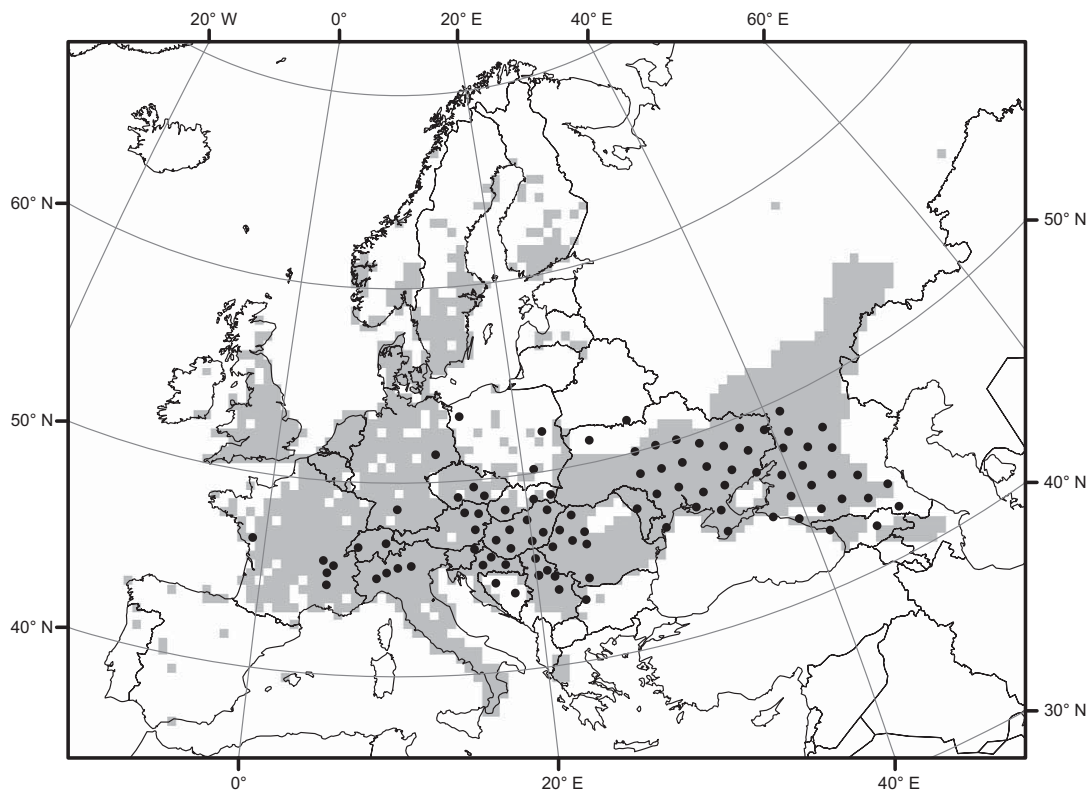


Fig. 2. The distribution (colonized grid cells of 50 × 50 km size are shown in grey) of *Ambrosia artemisiifolia* in Europe. Distribution data are based on Bullock *et al.* (2012), with additional records (D. S. Chapman, unpubl. data). Black points indicate heavily colonized areas with high level of allergies recorded (based on Déchamp, Méon & Reznik 2009).

difficult to reconstruct. In Canada and USA, the species is present in all provinces, states and territories, with the exception of Yukon and Nunavut (Flora North America (FNA) 2006). It has been argued that *A. artemisiifolia* is native only to the central part of North America (Bassett & Crompton 1975), but this assertion was based on a few old (19th century) herbarium specimens. Older specimens have since been recovered from southern Québec, which suggests that the native range was more extensive than previously thought (Lavoie, Jodoin & Goursaud de Merlis 2007). Nevertheless, common ragweed's North American range expanded greatly during the 20th century, and it is unlikely to be native in British Columbia, New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland and in the Northwest Territories (Brouillet *et al.* 2014). Except for Québec, there is no recent documentation of the spatial distribution and abundance of the species in Canada, but *A. artemisiifolia* is abundant and widespread in southern Ontario and Québec, especially along railways and paved roads, and in maize and soya bean crop fields (Bassett & Crompton 1975; Lavoie, Jodoin & Goursaud de Merlis 2007; Simard & Benoit 2010; Joly *et al.* 2011; Ngom & Gosselin 2014).

II. Habitat

(A) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

In its native range, *A. artemisiifolia* grows best under temperate, continental climates (Bassett & Crompton 1975).

Similarly, in Europe, the species has its optimum in temperate climates that are characterized by high heat sums during the growing period (Essl, Dullinger & Kleinbauer 2009; Cunze, Leiblein & Tackenberg 2013). In Central Europe, low mean temperature of the summer months has been identified as the most important limiting climatic factor (Essl, Dullinger & Kleinbauer 2009), as the species is not able to complete its life cycle. These thermal requirements also explain the absence of common ragweed from higher elevations in most parts of Europe. In southern Europe, *A. artemisiifolia* is largely absent from regions with a Mediterranean climate possibly because low rainfall during the summer months severely constrains growth (Chapman *et al.* 2014), and winter temperatures are too high to allow seed stratification (Shrestha *et al.* 1999).

(B) SUBSTRATUM

Ambrosia artemisiifolia colonizes a wide range of soil types without any particular preference in Europe (Fumanal *et al.* 2008), although it seems to show a preference for clays or sandy soils in North America (Bassett & Crompton 1975).

No Ellenberg indicator values for *A. artemisiifolia* are available for Great Britain (Hill *et al.* 1999) or for Central Europe (Ellenberg *et al.* 1992). However, for Austria, Ellenberg values of 3 are given for moisture (indicating a preference for dry soils), 8 for soil pH (grows best under moderately basic conditions) and 6 for nitrogen level (indicating

intermediate to high soil fertility) (BOKU 2014). Similar values are given for Switzerland (Landolt 2010).

III. Communities

Although *Ambrosia artemisiifolia* colonizes a wide range of disturbed habitats in Britain and Europe (Fig. S1; Brandes & Nitzsche 2007; Bullock *et al.* 2012), it was not recorded in any British Plant Community in the classification of Rodwell (2000).

In the more heavily colonized areas of Europe, *A. artemisiifolia* is most frequent in arable fields and on roadsides (Essl, Dullinger & Kleinbauer 2009; Pinke *et al.* 2013; Milakovic, Fiedler & Karrer 2014a). In regions currently less invaded, such as the British Isles, it is largely restricted to ruderal habitats, for example roadsides, railway embankments, construction sites and landfill sites (Bullock *et al.* 2012). The species is occasionally recorded in other habitats such as gravel beds of rivers or disturbed semi-dry grasslands (see section XI.). In its native range, *A. artemisiifolia* frequently contributes to the communities of disturbed habitats – along roadsides, in wastelands (Lavoie, Jodoin & Goursaud de Merlis 2007; MacKay & Kotanen 2008), in arable fields (e.g. Webster & Nichols 2012) and urban ruderal habitats (Ziska *et al.* 2003) – but is found rarely in communities of natural habitats (e.g. prairie grassland) (Bullock *et al.* 2012).

In accordance with common ragweed's habitat preferences, a large fraction of the most commonly associated species recorded in relevés within its Central and Eastern European range (Table 1) are diagnostic species of segetal vegetation of the class Stellarietea (i.e. summer annuals such as *Chenopodium album*, *Erigeron canadensis* and *Setaria pumila*) and of trampled vegetation of class Plantaginetea, Polygono—Poetea

(e.g. *Plantago major*, *Polygonum aviculare* agg.). In addition, diagnostic species of ruderal vegetation dominated by perennial species (class Artemisietea; e.g. *Artemisia vulgaris*, *Daucus carota* and *Elytrigia repens*) and of fertilized grasslands (class Molinio—Arrhenatheretea; e.g. *Medicago lupulina*, *Plantago lanceolata* and *Trifolium repens*) are found frequently in relevés containing *A. artemisiifolia*.

IV. Response to biotic factors

As an annual of open habitats, *Ambrosia artemisiifolia* is replaced by perennial plant species as the vegetation closes during succession (Bazzaz 1979; Brandes & Nitzsche 2007; Fumanal *et al.* 2008). Colonization of closed vegetation types (e.g. semi-dry grasslands, embankments along rivers) usually only occurs after disturbance has created gaps (Brandes & Nitzsche 2007). However, in continuously disturbed habitats, such as arable fields, *A. artemisiifolia* is highly competitive and can cause significant yield losses, especially in row crops (Kazinczi *et al.* 2008b; Novak *et al.* 2009; Bullock *et al.* 2012).

Ambrosia artemisiifolia shows little tolerance to trampling, because the main stems of mature individuals tend to break easily (Nitzsche 2010; Bullock *et al.* 2012); the broken stems often wilt above the fracture (Brandes & Nitzsche 2006). Under experimental conditions, Gard *et al.* (2013) showed that both native and introduced invasive *A. artemisiifolia* tolerate artificial defoliation, which did not affect reproduction, and plants could reallocate resources in shoots even after 90% of the leaf area had been removed.

Reports on the susceptibility of *A. artemisiifolia* to allelopathic effects of other plant species are rare (see section VI. F). In contrast, Kazinczi *et al.* (2008d) found that aqueous extracts from leaves of sunflower – and other donor plants –

Table 1. The plant species most commonly associated with *Ambrosia artemisiifolia* in Central and Eastern Europe (based on 220 phytosociological relevés from Germany, Romania, northern Italy and eastern France) (Nitzsche 2010, modified). Representation is indicated for the four phytosociological classes in which it is typical

Species	Stellarietea	Artemisietea	Molinio— Arrhenatheretea	Plantaginetea, Polygono—Poetea
<i>Achillea millefolium</i> agg.			x	
<i>Artemisia vulgaris</i>		x		
<i>Chenopodium album</i>	x			
<i>Convolvulus arvensis</i>		x		
<i>Daucus carota</i>		x		
<i>Echinochloa crus-galli</i>	x			
<i>Elytrigia repens</i>		x		
<i>Erigeron canadensis</i>	x			
<i>Lactuca serriola</i>	x			
<i>Lolium perenne</i>			x	x
<i>Medicago lupulina</i>	x	x	x	
<i>Plantago lanceolata</i>			x	
<i>Plantago major</i>				x
<i>Polygonum aviculare</i> agg.				x
<i>Setaria pumila</i>	x			
<i>Setaria viridis</i>	x			
<i>Taraxacum</i> sect. <i>Ruderalia</i>			x	
<i>Trifolium pratense</i>			x	
<i>Trifolium repens</i>			x	
<i>Tripleurospermum inodorum</i>	x			

promote rather than inhibit germination and growth of *A. artemisiifolia*, and they speculate that this may contribute to its invasion success under field conditions. Interspecific competition may limit its invasiveness in moist sites (see section V. C).

V. Response to environment

(A) GREGARIOUSNESS

Ambrosia artemisiifolia populations vary greatly in size and spatial extent in Europe. Whereas most populations in less invaded areas are small and ephemeral, very large populations (with millions of individuals), some at extremely high densities (up to 400 plants m⁻²), prevail in heavily invaded regions (Bullock *et al.* 2012).

(B) PERFORMANCE IN VARIOUS HABITATS

Ambrosia artemisiifolia thrives in a wide range of open and disturbed habitats, in both native and invasive ranges: along waterways, roadsides and railways, in old fields and industrial or urban wastelands, and in cultivated fields, particularly among maize, sunflower and soya bean (Bassett & Crompton 1975; DiTommaso 2004; Lavoie, Jodoin & Goursaud de Merlis 2007; Fumanal *et al.* 2008; Simard & Benoit 2010; Bullock *et al.* 2012; Ngom & Gosselin 2014).

During its spread in Europe and North America, common ragweed has undergone an expansion its range of habitats. In Québec, it first spread along river corridors, and later invaded fields (since the 1920s), roads and railways (since the 1930s) (Lavoie, Jodoin & Goursaud de Merlis 2007). In France, *A. artemisiifolia* was mostly confined to crop fields until the mid-20th century, as it was primarily introduced in contaminated seed imports from North America. Similarly, first occurrences of *A. artemisiifolia* in Hungary were as an arable weed as early as in the 1920s (Kazinczi *et al.* 2008a). However, from the 1950s, it was found increasingly along roads and railways in France (Chauvel *et al.* 2006). In Austria, a somewhat different pattern has been observed (Fig. 3): railways were invaded first, through spillage of contaminated crop seeds. Subsequently, ruderal habitats distant to railways (bird feeding places, etc.) were invaded. Those habitats currently with the largest populations have been colonized only recently: fields (since the 1960s) and roadsides (since the 1970s) (Essl, Dullinger & Kleinbauer 2009). Lavoie, Jodoin & Goursaud de Merlis (2007) suggested that the extension or the improvement (paving) of the road network during the 20th century may have facilitated the colonization of roadsides in Québec. In addition, the application of large quantities of de-icing salt may have contributed to this expansion. This might have led to the selection of salt-tolerant ecotypes of *A. artemisiifolia* with a competitive advantage over other roadside plant species (Joly *et al.* 2011). However, to date, salt-tolerant ecotypes have only been found in Québec (DiTommaso 2004; Eom, DiTommaso & Weston 2013).

(C) EFFECT OF FROST, DROUGHT, ETC

Ambrosia artemisiifolia plants are sensitive to freezing. In particular, late spring frosts kill seedlings (Leiblein-Wild, Kaviani & Tackenberg 2014) and the first autumn frosts terminate the growing season (Ziska *et al.* 2011). Leiblein-Wild, Kaviani & Tackenberg (2014) found that seedlings of common ragweed have higher frost tolerance in the European range than in the native range. Differences in frost tolerance were attributed partly to differences in seed mass, because on average, seeds are larger in Europe.

The net photosynthetic rate of *A. artemisiifolia* decreases during periods of reduced soil water content (Bazzaz 1973), but the plants recover rapidly from short-term droughts (Bazzaz 1973, 1974). *Ambrosia artemisiifolia* tolerates a high water-saturation deficit, in that water-saturated common ragweed leaves can lose up to 70% of their maximum water content without irreversible damage (Almádi 1976). In unusually dry years or on dry sites, common ragweed plants have stunted growth, but remain able to produce seeds, albeit in small quantities (Raynal & Bazzaz 1975; Leiblein & Lössch 2011). Furthermore, drought stress in spring has a disproportionately high negative impact on *A. artemisiifolia* germination and seedling establishment (Shrestha *et al.* 1999).

Although under experimental conditions *A. artemisiifolia* can germinate in soils with high water content and tolerates waterlogged conditions (Leiblein & Lössch 2011), it does not occur in waterlogged sites under field conditions. *Ambrosia artemisiifolia* has the highest net photosynthetic rates under moist soil conditions in the absence of other plant species (Leiblein & Lössch 2011), which suggests that interspecific competition is a main factor limiting the invasion of moist sites.

VI. Structure and physiology

(A) MORPHOLOGY

Ambrosia artemisiifolia is an annual erect plant, which is usually highly branched in the upper parts (Fig. 4), and shows only a weak apical dominance (Irwin & Aarssen 1996). Its height varies from 0.1 to 2.5 m according to environmental conditions and competition. Vegetative life-history traits such as height and volume of plants, shoot number and biomass are positively correlated with reproductive traits (e.g. seed and pollen production). Stems are sparsely to densely pubescent with relatively long hairs usually with minute, pustular bases and/or shorter, appressed hairs. Number of nodes ranges between 6 and 23, and basal stem diameter between 0.3 and 4 cm. Plants continue to grow after the onset of flowering, but only by elongation of the internodes. Branching starts at about 2–4 cm above soil level (at the first to the third node) and includes numerous side-branches (20–29) of first to third order. Additional shoots can develop from accessory buds, which are usually induced by physical damage (Karrer *et al.* 2011). The stem breaks easily because the internodes are hollow (Nitzsche 2010). Side-branches represent 54% of the dry

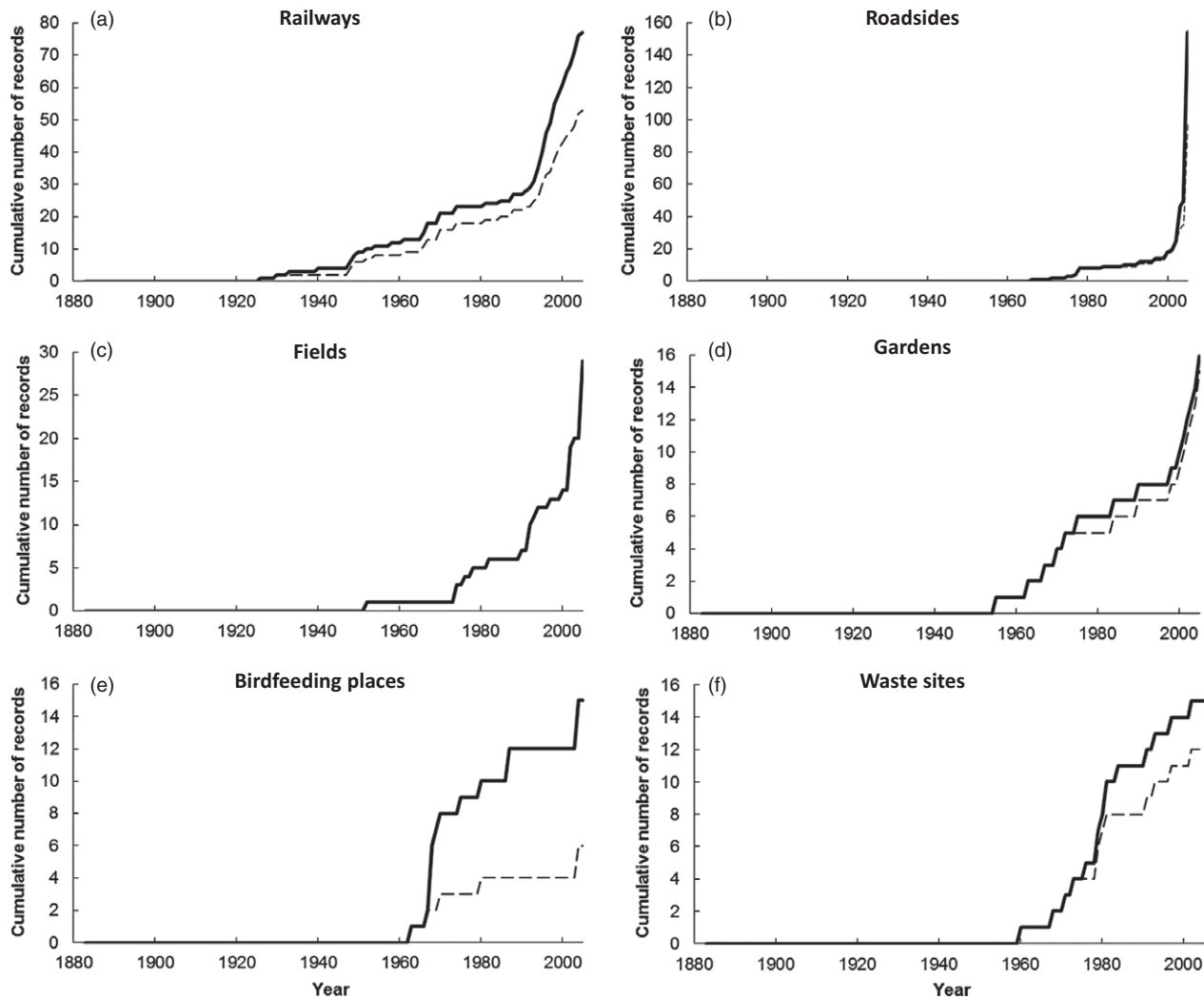


Fig. 3. Time course of invasion by *Ambrosia artemisiifolia* in six different habitats (a–f) in Austria. Results are shown as the cumulative number of records (solid line) and as cumulative number of colonized grid cells (dashed line) of the project ‘Floristic Mapping of Austria’ ($5 \times 3'$, c. 35 km^2). The two lines coincide for (c) fields (Essl, Dullinger & Kleinbauer, 2009, modified).

mass allocation, followed by 27% to roots and 18% to stems (Nitzsche 2010).

Leaves are opposite towards the stem base, but alternate towards the stem tip, with short to long, narrowly winged petioles. The length of the petiole diminishes from the basal to the median leaves, varying from obviously petiolate to sessile. Leaf blades are 3–10 cm long, ovate to broadly ovate in outline (the uppermost leaves are sometimes lanceolate to linear), 2–3 times pinnately lobed with more than five primary lobes (the uppermost leaves sometimes few-lobed to entire). The ultimate lobes are lanceolate to narrowly oblong, entire or few-toothed, the surfaces sparsely to moderately pubescent with short, somewhat broad-based hairs and sometimes appearing somewhat grey in colour (Tropicos 2014). The undersurface usually also has longer hairs along the main veins, and is not, or only slightly, paler than the upper surface.

The numerous male (staminate) capitula are arranged in leafless racemes (Fig. 5), but the female (pistillate) capitula are solitary or in small groups in the axils of the upper leaves. Staminate heads are in spike-like racemes, and the staminate

involucre is 2–4 mm wide, with 3–9 shallow lobes that are glabrous or sparsely hairy. Each involucre encloses one floret which develops to a one-seeded fruit (achene). At fruiting, it is 3–5 mm long, more or less ovoid and adnate to its involucre forming a syconium (Fig. 6). The sparsely to moderately hairy syconium develops a single series of 4–7 longitudinal ridges ending in spiny projections not or slightly flattened. Seeds are c. 3–4 mm long, 1.8–2.5 mm wide (Belcher 1985).

(B) MYCORRHIZA

Ambrosia artemisiifolia is considered obligately mycorrhizal in its native range (Crowell & Boerner 1988; Koide & Li 1991). In its French introduced range, 94% of 35 field populations studied were colonized by three main arbuscular mycorrhizal fungi (AMF): *Glomus mosseae*, *G. constrictum* and *Scutellospora* sp. (Fumanal *et al.* 2006). Fungal colonization levels were correlated with the habitat type. Populations from highly disturbed habitats (roadsides, ruderal habitats, riv-



Fig. 4. Appearance of *Ambrosia artemisiifolia*: (a) whole plant; (b) seedlings, together with seedlings of sunflower (*Helianthus annuus*); (c) juvenile plant; (d) female synflorescence; and (e) male racemes. © Essl (4×), B. Fumanal (1×), M. Smith (1×).

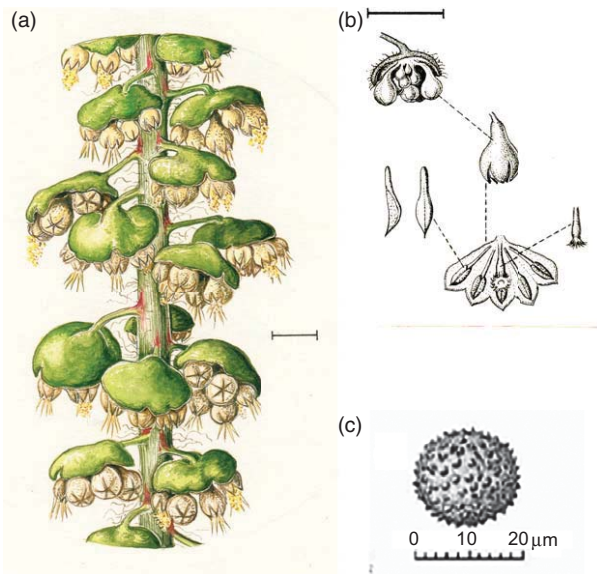


Fig. 5. Male capitula of *Ambrosia artemisiifolia*: (a) synflorescence; (b) single male flower; and (c) pollen. Scale bars for (a) and (b) represent 1mm. Drawings by Krisztina Bíró ©.

erbanks, but not fields) showed higher AMF colonization than those from less-disturbed habitats (orchard, old fallow). Experiments using various fungal inocula have shown that *Glomus etinacatum* facilitates phosphorus uptake in *A. artemisiifolia* (Koide & Li 1991) and that *G. intraradices* increases plant growth and developmental rates (Fumanal *et al.* 2006). In turn, common ragweed is able to stimulate both germination of *G. intraradices* spores (Schreiner & Koide 1993) and root colonization (File *et al.* 2012). File *et al.* (2012) report evidence of kin selection in juvenile *A. artemisiifolia* plants

through a common mycorrhizal network in that plants grown with siblings have greater mycorrhizal network sizes and root colonization rates than those grown with non-kin. These siblings having greater mycorrhizal association exhibited short-term benefits (e.g. fewer root lesions, higher total leaf nitrogen content) which could result in higher survival and fecundity.

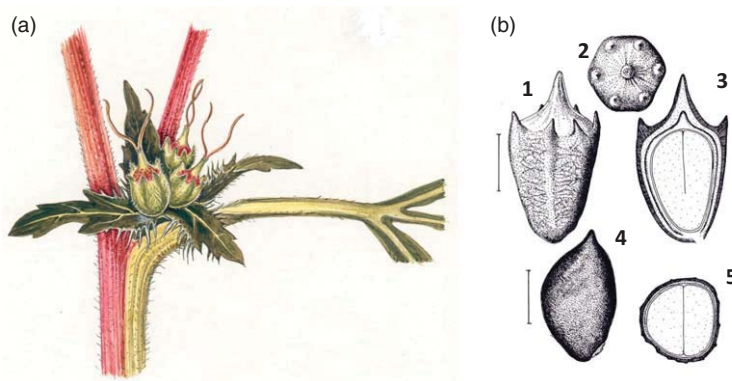
(C) PERENNATION AND REPRODUCTION

In North America, *A. artemisiifolia* is strongly self-incompatible and has high outcrossing rates (Friedman & Barrett 2008). Smaller and more isolated populations of wind-pollinated plants may experience an Allee effect because of pollen limitation (Friedman & Barrett 2011). It has thus been argued that natural selection may favour the evolution of selfing in the non-native range, as invading species frequently have small initial population sizes. However, Li *et al.* (2012) have demonstrated that no shift from outcrossing to selfing has occurred during *A. artemisiifolia*'s invasion of China. Similarly, outcrossing rates of common ragweed in Canada were found to be uniformly high. The maintenance of high outcrossing rates in colonizing populations of *A. artemisiifolia* is likely to be facilitated by the prodigious production of wind-borne pollen (Friedman & Barrett 2011).

(D) CHROMOSOMES

Chromosome number reported for *A. artemisiifolia* is $2n = 36$ (Stace 2010). According to Payne (1964) and Martin *et al.* (2014), the diploid state is frequent, but sometimes triploid and tetraploid individuals are found in North American popu-

Fig. 6. Female capitula of *Ambrosia artemisiifolia*: (a) racemes with achenes; (b) 1, one-seeded syconium viewed from the side; 2, syconium viewed from above; 3, syconium in longitudinal section; 4, achene; 5, syconium cross-section. Scale bars represent 1 mm. Drawings by Krisztina Bíró ©.



lations. Chromosome counts are available from North America and the introduced range in Europe and East Asia (see Tropicos 2014).

(E) PHYSIOLOGICAL DATA

Ambrosia artemisiifolia is a C3 plant and typically completes its life cycle within 115–183 days (Bassett & Crompton 1975; Béres 1994; Kazinczi *et al.* 2008b). Photoperiod and temperature (see section II. A) are the main factors controlling growth and development. The length of the photoperiod influences the sex ratio of flowers: under long day-conditions male flowers are predominant, whereas female flowers are favoured as the days shorten (Allard 1943).

Under experimental conditions, common ragweed leaves have the highest chlorophyll content (up to 8.8, SD: ± 0.6 mg g⁻¹), CO₂ uptake and photosynthetic rate under moist soil conditions (Leiblein & Löscher 2011). A lower chlorophyll content and insufficient opening of the stomata contribute to lower assimilation rates under less favourable (e.g. dry, waterlogged) conditions. Common ragweed grows best in full sunlight, but it grows well in moderate shade. Glasshouse-grown plants, which had experienced light availability only c. 39% of that outside, approached photosynthetic light saturation at a PAR of c. 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas field-grown plants did not saturate at c. 730 $\mu\text{mol m}^{-2} \text{s}^{-1}$; field-grown plants also had fivefold higher rates of photosynthesis (Bazzaz 1973). In a further experiment, field-grown, mature *A. artemisiifolia* plants did not saturate at a PAR of c. 1450 $\mu\text{mol m}^{-2} \text{s}^{-1}$; the photosynthetic rate at optimal light flux, temperature, water potential and 300 ppm CO₂ was c. 35 mg dm⁻² h⁻¹ (Bazzaz 1974). Their optimal temperature for photosynthesis was 20°C, and the high rate of photosynthesis was accompanied by a high transpiration rate (3 g H₂O dm⁻² h⁻¹) (Bazzaz 1974). Consequently, *A. artemisiifolia* utilizes substantially more water to produce an equivalent amount of biomass than maize (Bassett & Crompton 1975).

Leskovšek *et al.* (2012a,b) showed that high nitrogen levels lead to a greater allocation of biomass to the top stratum of the plants, thus increasing their ability to compete for light. Elevated atmospheric CO₂ concentrations led to a marked increase in growth (Bazzaz 1974), seed yield and pollen production (Ziska *et al.* 2003) as well as a heightened pollen

allergenicity (Singer *et al.* 2005). A doubling of the CO₂ concentration stimulated pollen production by 61% (Wayne *et al.* 2002).

(F) BIOCHEMICAL DATA

Ambrosia artemisiifolia contains various secondary metabolites with antibiotic properties, such as sesquiterpene lactones, including ambrosin, isabelin, psilostachya, cumarin and peruvian, as well as triterpenoids of the α - and β -amyrin type and derivatives of caffeic acid (Solujić *et al.* 2008). The sesquiterpene lactones are characterized by an α,β -unsaturated γ -lactone moiety 14 and possess antibacterial, antifungal, antiprotozoal, anthelmintic and schistosomicidal activities (Brückner, Lepossa & Herpai 2003).

These substances produced by *A. artemisiifolia* have an inhibitory effect on growth of different plant species (e.g. Fisher & Quijano 1985; Wang & Zhu 1996; Brückner, Lepossa & Herpai 2003; Lehoczky *et al.* 2011; Vidotto, Tesio & Vidotto 2013). Experiments show variation in the intensity of inhibition among extracts of different plant parts (roots, leaves, male inflorescences, achenes). The extract of male inflorescences had the highest impact on germination of plant seeds tested (Brückner, Lepossa & Herpai 2003). In a recent study, Vidotto, Tesio & Vidotto (2013) showed under laboratory and greenhouse conditions that residues of dead plant material of *A. artemisiifolia* in soil affected the germination and seedling growth of crop and weed species. Tomato (*Solanum lycopersicum*) was the most sensitive crop species as growth was reduced by more than 50% compared to the control. Among tested weed species, *Digitaria sanguinalis* suffered a large reduction in germination (90%) after incorporation of 3 g of residues of *A. artemisiifolia* in 150 g of an experimental soil mixture (alluvium soil and silica sand). Allelopathic effects in the field have not been tested, but current research suggests that they might play a role in facilitating the invasion of *A. artemisiifolia*.

VII. Phenology

Ambrosia artemisiifolia's life cycle is typical of a short-day annual (Deen, Hunt & Swanton 1998b). Germination in Europe occurs in early to mid-spring (late March and April), although a small proportion germinates later (Bassett & Crompton 1975;

Baskin & Baskin 1977). Following seedling emergence, the rate of vegetative growth depends on temperature (Deen, Hunt & Swanton 1998b), but development occurs over a wide thermal range (8–30°C) (Deen, Hunt & Swanton 1998b).

The onset of reproductive development is marked by a switch from the production of opposite leaves to the appearance of alternate leaves. In the native range, and in heavily invaded parts of Europe, flowering begins in late July or early August (Brandes & Nitzsche 2006; Ziska *et al.* 2011). Flowering is triggered by declining day lengths after the summer solstice, with reproductive development being delayed at photoperiods longer than 14 h (Deen, Hunt & Swanton 1998a). Flowering is monoecious with overlap in the period when flowers of both sexes are present. The first male flowering usually occurs a few days before the first female flowering (Deen, Hunt & Swanton 1998b; Friedman & Barrett 2011). However, the relative timing of male and female flowering is plastic, for example shading triggers earlier male flowering (Friedman & Barrett 2011). Termination of flowering occurs with frosts from late September or October that kill the plants (Dahl, Strandhede & Wihl 1999; Ziska *et al.* 2011; Prank *et al.* 2013). This also marks the end of the period for the development of viable mature seeds.

Although the phenology of *Ambrosia artemisiifolia* conforms to this general pattern, there is significant variation across its range. A common garden study using native seeds demonstrated that plants from northern latitudes flowered earlier in a northern garden (Allard 1943; Dickerson & Sweet 1971). Similar latitudinal clines in flowering phenology have been found in Europe (Genton *et al.* 2005; Chun *et al.* 2011; Hodgins & Rieseberg 2011; Leiblein-Wild & Tackenberg 2014). For instance, late growth and flowering phenology in a common garden experiment were highly correlated with latitude, that is individuals from northern populations grew smaller and flowered and dispersed pollen and seeds up to five weeks earlier than individuals from southern populations (Leiblein-Wild & Tackenberg 2014). This may be responsible for the remarkable level of synchronization in the start of the pollen season observed across the native range (Ziska *et al.* 2011).

VIII. Floral and seed characters

(A) FLORAL BIOLOGY

Common ragweed is exclusively wind pollinated. Male capitula are short stalked (2–5 mm) and arranged in numerous dense but elongating racemes. The phyllaries form a funnel-shaped involucre (Payne 1964). Raceme number (5–2878, mean = 142, $n = 203$), capitulum number per raceme (15–93, mean = 55, $n = 1015$) and florets per capitulum (9–39, mean = 18, $n = 1015$) can be very variable according to the plant size but are strongly positively correlated with plant dry mass (Fumanal, Chauvel & Bretagnolle 2007; Simard & Benoit 2011). Female heads are clustered in the axils of foliar leaves below the terminal male racemes in small groups (1–5 (10)) surrounded by small bracts. High-ranking lateral shoots tend to develop female heads. Lateral regrowth from early

cutting (mid-July) produces significantly more male racemes than branches from late cutting (mid-August) (Barbour & Meade 1981). Basal lateral branches of plants cut in September develop almost exclusively female flowers (M. Leitsch-Vitalos, unpubl. data). Some individuals in a few European populations have 100% pistillate flowers – even the terminal racemes consist only of females. In North American populations, c. 5% of the individuals have exclusively pistillate flowers (Gebben 1965).

Anthers open with a rise in temperature and low relative humidity (Martin, Chamecki & Brush 2010), that is usually in the morning after sunrise, and pollen release from a flower lasts only up to 6 h. Although *A. artemisiifolia* is exclusively anemophilous, the pollen (Fig. 6c) is sticky directly after release, but after some hours, it is dry enough to be dispersed by wind. The pollen production varies among plants and years from 0.1 to 3.8 billion pollen grains per plant (Fumanal, Chauvel & Bretagnolle 2007), according to plant size. Pollen grain diameter ranges from 18 to 22 μm (Taramarcas *et al.* 2005). The pollen load is high enough for effective pollination from August to end of October.

There is experimental evidence for some degree of self-pollination (Bassett & Crompton 1975) but also for 100% outcrossing (Friedman & Barrett 2008). Population genetic data indicate heterozygosity deficits, probably through some degree of selfing (Genton, Shykoff & Giraud 2005; Chun *et al.* 2010; Gaudeul *et al.* 2011; Karrer *et al.* 2011).

(B) HYBRIDS

Hybrids of *A. artemisiifolia* with congeners have been reported rarely. Hybrids between *A. artemisiifolia* and *A. psilostachya* (*A. ×intergradiens* W. H. Wagner) have been observed rarely in North America (Wagner & Beals 1958). However, this hybrid fails to produce viable seeds.

Ambrosia ×helenae Rouleau is a hybrid between *A. artemisiifolia* and *A. trifida* (Vincent & Cappadocia 1988; Flora North America (FNA) 2006), which has also been found infrequently in North America (Steyermark 1963). Gilles, Lauzer & Cappadocia (1988) created hybrids with *A. trifida* through cross-fertilization that resemble *A. trifida* but are sterile (Bassett & Crompton 1975). No hybrids have yet been found in the non-native range of *A. artemisiifolia*.

(C) SEED PRODUCTION AND DISPERSAL

Seed production of common ragweed is closely related to plant biomass (Dickerson & Sweet 1971; Fumanal, Chauvel & Bretagnolle 2007). Therefore, habitat suitability and competition are likely to be the most important determinants of the number of seeds. A survey of five ragweed populations in France showed an average seed number of 2518 (± 271 SD) seeds per plant (Fumanal, Chauvel & Bretagnolle 2007). Planted individuals in the native range had higher seed production, ranging from 3135 to 32 485 seeds per plant (Dickerson & Sweet 1971). However, the highest reported numbers of seeds per plant have been found in Hungary (without intra-

and interspecific competition generally between 18 000 and 48 000, but an extreme value of 94 900 seeds was also counted for a plant; G. Kazinczi, unpubl. data) and Russia (62 000 seeds; Fijunov 1984). Individuals from ruderal habitats had lower average seed production (between c. 300 and 2500 plant⁻¹) than individuals from arable fields (c. 2300–6000 plant⁻¹; Fumanal, Chauvel & Bretagnolle 2007). Seed production in populations on arable fields is negatively affected by the density of crops (Chikoye, Weise & Swanton 1995; Nitzsche 2010).

Seed mass is highly variable within individual plants and differs between populations (Fumanal *et al.* 2007). Mean seed mass in different populations in France ranged from 1.72 to 3.60 mg (Fumanal *et al.* 2007). Nitzsche (2010) found a mean seed mass around 5 mg for several populations from Germany and Hungary and a high mean of 10 mg for one experimental population in Germany. Similarly, Karrer (unpubl. data) found a mean of 4.65 mg for 24 populations in Europe and China. Seeds take about 4–6 weeks to develop to maturity following pollination (Béres 1981; G. Karrer, unpubl. data). Seeds tend to stay on the plants for one or 2 weeks after ripening.

In North America, Gebben (1965) stated that seed dispersal by birds plays a role in the spread of *A. artemisiifolia* and dispersal (epizoochory) by animals (*Bison bison*) has also been shown (Rosas *et al.* 2008). Bullock *et al.* (2012) found little evidence for seed dispersal by animals in Europe, although there are reports of caching of ragweed seeds by rodents and of seed dispersal by birds (Nitzsche 2010). Zoochory and dispersal of floating seeds by water (hydrochory) (Fumanal *et al.* 2007) seems to have minor importance.

While the achenes have no obvious morphological adaptations for vectors of long-distance dispersal, it is obvious that simple dissemination of seeds by gravity and wind cannot explain the observed spread rates at the landscape scale, which are probably achieved through seed dispersal by human activities (Bullock *et al.* 2012). Dispersal experiments with sticky plastic sheets around single plants of common ragweed gave a median dispersal distance of 0.45 m and a 99% percentile of 1.05 m (A. Lemke, unpubl. data). This is in accordance with Dickerson (1968) who showed that dispersal by wind is restricted to 2 m around the mother plant.

(D) VIABILITY OF SEEDS AND GERMINATION

Ambrosia artemisiifolia forms a persistent soil seed bank as a result of complex germination strategies (Bazzaz 1970; Thompson, Bakker & Bekker 1997). Seeds are dormant following their dispersal in autumn. This primary (innate) dormancy is then broken by low winter temperatures (optimally a few days around 4°C; Willemsen 1975) and seeds that do not germinate the next spring enter secondary (induced) dormancy (Bazzaz 1970, 1979; Willemsen & Rice 1972; Willemsen 1975; Baskin & Baskin 1980). Secondary dormancy can also be induced by dark, low temperature fluctuations and high CO₂ concentration (Bazzaz 1979). Under field conditions, secondary dormancy may also be induced during hot dry summer periods.

Germination and early seedling establishment of *A. artemisiifolia* are mostly related to disturbance and the lack of competition (Bazzaz 1979; Rothrock, Squiers & Sheeley 1993). In a field experiment, Fumanal, Gaudot & Bretagnolle (2008) observed that recruitment from the seed bank in an invaded set-aside field was doubled when competitors were removed and twofold to twelvefold higher when the soil surface was disturbed. Furthermore, Fenesi, Albert & Ruprecht (2014) showed reduced and delayed germination with the presence of adult plant competitors.

Seed dormancy can be broken by wet, dark stratification at 4°C for 2 weeks to obtain about 75% of germination (Baskin & Baskin 1987; Fumanal *et al.* 2006). However, freshly harvested dormant seeds do not germinate at their optimum after stratification as they need to ripen for some months before stratification (Brandes & Nitzsche 2006). Under natural conditions, seed dormancy is broken from January to February (Willemsen 1975; Béres & Hunyadi 1984). Fumanal, Gaudot & Bretagnolle (2008) observed in France that dormancy could be broken until May (2–6% of dormant seeds in the 0–20 cm soil layer) and germination rate then increases up to 79% until mid-July. According to Baskin & Baskin (1985), the dormancy period starts in May in the native region.

Because of secondary dormancy, *A. artemisiifolia* seeds can remain alive in the soil for decades (Toole & Brown 1946; Stoller & Wax 1974). Darlington (1922) showed that 4% of common ragweed seeds from the experiment initiated by Beal in 1879 were still able to germinate after 40 years. These results do not necessarily indicate the maximum life span of seeds but their ability or inability to germinate in time under specific experimental conditions (Baskin & Baskin 1977). Likewise, in field conditions, the survival of seeds depends on their burial depth. In total, 21% and 57% of seeds buried in the soil at 8 cm and 22 cm, respectively, germinated *in vitro* 30 years after Duvel's experiment started in 1902, and 6% of seeds buried at 22 cm did so after 39 years (Toole & Brown 1946). Unburied seeds quickly lose their viability over 4 years (Béres 2003). Viability decreased by 82% after five years for seeds stored in paper bags at room temperature (Kazinczi and Novák 2014).

Seed-bank densities of *A. artemisiifolia* in field-crop habitats have been analysed by a number of authors (Raynal & Bazzaz 1973; Bigwood & Inouye 1988; Gross 1990; Rothrock, Squiers & Sheeley 1993; Webster, Cardina & White 2003). Fumanal, Gaudot & Bretagnolle (2008) studied the seed bank in different invaded habitats and found on average 536 (in waste land) to 4477 (in set-aside habitats) seeds m⁻² in the upper 20 cm of soil. Seed banks in crop fields were larger than in ruderal and set-aside habitats. The number of extant seeds in the upper soil layer (0–5 cm) was lower (mean = 592, *n* = 240) than in the deeper layer (5–15 cm) (mean = 1630, *n* = 240) for frequently ploughed habitats such as crop fields, whereas the opposite pattern was observed for less-disturbed conditions (wasteland and set-aside habitats) (upper soil layer, mean = 1066; deeper soil layer, mean = 585, *n* = 250). The horizontal distribution of

A. artemisiifolia seed bank is spatially aggregated irrespective of the intensity of soil disturbance.

Under experimental conditions (after stratification), seed germination is highest for seeds on the soil surface and decreases with increasing depth, ceasing below 8 cm (Gebben 1965; Dickerson 1968; Stoller & Wax 1975; Guillemain & Chauvel 2011). Depending on the habitat type, germination is positively correlated with seed mass (Fumanal, Gaudot & Bretagnolle 2008) or not (Guillemain & Chauvel 2011). Germination in the field depends on various factors, such as soil temperature, rhythm of temperature changes, light, humidity and CO₂ concentration (Bazzaz 1968, 1970; Pickett & Baskin 1973; Raynal & Bazzaz 1973; Baskin & Baskin 1980; Shrestha *et al.* 1999). Under controlled conditions and at constant temperature, germination of stratified seeds increases from 5 to 25°C and decreases up to 40°C (Shrestha *et al.* 1999; Nitzsche 2010; Sang, Liu & Axmacher 2011). Guillemain & Chauvel (2011) observed 80% germination of stratified seeds at 15/10°C and 90% at 25/20°C with a 16 h day/8 h night photoperiod. In natural conditions, even if most of the seeds are able to germinate early in spring (Fumanal, Gaudot & Bretagnolle 2008), recruitment rates of buried seeds from the upper soil layers are relatively low and variable – from 2.3 to 42% – according to the habitat and amount of disturbance (Forcella *et al.* 1992; Rothrock, Squiers & Sheeley 1993; Webster, Cardina & White 2003; Fumanal, Gaudot & Bretagnolle 2008).

Germination is delayed by low temperatures (Willemsen 1975; Pickett & Baskin 1973; Guillemain *et al.* 2013), low moisture (Shrestha *et al.* 1999; Guillemain *et al.* 2013), low light (Pickett & Baskin 1973; Guillemain & Chauvel 2011) or high salinity (DiTommaso 2004). The minimum temperature for germination ranges from 3.4 to 3.6°C and minimum water potential from –0.8 to –1.28 MPa (Shrestha *et al.* 1999; Sartorato & Pignata 2008; Guillemain *et al.* 2013). However, according to Sang, Liu & Axmacher (2011), the germination of seeds decreases near-linearly with decreased osmotic potential to –1.6 MPa (no germination). Therefore, *A. artemisiifolia* can germinate under a very high water deficit as well as under water-logged conditions (Martinez *et al.* 2002). *Ambrosia artemisiifolia* is also able to germinate in distilled water over a large range of pH values, from 4 to 12 (at least 48% germination) with an optimum between pH 5–8 and a maximum germination rate of 98.2% at pH 5.57 (Sang, Liu & Axmacher 2011). It is also able to maintain high germination rates (70–80%) under moderate salinity of about 200 mmol L⁻¹ of NaCl (Sang, Liu & Axmacher 2011; Eom, DiTommaso & Weston 2013) and can germinate (from 5 to 12%) at high NaCl concentrations (i.e. 400 mmol L⁻¹). DiTommaso (2004) observed that populations growing in saline, road-side habitats show higher germination rates than field-crop populations and were very competitive in such environments.

(E) SEEDLING MORPHOLOGY

Germination is epigeal (Dickerson 1968; Fig. 7). The cotyledons are elliptic, short-stalked, hairless and show a purple pigmentation of the margins that often extends to the lower



Fig. 7. Germination and seedling development of *Ambrosia artemisiifolia*. Drawings by Krisztina Bíró ©.

surface. They become green shortly after they emerge from the soil and start to be photosynthetically active (Bazzaz 1973). The primary leaves are ovate in outline, pinnate and minutely hairy (Kazinczi *et al.* 2008a). The first foliar leaf appears within few days after germination. Seedling size is positively correlated with the mass of the seed. The hypocotyl and epicotyl are glabrous and often purplish in colour.

IX. Herbivory and disease

(A) ANIMAL FEEDERS OR PARASITES

In Eurasia, some 50 insect and one acarine species have been found on *A. artemisiifolia* and nearly all were recorded in the former Yugoslavia, Hungary and Russia (Table 2; Gerber *et al.* 2011). The only exception is the moth *Ostrinia orientalis* Mutuura & Munroe (Crambidae), which has been found on *A. artemisiifolia* in China (Wan *et al.* 2003). However, many of these species are polyphagous and cause little damage to *A. artemisiifolia* (Gerber *et al.* 2011). In Hungary, hemipterans dominated the insect fauna in a survey on *A. artemisiifolia* with *Eupteryx atropunctata* and *Emelyanoviana mollicula* being most often recorded (Kiss, Rédei & Koczor 2008). In Hungary (and probably elsewhere), *A. artemisiifolia* is a host to several Thysanoptera species including *Frankliniella occidentalis* and *Thrips tabaci* that are vectors of the tomato spotted wilt virus, and *T. tabaci* has been shown to transmit this virus to *A. artemisiifolia* (Jenser, Kiss & Takács 2009). Recently, the beetle *Ophraella communa* (Fig. 8) has been detected for the first time in Europe in southern Switzer-

Table 2. Herbivores and pathogens recorded on *Ambrosia artemisiifolia* in its introduced range in Europe (modified from Gerber *et al.* 2011). Fungal taxonomy is in accordance with Index Fungorum (<http://www.indexfungorum.org/Index.htm>)

Taxon	Country	Source
Insecta		
Coleoptera		
Cerambycidae		
<i>Agapanthia dahli</i> Richter	Hungary	12
Chrysomelidae		
<i>Cryptocephalus sericus</i> L.	Former Yugoslavia	16
<i>Galeruca tanacetii</i> L.	Former Yugoslavia, Slovakia	16, 27
<i>Ophraella communis</i> Le Sage	Italy, Switzerland	17
<i>Zygogramma suturalis</i> F.	Russia, Croatia	10, 22
Curculionidae		
<i>Lixus</i> sp.	Former Yugoslavia	16
<i>Phyllobius pyri</i> L.	Former Yugoslavia	16
<i>Sitona suturalis</i> Steph.	Former Yugoslavia	16
<i>Tanymecus pallidus</i> R.	Russia, former Yugoslavia	16
<i>Coniocleonus nigrosuturatus</i> Goeze	Hungary	9
Mordellidae		
<i>Morellistena</i> sp.	Russia	16
HETEROPTERA		
Cercopidae		
<i>Philaenus spumarius</i> L.	Hungary, former Yugoslavia, Sweden	13, 28
<i>Coreus marginatus</i> L.	Russia, former Yugoslavia, Slovakia	16, 27
<i>Adelphocoris lineoletus</i> Goeze	Hungary	13
<i>Lygus rugulipennis</i> Poppius	Hungary, Slovakia, Sweden	13, 27, 28
<i>Lygus pratensis</i> (L.)	Slovakia	27
<i>Eurydema oleraceum flanata</i> Schr.	Former Yugoslavia	16
<i>Eurydema oleraceum interrupta</i> Ry.	Former Yugoslavia	16
<i>Eurydema ornatum</i> (L.)	Slovakia	27
HOMOPTERA		
Aphididae		
<i>Aphis fabae</i> Scopoli	Hungary, former Yugoslavia, Slovakia	13, 27
<i>Aphis</i> sp.	Former Yugoslavia	16
<i>Brachycaudus helichrysi</i> (Kaltenbach)	Hungary, former Yugoslavia	2
<i>Myzus persicae</i> (Sulzer)	Hungary	2
<i>Protaphis</i> sp.	Russia	16
Cicadellidae		
<i>Cicadella viridis</i> (L.)	Sweden	
<i>Emelyanoviana mollicula</i> (Boheman)	Hungary	13
<i>Eupteryx atropunctata</i> (Goeze)	Hungary	13
Membracidae		

(continued)

Table 2. (continued)

Taxon	Country	Source
<i>Stictocephala bisonia</i> Kopp et Yonke	Slovakia	27
Diaspididae		
<i>Parthenolicaneum corni</i> Bouché	Russia	28
Psyllidae		
<i>Psyllid</i> sp.	Sweden	28
LEPIDOPTERA		
Crambidae		
<i>Ostrinia nubialis</i> Hbn.	Former Yugoslavia	16
Geometridae		
<i>Cosymbia</i> sp	Former Yugoslavia	16
Unidentified	Former Yugoslavia	16
Unidentified	Former Yugoslavia	16
Lymantriidae		
<i>Orgyia recens</i> Hbn.	Former Yugoslavia	16
Noctuidae		
<i>Autographa confusa</i> Steph.	Russia	14
<i>Autographa gamma</i> L.	Russia, former Yugoslavia	14
<i>Chloridea scutosa</i> Schiff.	Russia	16
<i>Helicoverpa armigera</i> (Hübner)	Italy, Slovakia	27
<i>Hyponomeuta proboscidalis</i> L.	Former Yugoslavia	16
<i>Peridroma saucia</i> Hbn.	Former Yugoslavia	16
<i>Scotia ipsilon</i> Rott.	Russia	14
<i>Tarachidia candefacta</i> Hübner	Russia, Serbia	20, 23
ORTHOPTERA		
Acrididae		
<i>Chortippus paralellus</i> Zett.	Former Yugoslavia	16
<i>Chortippus</i> sp.	Former Yugoslavia	16
Decticinae		
<i>Pholidoptera</i> sp.	Former Yugoslavia	16
Gryllidae		
<i>Oecanthus pellucens</i> Scop.	Former Yugoslavia	16
Tettigidae		
<i>Tetrix undulata</i> Serv.	Former Yugoslavia	16
<i>Leptophytes bosci</i> Fieb.	Former Yugoslavia	16
THYSANOPTERA		
Thripidae		
<i>Aeolothrips intermedius</i> Bagnall	Hungary	11
<i>Frankliniella intonsa</i> (Trybom)	Hungary	11
<i>Franliniella occidentalis</i> (Pergande)	Hungary	11
<i>Haplothrips aculeatus</i> (Fabricius)	Hungary	11
<i>Microcephalothrips abdominalis</i> (D. L. Crawford)	Hungary	11
<i>Thrips fuscipennis</i> Haliday	Hungary	11
<i>Thrips nigropilosus</i> Uzel	Hungary	11
<i>Thrips tabaci</i> Lindeman	Hungary	11
ACARINA		
Tetranychidae		
<i>Tetranychus urticae</i> Koch.	Russia	16
Eriophyidae		
<i>Aceria</i> sp.	Serbia	29

(continued)

Table 2. (continued)

Taxon	Country	Source
FUNGI		
OOMYCOTA		
OOMYCETES		
ALBUGINALES		
Albuginaceae		
<i>Pustula tragopogonis</i> (Pers.) Thienes (<i>Albugo tragopogonis</i> (D.C.) S.F. Gray)	Hungary, Austria	6, 26
PERONOSPORALES		
Peronosporaceae		
<i>Plasmopara angustiterminalis</i> Novot.	Ukraine	8
<i>Plasmophora halstedii</i> (Farl.) Berl. & De Toni	Hungary	24
ASCOMYCOTA		
DOTHIDEOMYCETES		
BOTRYOSPHAERIALES		
Botryosphaeriaceae		
<i>Macrophomina phaseolina</i> (Tassi) Goid	Hungary	4
CAPNODIALES		
Mycosphaerellaceae		
<i>Septoria ambrosiae</i> Hemmi & N. Naito	Japan	18
<i>Septoria epambrosia</i> D.F. Farr	Hungary	5
PLEOSPORALES		
Pleosporaceae		
<i>Alternaria alternata</i> (Fr.) Keissl (<i>Alternaria tenuis</i> Nees)	China	15
Incertae sedis		
<i>Phoma</i> sp.	Hungary	3
LEOTIOMYCETES		
HELOTIALES		
Sclerotiniaceae		
<i>Botrytis cinerae</i> Pers.	Hungary	6
<i>Sclerotinia sclerotiorum</i> (Lib.) de Bary	Hungary	4
ERYSIPHALES		
Erysiphaceae		
<i>Golovinomyces cichoracearum</i> (DC.) V.P. Heluta (<i>Erysiphe cichoracearum</i> DC.)	Korea, Mauritius	19, 22
<i>Golovinomyces cichoracearum</i> var. <i>latisporus</i> (U. Braun) U. Braun (<i>Erysiphe cichoracearum</i> var. <i>latispora</i> U. Braun)	Germany	7
<i>Leveillula taurica</i> (Lév.) G. Arnaud	Former USSR	1
SORDARIOMYCETES		
HYPOCREALES		
Netriaceae		
<i>Fusarium avenaceum</i> (Fr.) Sacc.	China	15

(continued)

Table 2. (continued)

Taxon	Country	Source
INCERTAE SEDIS		
Plectosphaerellaceae		
<i>Verticillium dahliae</i> Kleb.	Hungary	6
PHYLLACHORALES		
Phyllachoraceae		
<i>Phyllachora ambrosiae</i> (Berk. & M.A. Curtis) Sacc.	Hungary	24
AGARICOMYCETES		
CANTHARELLALES		
Ceratobasidiaceae		
<i>Thanatephorus cucumeris</i> (A.B. Frank) Donk (<i>Rhizoctonia solani</i> J.G. Kühn)	Hungary	6
EXOASIDIOMYCETES		
ENTYLOMATALES		
Entylomataceae		
<i>Entyloma polysporum</i> (Peck) Farl.	Hungary	25
INCERTAE SEDIS		
<i>Athelia rolfsii</i> (Curzi) C.C. Tu & Kimbr. (<i>Sclerotium rolfsi</i> Sacc.)	China	15

Sources: (1) Amano (1986); (2) Basky (2009); (3) Bohár *et al.* (2009); (4) Bohár & Kiss (1999); (5) Bohár & Schwarzinger (1999); (6) Bohár & Vajna (1996); (7) Braun (1995); (8) Dudka & Hayova (2007); (9) Horváth, Kazinczi & Keszthelyi (2014); (10) Igrc, DeLoach & Zlof (1995); (11) Jenser, Kiss & Takács (2009); (12) Kiss (2009); (13) Kiss, Rédei & Koczor (2008); (14) Kovalev (1971b); (15) Li & Li (1993); (16) Maceljski & Igrc (1989); (17) Müller-Schärer *et al.* (2014); (18) Naito (1940); (19) Orioux & Felix (1968); (20) Poltavsky & Artokhin (2006); (21) Reznik (1991); (22) Shin (2000); (23) Stojanović *et al.* (2011); (24) Vajna (2002); (25) Vanky *et al.* (1988); (26) Voglmayr & Riethmüller (2006); (27) P. Toth (unpubl. data); (28) J. Stephan, M. Kniest, C. Marchal, H. Tran & R. Scalone *et al.* (unpubl. data); (29) Petanović & Vidović (unpubl. data).

land (Ticino) and northern Italy (Lombardia, Piemonte and Emilia-Romagna; Fig. S2; Müller-Schärer *et al.* 2014). Despite its recent arrival in Europe, data from the rapidly expanding colonized area suggest that this species, which was accidentally introduced into China and now is used there as a successful biocontrol agent (Zhou *et al.* 2010), reduces growth and seed production of *A. artemisiifolia* substantially.

In its native range, *A. artemisiifolia* is attacked by a wide variety of invertebrate herbivores, for example by the beetle *Zygotogramma suturalis* (see section XI.) and several polyphagous consumers including beetles, bugs and moths. While most of these herbivores are leaf-chewing insects, the plant is also attacked by stem-galling moths of the genus *Epiblema* (MacKay & Kotanen 2008). Goeden & Palmer (1995) identified up to 70 species of insects and mites associated with *A. artemisiifolia* in the native range. In total, as many as 450 herbivores have been found on the various native *Ambrosia* spp. in North and South America (Goeden & Palmer 1995), of which some 109 species are likely to be specialists, associated with plants from the subtribe Ambrosiinae (Gerber *et al.*



Fig. 8. *Ophraella communa* on *Ambrosia artemisiifolia* in northern Italy: (a) Eggs; (b) Larva; (c) Pupa; (d) Adult; (e) Content of a sweep net after 10 sweeps in a field infested with *A. artemisiifolia* near Milano (Corbetta, 24 September 2013).

2011). Moreover, seed predation by ground beetles (*Harpalus* spp.; Coleoptera, Carabidae) and snails (*Trichia striolata*; Gastropoda, Hygromiidae) has been reported by MacKay & Kotanen (2008). In contrast, the insect complex associated with *A. artemisiifolia* in Europe consists mainly of polyphagous species, including some known agricultural pests, and most native herbivores occur only at low densities (Table 2). *Ambrosia artemisiifolia* is wind pollinated, so insects only visit flowers to eat the pollen (Bassett & Crompton 1975).

MacKay & Kotanen (2008) showed that in the native range, experimental populations of common ragweed isolated from existing populations by as little as 100 m experienced reduced levels of damage by invertebrate folivores and seed predators. These results indicate that common ragweed can escape natural enemies by dispersing to new sites. Although MacKay & Kotanen (2008) and MacDonald & Kotanen (2010) found only slight effects of reduced levels of folivory, seed predation, soil pathogens and perhaps losses to seed pathogens, they proposed that enemy release can occur for native as well as exotic populations of this species, linking possible mechanisms of local spread with long-distance invasion. Similarly, in its invaded range, this plant has been shown to have escaped insect folivores (Genton *et al.* 2005), consistent with the Enemy Release Hypothesis, that is the absence of specialized herbivores in the introduced range (Colautti *et al.* 2004).

(B, C) PLANT PARASITES AND DISEASES

Ambrosia artemisiifolia is only rarely attacked by plant parasites. In North America (Bassett & Crompton 1975; Krumbiegel 2007) as well as in Europe (S. Follak and G. Karrer, unpubl. data), *A. artemisiifolia* is sometimes attacked by a parasitic dodder (*Cuscuta campestris*), which is also native to North America and has been introduced into Europe. In the native range, numerous fungal pathogens are associated with *Ambrosia* species (Bassett & Crompton 1975). Of the 20 fungal pathogens associated with *Ambrosia* species in Eurasia (Table 2; Gerber *et al.* 2011) 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. (Acomycota: Phyllachorales) and *Plasmodiopsis halstedii* (Farl.) Berl. & De Toni (Oomycota: Peronosporales), were recorded in Hungary in 1999 and 2002 (Vajna, Bohár & Kiss 2000; Vajna 2002).

X. History

INTRODUCTION AND HISTORICAL SPREAD

Ambrosia artemisiifolia was first recorded in Europe in botanical gardens. Bullock *et al.* (2012) report that in France, *A. artemisiifolia* was present in at least three botanical gardens in the 18th century (Lyons, 1763; Paris, 1775; Poitiers, 1791) and during the first half of the 19th century in at least another five botanical gardens (Alençon, Angers, Avignon, Montpellier, Strasbourg). In the wild, *A. artemisiifolia* was first recorded as a casual in Britain in 1836 (Lockton & Crocker 2014). For Central and Eastern Europe, the first publication summarizing its early invasion history was by Ascherson (1874). First records have been collected for the second half of the 19th century in most countries: Germany (1860; Ascherson 1874; Brandes & Nitzsche 2007; Poppendieck 2007), France (1863; Bonnot 1967; Chauvel *et al.* 2006), Switzerland (1865; <http://www.ambrosia.ch/vorkommen-pflanze/vorkommen-von-ambrosia/>), Austria (1883; Essl, Dullinger & Kleinbauer 2009), Czech Republic (1883; Pyšek, Sádlo & Mandák 2002), Hungary (1888; Kazinczi *et al.* 2008a), Italy (1902; Mandrioli, Di Cecco & Andina 1998), Romania (1907; Csontos *et al.* 2010) and Russia (1918; Centre for Agricultural Bioscience International (CABI) 2014).

Most early records of *A. artemisiifolia* in Europe which pertain to ephemeral, casual populations have been made in cities and were probably related to repeated introduction events, for example the import of contaminated grain, oil-seed and seeds of forage species from North America (Brandes &

Nitzsche 2006; Chauvel *et al.* 2006). Only after the occurrence of the first naturalized populations and the associated local expansion of populations to adjacent areas first invasion foci in Europe emerged. A *post hoc* analysis of *A. artemisiifolia* invasion in Central and Eastern Europe reveals four distinct invasion stages (Kazinczi *et al.* 2008a; Essl, Dullinger & Kleinbauer 2009; Csontos *et al.* 2010) (Fig. S3):

1 *Rare introductions (19th century–c. 1930)*: the few records of *A. artemisiifolia* are of small scattered populations; spread is mediated largely by anthropogenic long-distance dispersal and repeated introductions (e.g. in Austria, 80% of early records are associated with railways; Essl, Dullinger & Kleinbauer 2009), few first naturalized populations are recorded in the 1920s from the climatically most favourable regions (e.g. Kazinczi *et al.* 2008a; Csontos *et al.* 2010).

2 *Incipient spread and local naturalization (c. 1930–c. 1960)*: numbers of records increase considerably, in particular in the Pannonian Basin; but in most countries, *A. artemisiifolia* continues to be rare; reproduction and local spread from an increasing, yet still limited, number of naturalized populations gain importance.

3 *Increased spread and naturalization (c. 1960–c. 1990)*: numbers of records increase, especially of naturalized populations; in the climatically most favourable regions, large populations in fields emerge (Novak *et al.* 2009); local spread is becoming dominant.

4 *Rapid spread and increasing abundance (c. 1990–ongoing)*: a great increase in the numbers of records, *A. artemisiifolia* is naturalized in increasingly larger regions in Europe, with large populations expanding into climatically less favourable regions, often along major roads.

In climatically less suitable regions, where the occurrence of these invasion phases is delayed, for example in the British Isles, Germany, the Czech Republic and Poland, *A. artemisiifolia* invasion can currently be classified as the phase of increased spread and naturalization (Rich 1994, Rybnicek *et al.* 2000; Brandes & Nitzsche 2006; Tokarska-Gudzic *et al.* 2011). In Europe, the saturation phase of the invasion – that is when the rate of invasion of new areas slows down (Pyšek & Hulme 2005) – has, with the exception of the most heavily invaded regions, apparently not been reached yet.

PATHWAYS

The medium-distance and long-distance spread of *A. artemisiifolia* is driven by human agency, whereas local population growth and short-distance spread are dependent on natural dispersal mechanisms as well (Bullock *et al.* 2012). Seeds of *A. artemisiifolia* stay close (within a few metres) of the parent plant (barochory) (see section VIII. C). However, *A. artemisiifolia* can be dispersed by human activities in many ways with differing relative importance and spatial range (Table 3; Bullock *et al.* 2012).

Common ragweed is able to disperse quickly and efficiently along the transport network (roadsides, railways) as observed, for example in Austria (Essl, Dullinger &

Kleinbauer 2009) and France (Chauvel *et al.* 2006). However, experimental quantification of dispersal by vehicles suggests rather small frequencies of seeds transported by the windslip of vehicles (Vitalos & Karrer 2009; von der Lippe *et al.* 2013; Milakovic, Fiedler & Karrer 2014a). Distances bridged by this vector are higher than primary dispersal by gravity and wind but not as high as to foster long-distance dispersal along roads. Dispersal kernels after 80 passes of a car at 30 mph (48 km h⁻¹) showed a median distance of one metre and a 99% quantile of 9 m (von der Lippe *et al.* 2013). Another vector that could explain rapid spread along roadsides is dispersal by mowing machinery. Vitalos & Karrer (2009) report a mean of 53.1 seeds of common ragweed seeds attached to roadside mowing machinery in infested areas.

The spread of *A. artemisiifolia* through commercial bird feed and small domestic pet food has been investigated in several studies (EFSA 2010; Bullock *et al.* 2012). They showed that bird feed was often contaminated with significant quantities of seeds of *A. artemisiifolia*. This pathway is mainly responsible for introductions into private gardens and parks. However, an EU-wide legislation restricting the amount of seeds of *A. artemisiifolia* in food containing whole grain and seeds has recently been adopted (European Union (EU) 2012). Subsequently, the importance of this pathway currently seems to be decreasing. However, it is likely that the species is also dispersed through other contaminated commodities (e.g. seed mixtures for slopes and embankments, animal fodder), but information on frequency and levels of contamination is relatively sparse (Song & Prots 1998; Chauvel *et al.* 2004; Karrer *et al.* 2011).

Agricultural machinery is strongly implicated in the transport of seeds of *A. artemisiifolia* within and between fields (Tamarcaz *et al.* 2005; Chauvel *et al.* 2006). For example, Karrer *et al.* (2011) found heavy but varying levels of contamination of soya bean harvesters of several dozens up to 31 133 seeds per harvester in eastern Austria.

The transportation of soil, gravel, construction material and landfill waste is involved in the spread of *A. artemisiifolia* as well (Tamarcaz *et al.* 2005; Bullock *et al.* 2012). Consequently, several authors list construction (e.g. Essl, Dullinger & Kleinbauer 2009) or landfill sites (Rich 1994) as one of the habitats invaded by *A. artemisiifolia*.

FUTURE SPREAD

Several European modelling studies predict common ragweed's future or potential spread due to climate change (Table 4). There is consensus among continental-scale models that warmer summers and later autumn frosts will allow northward and uphill spread. For instance, under medium climate change scenarios, warmer summers and delayed frosts expand the climatically suitable regions by the mid 21st century in Europe as far north as southern Scandinavia and the British Isles (Cunze, Leiblein and Tackenberg 2013; Chapman *et al.* 2014; Storkey *et al.* 2014). In contrast, parts of the currently southernmost distribution range in Europe will become

Table 3. Dispersal pathways for *Ambrosia artemisiifolia* in Europe. Shown are their spatial range (short distance < 1 km; medium distance 1–100 km; long distance > 100 km), their putative relative contribution to dispersal and their putative temporal trends in importance (red = increasing; orange = stable; yellow = decreasing)

Pathway	Spatial range	Relative importance	Temporal trend in importance	Selected References
<i>Natural seed dispersal</i>				
Barochory	Short distance	Low	→	Bassett & Crompton (1975)
Hydrochory	Short/medium distance	Low	→	Fumanal <i>et al.</i> (2007)
<i>Human-mediated seed dispersal</i>				
Grain, oil seeds, seeds for planting	Medium/long distance	Medium	→	Song & Prots (1998), Karrer <i>et al.</i> (2011)
Animal fodder/bird seed	Long distance	Medium	↘	European Food Safety Authority (EFSA) (2010)
Agricultural machinery	Short/medium/long distance	High	↗	Karrer <i>et al.</i> (2011)
Mowing machines	Medium distance	High	↗	Vitalos & Karrer (2009)
Vehicles (traffic)	Short distance	Medium	→	Vitalos & Karrer (2009)
Contaminated soil	Short/medium/long distance	High	↗	Tamarcaz <i>et al.</i> (2005)

climatically unsuitable due to the combined effect of increasing summer droughts and high temperatures. Drought in particular, expected to strengthen in southern Europe (Jacob *et al.* 2013), may limit for common ragweed. Indeed, some models predict population declines because of drought in regions that are currently colonized (e.g. southern Russia and Ukraine). With regard to Britain, cool summers and common ragweed's preference for a continental climate may remain limiting factors in all but south-east England. In addition to latitudinal range shifts, *A. artemisiifolia* is also predicted to invade higher elevations in mountain areas (Petitpierre 2014).

Using the distribution of *A. artemisiifolia* in North America, Eurasia and Australia reported by Petitpierre *et al.* (2012), detailed climatic niche conservatism analyses (see Guisan *et al.* 2014) were conducted, which revealed that the climatic niche of *A. artemisiifolia* has remained mostly stable in analogue climates between its native and non-native ranges (i.e. negligible expansion and limited unfilling; Petitpierre *et al.* 2012; Appendix S1), allowing species distribution models (SDMs; Guisan & Thuiller 2005) to be fitted and projected across ranges. Thus, SDMs were constructed to depict the current and future distributions based on the current species' climatic niche (Fig. 9; see Appendix S1 for details). The evaluation of SDMs' ability to depict the potential distribution of *A. artemisiifolia* is excellent (see Appendix S1 for information about evaluation indices). Annual mean temperature is far more important (0.814) than other variables (all between 0.07 and 0.2; Fig. S4). Outside the known distribution of *A. artemisiifolia* used to calibrate SDMs, several areas are predicted to be highly suitable for the species (Fig. 9): southern Brazil, Paraguay, Uruguay, Argentina and Chile in South

America, the southern rim of South Africa, and, in Asia, China, South Korea and Japan. Finally, New Zealand is the most suitable country in Oceania. SDMs predict that the potential distribution will increase globally – and also in the British Isles – under climate change. Among the 8151 grid cells (resolution = 0.5°, c. 50 km) currently suitable, only 1579 are predicted to become unsuitable (potential range contraction), whereas 5023 grid cells are predicted to become suitable in a warmer climate in 2100 (potential range expansion, Fig. S5). These latter cells occur mainly on the north-eastern front of the invaded range in Eurasia (Fig. S5).

However, there is uncertainty in predicting the spread of any invasive species (Gallien *et al.* 2010). Modelling is hampered by *A. artemisiifolia*'s non-equilibrium distribution, poor mapping of spread at the continental scale, poor mapping of variation in population sizes and inadequate models for anthropogenic dispersal pathways (Bullock *et al.* 2012). Only regional-scale models operating in well-mapped countries have been able to fit spread dynamics to time series of *A. artemisiifolia*'s distribution (Smolik *et al.* 2010; Richter *et al.* 2013a,b).

Several factors beyond climate may also influence future spread. Ongoing agricultural abandonment in Eastern Europe (Spangenberg *et al.* 2012) may profoundly influence *A. artemisiifolia*'s invasion (Bullock *et al.* 2012). Proliferation in the early stages of post-abandonment succession will likely be followed by longer-term decline. Control efforts such as deliberate eradication or enhanced phytosanitary regulation of the seed trade may restrict invasion (Bullock *et al.* 2012; Richter *et al.* 2013a,b). Other important anthropogenic effects such as greater herbicide and fertilizer use in north-west Europe have yet to be included in the models. Finally, in coun-

Table 4. Summary of models predicting the effects of climate change on the future spread of *Ambrosia artemisiifolia* in Europe

Model	Scale (resolution)	Approach	Climate variables	Other variables	End year	Future climate scenarios	Spread prediction summary
Cunze, Leiblein & Tackenberg (2013)	Europe (5' x 5')	Correlative species distribution model fitted to native occurrences	Mean diurnal temperature range, temperature seasonality, mean temperature of warmest quarter, precipitation seasonality, precipitation of wettest quarter, precipitation of warmest quarter	–	2080	IPCC A1, A2, B2	Northwards spread as far as southern Britain and central Scandinavia. Extinction of current populations in drier parts of the range (e.g. southern Russia and Ukraine)
This MS; based on Petitpierre <i>et al.</i> (2012)	World-wide (50 x 50 km)	Correlative species distribution model fitted to native and non-native (North America, Eurasia, Australia) occurrences	Annual mean temperature, temperature seasonality, minimum temperature of the coldest annual quarter, maximum temperature of the hottest annual quarter, precipitation of the wettest quarter, precipitation seasonality, annual moisture and moisture seasonality	–	2050, 2100	IPCC A1b	Annual mean temperature is the by far most important variable. Potential distribution will increase globally under climate change, in particular in north-eastern Europe and Siberia
Chapman <i>et al.</i> (2014)	Europe (5 x 5 km)	Mechanistic phenology model driven by temperature and photoperiod. Range predicted as region where ragweed completes life cycle before frost.	Daily minimum and maximum temperature	Photoperiod	2050	IPCC A2a	Warmer summers and delayed frosts allow modest northwards spread as far as central Scandinavia. No representation of southern range margin
Storkey <i>et al.</i> (2014)	Europe (points > 100 km apart)	Mechanistic plant growth simulator representing competition for light, water and nutrients, reproduction and seed-bank dynamics. Predicts range as region with positive population growth rate	Daily temperature and precipitation	–	2070	IPCC A1b	Warmer summers and delayed frosts allow northwards spread as far as Britain and southern Scandinavia. Little change in southern margin

(continued)

Table 4. (continued)

Model	Scale (resolution)	Approach	Climate variables	Other variables	End year	Future climate scenarios	Spread prediction summary
Vogl <i>et al.</i> (2008), Richter <i>et al.</i> (2013a,b)	Central Europe (3' × 5')	'Hybrid model' coupling species niche with dispersal kernel to simulate spread dynamics. Fitted to data on spread in study region.	Mean annual temperature, mean annual precipitation	Crop and urban land cover, length of roads	2050	IPCC A1b (lower & upper range: +1.5 °C, +2.4 °C)	Spread by infilling from multiple current occurrences is ~25% (lower range) and ~50% (upper range) worse under climate change
Bullock <i>et al.</i> (2012)	Europe (5 × 5 km)	'Hybrid model' coupling species niche with dispersal kernel, extinction model and ragweed introduction through trade to simulate spread dynamics. Calibrated against current distribution	Growing season temperature and precipitation, temperature seasonality	Crop and urban land cover, national seed import rates	2080	IPCC A1b, A2a, B2	Warmer summers allow northwards spread as far as Britain and southern Scandinavia. Southern Europe becomes too hot and dry for ragweed. Loss of cropland in Eastern Europe promotes range contraction and restricts spread

tries where the species is still spreading, coupling dispersal with environmental suitability modelling has shown to improve predictions and allows reconstructing the most likely introduction pathways (Bullock *et al.* 2012).

Finally, all the models assume temporal and spatial conservatism of the ecological niche, that is that populations of *A. artemisiifolia* have retained the same climatic tolerances in all places at all times. Evidence of evolutionary adaptation during invasion has been found in its frost tolerance of germination (Leiblein-Wild, Kaviani & Tackenberg 2014) and phenology (Genton *et al.* 2005; Chun, Le Corre & Bretagnolle 2011; Hodgins & Rieseberg 2011), but this has not been detected at the level of the realized macro-climatic niche (Petitpierre *et al.* 2012). At finer scale (e.g. habitat level), ongoing adaptation may allow common ragweed to extend its range into areas currently too cold or dry for invasion, presenting a significant challenge for predictive modelling of invasion.

GENETIC VARIATION

Introduced populations in Europe and Asia are probably a mixture of different native populations (Genton, Shykoff & Giraud 2005; Chun *et al.* 2010; Li *et al.* 2012). Most observed genetic variation occurs within rather than between populations, which indicates little genetic differentiation. This holds in Europe as well as North America, and both native and non-native populations show similar overall genetic diversity (Genton, Shykoff & Giraud 2005; Fumanal 2007; Chun *et al.* 2010; Martin *et al.* 2014). According to Genton, Shykoff & Giraud (2005), range expansion of *A. artemisiifolia* occurred in France after a series of bottleneck events associated with the initial introduction of the species whereas no such effect was observed in China (Li *et al.* 2012). Nuclear and chloroplast microsatellites used in these studies suggested multiple introductions of common ragweed within countries in most parts of its non-native range, leading to high levels of genetic diversity. Genetic differences exist between populations from Western Europe introduced at the end of the 19th century and populations established in the middle of the 20th century in Central and Eastern Europe (Gaudeul *et al.* 2011; Gladieux *et al.* 2011), which could be explained by different regions of origin in North America. Martin *et al.* (2014) found weak but significant isolation by distance at least in the two geographical Eastern and Western clusters in Europe. In North America, a significant pattern of isolation by distance was detected along an east to west cline (Genton, Shykoff & Giraud 2005; Gaudeul *et al.* 2011). A hypothesis for the European findings is that separate vectors of introductions from two source areas in North America have occurred in Europe. This admixture of introduced populations may have increased genetic diversity and additive genetic variance and may have promoted rapid evolution and adaptation (Chun, Le Corre & Bretagnolle 2011).

Changes of genetic diversity over time have been reconstructed using herbarium specimens from the 19th and 20th centuries. Recent populations in France show greater allelic and genetic diversity than older ones. This suggests that current populations have arisen from active gene flow between

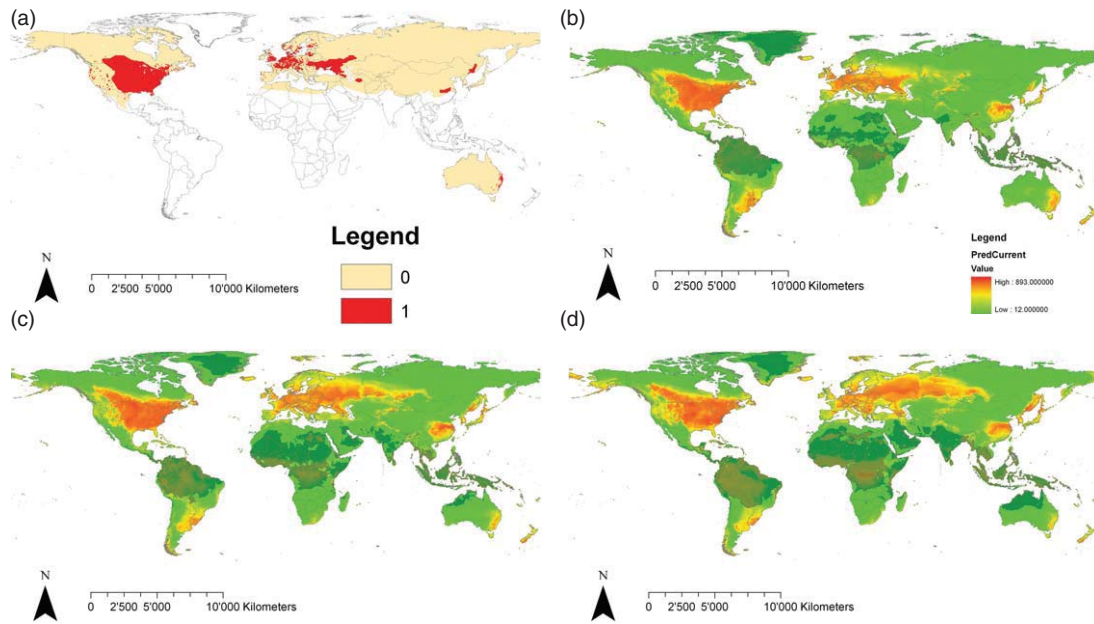


Fig. 9. World-wide potential distribution of *Ambrosia artemisiifolia*. Information about species occurrences in North America and for the non-native distribution in Eurasia and Australia (a) were used to calibrate SDMs providing potential distribution under current (b) and warmer (c) and (d) climates. The projection of future habitat suitability is shown for a severe climate change scenario (the A1b-SRES-scenario) for the year 2050 (c) and 2100 (d) using the CSIRO MK3.0 Global Circulation Model. Shaded area represents non-analogue climate where predictions are not reliable. For details, see Appendix S1.

older populations, incorporating new alleles from new introductions from native areas (Chun *et al.* 2010) and also from crop seeds traded between European countries.

The molecular basis of invasiveness of *A. artemisiifolia* was studied by Hodgins & Rieseberg (2011) by comparing the expression of more than 45 000 genes between native and introduced populations subjected to light or nutrient stress. This genomewide approach identified 180 candidate genes expressed differently under these conditions. Among those genes, several are potentially involved in the metabolism of secondary compounds and in stress responses. They may therefore be involved in an increase of growth rate and reproduction observed in the same population sample in a previous study (Hodgins & Rieseberg 2011). These results suggest that abiotic conditions might have exerted selection pressures on *A. artemisiifolia* populations, such that populations at higher altitudes or latitudes have evolved a greater reproductive allocation. The results of Chun, Le Corre & Bretagnolle (2011) indicated that a proportion of genes may be differentially expressed within native and non-native populations and may modify the response of common ragweed to abiotic conditions.

XI. Conservation, impacts and management

IMPACTS

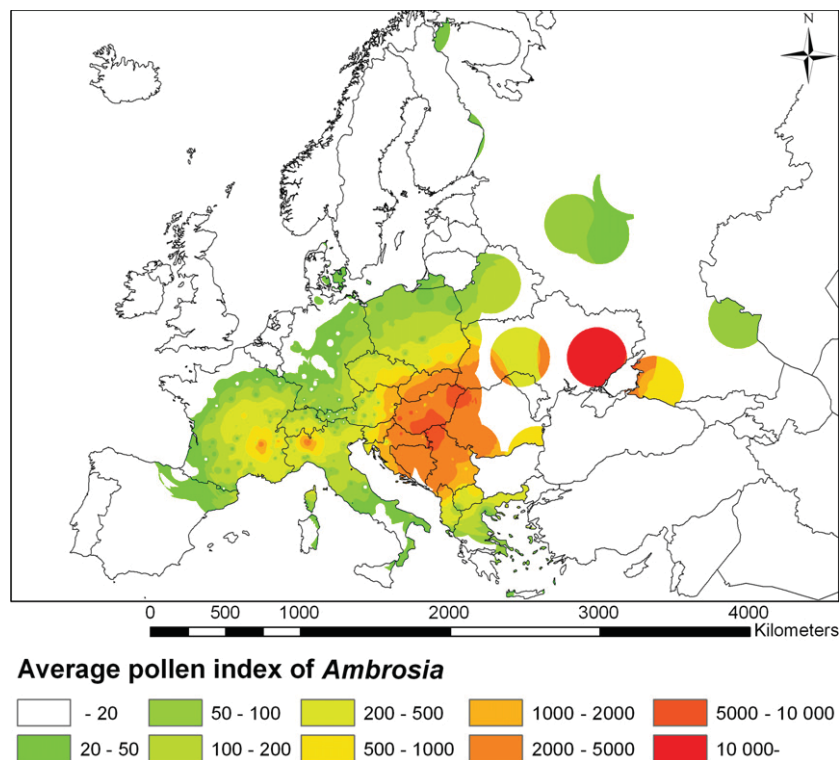
Agriculture

In Central and Eastern Europe, in particular in the Pannonian Plain, *A. artemisiifolia* has become a dominant weed in arable fields (Týr, Vereš & Lacko-Bartošová 2009; Novak *et al.* 2009; Galzina *et al.* 2010; Follak & Fertsak

2012). For instance, *A. artemisiifolia* increased from 21st (1950) to 8th (1970), to 4th (1988) and to 1st (1996–1997; 2007–2008) in place in terms of weed abundance in winter wheat and maize fields in Hungary (Novak *et al.* 2009). In 2003, it was recorded on 5.4 million hectares in Hungary, out of which 700 000 ha were considered to be heavily infested. In Western and northern Central Europe, large populations in fields are known from France (Rhône Valley) (Chauvel *et al.* 2006), locally from Switzerland (Bohren, Mermillod & Delabays 2006) and recently from eastern Germany (Schröder & Meinlschmid 2009). Spring-sown row crops like sunflower, maize and soya bean are most heavily invaded followed by sugar beet, oil-pumpkin, potatoes, various legumes and vegetables.

The species' temporal emergence pattern, rapid and plastic growth, and strong ability to regenerate after cutting contribute to its success as a weed (Bassett & Crompton 1975). Yield loss can be substantial (particularly so in low-growing crops such as beets; Buttenschøn, Waldspühl and Bohren 2009), but depends largely on the crop type, the time of emergence of *A. artemisiifolia* relative to the crop and the density of *A. artemisiifolia* infestation (Chikoye, Weise & Swanton 1995; Cowbrough, Brown & Tardif 2003). Damage is especially high in crops with a low canopy height and when *A. artemisiifolia* emerges together with the crop. In Europe, the impact of various densities of *A. artemisiifolia* on the yield of sunflower, sugar beet and maize has been documented by some authors (Bosak & Mod 2000; Varga, Beres & Reisinger 2002; Varga *et al.* 2006; Kazinczi *et al.* 2009; Nitzsche 2010; Bullock *et al.* 2012). For example, Kazinczi *et al.* (2009) demonstrated that *A. artemisiifolia* at densities of 5 and 10 plants m^{-2} caused 21 and 33% yield reduction in

Fig. 10. A spatial assessment of the density of naturalized *Ambrosia artemisiifolia* populations with flowering potential for the years 2000–2009. The map is based on the mean annual pollen index of *Ambrosia artemisiifolia* from 368 stations in Europe, simple interpolation, buffer zones of 200 km and presence/absence information in Flora Europea. The map is based on data stored in the European Aeroallergen Network data base (<https://ean.polleninfo.eu/Ean/>). In Eastern Europe, there are gaps resulting from a lack of pollen stations (Smith *et al.* 2013, modified).



sunflower and almost 30% in maize at both densities. In sugar beet, plots infested with *A. artemisiifolia* at a density of 2–5 plants m⁻² resulted in an average loss of 50% of sugar yield compared to weed-free plots (Bosak & Mod 2000). In these studies, considerable crop-yield losses occurred even at low weed densities. More data are available from North American studies (e.g. Coble, Williams & Ritter 1981; Cowbrough, Brown & Tardif 2003), but these results can only be transferred with caution to the European situation because of differing climatic conditions and cropping practices. Coble, Williams & Ritter (1981) calculated soya bean yield losses of 8% at an *A. artemisiifolia* density of four plants per 10 m of row. Weaver (2001) also found *A. artemisiifolia* was highly competitive with maize and soya bean crops in Ontario (Canada). For high *A. artemisiifolia* density, the maximum yield loss in soya bean was 65 and 70%, and in maize, it varied between 20% and 80% in 1991 and 1993, respectively.

Health

Ambrosia artemisiifolia is a noxious plant that has highly allergenic pollen (Fig. 10), which causes symptoms in late summer and autumn (typically from August to October in the Northern Hemisphere) and reportedly induces asthma about twice as often as other pollen types (Dahl, Strandhede & Wihl 1999 and references therein). *Ambrosia artemisiifolia* has become a major cause of pollen allergy in its native (White & Bernstein 2003) and introduced ranges (Smith *et al.* 2013).

Allergic cross-reactivity is frequent between species within the genus *Ambrosia* as well as with *Artemisia* species (White & Bernstein 2003). The closely related genera have clinical

relevance because sufferers of *Artemisia* pollen allergy frequently also react to *Ambrosia* pollen allergens (Taramarcas *et al.* 2005). For instance, immunoglobulin E (IgE) against *Artemisia* was also detected in 31% of ragweed-sensitized patients in Hungary (Páldy *et al.* 2010). Cross-reactive *Ambrosia* and *Artemisia* pollen allergens can be divided into allergen groups with restricted species distribution (Amb a 1 and Amb a 5 from *Ambrosia* as well as Art v 1 from *Artemisia*) and pan-allergens (profilins, polcalcins and the nsLTPs) (Wopfner *et al.* 2005). The allergenicity of *Ambrosia* pollen can change under different environmental conditions such as increased concentrations of atmospheric CO₂ which have been shown to increase Amb a 1 expression (Singer *et al.* 2005).

The majority (> 90%) of *Ambrosia* pollen-allergic patients are sensitized to Amb a 1, which is a 38-kDa non-glycosylated protein that belongs to the family of pectatelyase proteins, and as such it represents the major allergen in *Ambrosia* pollen (Adolphson, Goodfriend & Gleich 1978; Gadermaier *et al.* 2008; Gadermaier, Hauser & Ferreira 2013) and is considered to be a good marker for specific *Ambrosia* sensitization (Smith *et al.* 2013). Clinical relevance of sensitization to *Ambrosia* pollen allergen determined in 14 European countries (3034 patients), showed that the clinically relevant sensitization rate to *Ambrosia* in Europe was 10.7% [ranging from 1.4% in Finland to 49.7% in Hungary; Burbach *et al.* 2009a]. The prevalence of sensitization to *Ambrosia* pollen has increased over time in Europe (Burbach *et al.* 2009b), for example as documented for northern Italy where *Ambrosia* pollen allergy has recently become a serious problem for public health (Asero 2007). Consequently, as the incidence of allergy in a human population increases with the time it is

exposed to *Ambrosia* pollen and it is not possible to ascertain the consequences of high *Ambrosia* pollen concentrations over the short term (Tosi *et al.* 2011).

It has been suggested that the atmospheric concentrations of *Ambrosia* pollen required to induce symptoms may be very low, for example 1–3 pollen grains $\text{m}^{-3} \text{day}^{-1}$ (Comtois & Gagnon 1988), but the typical range is 5–20 pollen grains m^{-3} (Bullock *et al.* 2012). As a result, the long-distance transport of *Ambrosia* pollen from centres of *Ambrosia* distribution into areas where the plant is not frequently found or absent (Stach *et al.* 2007; Smith *et al.* 2008; Šikoparija *et al.* 2009, 2013) is also a concern for allergy (Bullock *et al.* 2012; Prank *et al.* 2013). The allergenic capacity of *Ambrosia* pollen transported over long distances remains uncertain (Cecchi *et al.* 2010), but a recent study showing the presence of Amb a 1 in samples containing *Ambrosia* pollen collected during episodes of long-distance transport (Grewling *et al.* 2013) indicates that these pollen grains have the potential to induce allergic reactions in sensitized individuals.

Nature conservation

The synthesis of habitat affiliation of *A. artemisiifolia* in Europe by Bullock *et al.* (2012) reveals that it only rarely invades habitats of high nature conservation value, and most of such occurrences have been recorded in the centre of its current distribution in Europe. Occurrences in dry grasslands have been documented several times for Central and Eastern European Countries (Austria: F. Essl, G. Karrer, unpubl. data; Germany: Alberternst, Nawrath & Klingenstein 2006; Hungary: Mihály & Botta-Dukát 2004; Ukraine: Protopopova, Shevera & Mosyakin 2006), but these seem mostly to be a consequence of disturbances (e.g. grazing) that have created patches of open soil. Similarly, open sand and gravel banks along rivers are invaded, most regularly in the Pannonian Basin (Bullock *et al.* 2012). However, so far no discernible negative impact on the invaded communities has been identified (Fried *et al.* 2014). Common ragweed may occasionally colonize other habitats of high conservation value (e.g. tall herb communities, open forests). Usually, these populations occur in low densities and are ephemeral. Accordingly, the environmental consequences of invasion of *A. artemisiifolia* in Europe qualify as ‘no impact’ according to the impact assessment scheme of Blackburn *et al.* (2014). Management measures against *A. artemisiifolia* may affect other plant species and thus have an indirect nature conservation impact (Bullock *et al.* 2012).

MANAGEMENT

Physical management

The physical management of *A. artemisiifolia* can have two complementary approaches: prevention of anthropogenic seed dispersal and mechanical control of already established populations. Preventive measures have to be designed specifically

for the various introduction pathways. Strict standards for limiting the contamination of feed stuff by ragweed seeds have been in place in the EU since 2012. This regulation limits the maximum allowed amount of *A. artemisiifolia* seeds in bird seeds (since 1 January 2012; European Union (EU) 2012) and in animal feed material (since 1 January 2013; European Union (EU) 2012) to 50 mg kg^{-1} , which is equivalent to c. 10–12 seeds. Accordingly, imported and exported containments must now be kept almost free of seeds; this can be best achieved by sieving techniques. *Ambrosia artemisiifolia* seed loads on roadside cutting machines (Vitalos & Karrer 2009) and crop harvesting machinery (Karrer *et al.* 2011) can reach several tens of thousand seeds per machine. Thus, in order to avoid the transport of seeds from infested fields and roadsides, machinery must be thoroughly cleaned (Karrer *et al.* 2011). Transport of contaminated soil is an additional serious source for new infections. Currently, Switzerland is the only European country with legal regulations concerning this pathway.

Once common ragweed is established in a region, several mechanical techniques for control are available (Kazinczi *et al.* 2008c; Buttenschön, Waldspühl & Bohren 2009; Karrer *et al.* 2011; Bullock *et al.* 2012). However, *A. artemisiifolia* tolerates substantial physical damage such as removal of the stem apex and leaves, as the plants regenerate from buds from the base or increase growth of existing lateral stems (Irwin & Aarssen 1996; Nitzsche 2010; Simard & Benoit 2010; Patracchini, Vidotto & Ferrero 2011). The cutting of vegetative plants is reported to delay the initiation of flowering but does not prevent reproduction (Nitzsche 2010). Therefore, the most effective, but also very laborious, mechanical control option is hand pulling (Bohren, Mermillod & Delabays 2006). Pulling of plants with ripened seeds requires treatments that destroy the germination ability (e.g. burning or heating in composters; Karrer *et al.* 2011), and it must be done carefully to avoid seed losses. It is best to act before the onset of (male) flowering and to wear gloves in order to prevent skin irritations due to contact dermatitis.

Mowing is the most widely applied mechanical control technique. As the regrowth potential from buds below cutting height is very high (Bassett & Crompton 1975; Barbour & Meade 1981; Bohren, Mermillod & Delabays 2006, 2008; Meiss *et al.* 2008; Karrer *et al.* 2011), to avoid branch multiplication, cutting should be done as close to the soil surface as possible (Bohren, Mermillod & Delabays 2006). Accessory buds that develop to additional branches enable prolongation of seasonal growth (Karrer *et al.* 2011). Patracchini, Vidotto & Ferrero (2011) showed that early cutting (when plants are c. 20 cm tall) leads to only moderate reductions in the number of male racemes and released pollen, whereas cutting before the onset of flowering (mid to end of July under the climatic conditions of southern Central Europe, Kazinczi *et al.* 2008c; Milakovic, Fiedler & Karrer 2014a) is optimal to minimize pollen production. To reduce seed set effectively, however, the first cut should be done 2–3 weeks after the beginning of male flowering (Milakovic, Fiedler & Karrer 2014b). Subsequent cuts every 3 weeks are important to pre-

vent the production of seeds from resprouts (Karrer *et al.* 2011; Karrer & Pixner 2012).

Tillage (ploughing, grubbing, hoeing) may kill *A. artemisiifolia* plants. Various mechanical hoeing techniques have been shown to reduce ragweed densities in crops (Buttenschön, Waldispühl & Bohren 2009). Control of *A. artemisiifolia* on stubble fields can be achieved by early ploughing after crop harvest (Bohren, Mermillod & Delabays 2008). Shallow ploughing or grubbing every 4–6 weeks during the germination period in spring leads to the depletion of the soil seed bank within few years (Swanton *et al.* 2000; Murphy *et al.* 2006; Karrer *et al.* 2011).

Introducing crop rotation, including crops that are less susceptible to *A. artemisiifolia*, has been suggested as a control method (Béres 2004; Kazinczi *et al.* 2008c). However, the persistent soil seed bank and plasticity in germination dates limit the applicability of this technique (Karrer *et al.* 2011).

Experimental thermal treatments (hot steam, flaming) have been found to control ragweed (Buttenschön, Waldispühl & Bohren 2009; U. Starfinger *et al.*, unpubl. data). Such techniques can be applied to small *A. artemisiifolia* populations, and they may also kill some non-target species.

Establishing a closed vegetation cover in combination with mowing has been shown to be effective in reducing densities of *A. artemisiifolia* (MacDonald & Kotanen 2010). In experiments that combined planting *Medicago sativa* with intensive cutting, *A. artemisiifolia* was rapidly out-competed (Meiss *et al.* 2008; Meiss 2010). *Ambrosia artemisiifolia* grown with restoration seed mixtures showed identical results (Karrer *et al.* 2011). In a glasshouse experiment, *Lolium perenne* and *Dactylis glomerata* out-competed *A. artemisiifolia* (Milanova, Vladimirov & Maneva 2010). *Ambrosia artemisiifolia* biomass was reduced most by *Lolium perenne* (by more than 95%). *Medicago sativa* also showed an inhibitory effect on *A. artemisiifolia*, reducing its biomass by 91%.

Chemical management

For 50 years, herbicides have been widely used in agriculture to control *A. artemisiifolia*, for example 2,4-D in USA. In major crops, *A. artemisiifolia* can be controlled with pre- and post-emergence herbicides, while in minor crops (e.g. oil-pumpkin, vegetables, various legume crops), a limited number of less effective herbicides can be applied (e.g. Kazinczi *et al.* 2008c; Buttenschön, Waldispühl & Bohren 2009; Schröder & Meinschmid 2009; Gauvrit & Chauvel 2010).

Yield losses are most important in certain spring crops (sorghum, soya bean) and more particularly in sunflower, which is also in the Asteraceae, and thus, the potential of herbicide application is greatly reduced. The cultivation of sunflower cultivars that are tolerant to certain herbicides (e.g. imazamox, tribenuron-methyl) might be an alternative for infested fields (Schröder & Meinschmid 2009; Kukorelli *et al.* 2011). In non-crop areas, non-selective active ingredients such as glyphosate and glufosinate are appropriate to control both pollen and seed production of *A. artemisiifolia* (Gauvrit & Chauvel 2010), but they also have strong impacts on other plant

species. The efficacy of several active ingredients against the species is influenced by the plant growth stage at application (Bohren, Mermillod & Delabays 2008). *Ambrosia artemisiifolia* is most susceptible at the 2–4 leaf stage, while larger individuals often survive. Sequential treatments may improve herbicide efficiency, and a combination of leaf and soil active ingredients is recommended to achieve a lasting control, because the species has a long germination period (Buttenschön, Waldispühl & Bohren 2009; Schröder & Meinschmid 2009). Moreover, herbicide application should be combined with crop rotation as autumn-sown crops with high plant densities (e.g. cereals) are less infested. Kazinczi *et al.* (2008c) and Kazinczi & Novák (2014) provide an exhaustive list of active ingredients and application methods, which are recommended for the control of *A. artemisiifolia* in main crops in Hungary.

The dependence upon herbicides for control of *A. artemisiifolia* in fields has led to the development of herbicide-resistant ecotypes. Herbicide-resistant populations of common ragweed have been detected in various crops since the mid-1970s in Canada and USA. At first, some resistance to herbicides inhibiting photosynthesis was observed in common ragweed infesting maize in USA (atrazine; Stephenson *et al.* 1990) and in Canada in ragweed infesting carrots (linuron; Saint-Louis, DiTommaso & Watson 2005). Cross-resistance was observed between triazine and substituted urea herbicides (Heap 2014). During the last two decades, many cases of resistance of *A. artemisiifolia* to ALS inhibitors and glyphosate have been observed in North America (Patzoldt *et al.* 2001; Taylor *et al.* 2002; Brewer & Oliver 2009).

In Europe, as a consequence of its intensive application since the 1960s, an atrazine-resistant ecotype was found in Hungary (Cseh, Cernak & Taller 2009). Although this case of resistance seems to be isolated, the risk that common ragweed populations become resistant to herbicides that target the enzyme acetolactate synthase (ALS) is important because of the increasing cultivation of ALS inhibitor tolerant sunflower varieties (Chauvel & Gard 2010). More generally, the intensive use of ALS inhibitors (alone or in mixtures) in the whole crop rotation cycle may lead rapidly to resistance whether integrated cultural practices are not introduced in the cropping system to reduce common ragweed density. Therefore, a major objective of farmers and land managers in Europe is to avoid the selection of resistant plants in fields and on roadsides by alternating active ingredients (Grangeot, Chauvel & Gauvrit 2006) and by diversifying control methods.

Biological management

Common ragweed has been a target for biological management both in parts of its native range (Cartwright & Templeton 1988; Teshler *et al.* 2002) as well as in the invaded range in Europe (Gerber *et al.* 2011), Australia (Palmer, Heard & Sheppard 2010) and Asia (Zhou *et al.* 2010). In Europe, very few native natural enemies reach high enough densities to inflict significant damage on *A. artemisiifolia*. Therefore, using specialist natural enemies from the native range for the

classical biological control of *A. artemisiifolia* in Europe was initiated in the 1960s, and the release of the North American noctuid moth *Tarachidia candefacta* Huebner in the Krasnodar region in Russia in 1969 was the first intentional introduction of a biological control agent against an invasive non-native plant in Europe (Kovalev 1971a). More recently, *T. candefacta* has also been recorded in the Ukraine (Poltavsky & Artokhin 2006) and Serbia (Stojanović *et al.* 2011). According to Poltavsky & Artokhin (2006), this moth has suffered from the harsh continental climate in the region, but a series of mild winters between 2002 and 2005 has promoted the build-up of large populations.

In 1978, the leaf beetle *Zygogramma suturalis* F. was released and quickly established in the North Caucasus (Julien & Griffiths 1998). 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 released in former Yugoslavia (now Croatia) in 1985 and again in 1990 (Igrc, DeLoach & Zlof 1995). At first, the results obtained with this beetle in Russia were very promising (Reznik 1991). It reached densities as high as 5000 m⁻² in an arable field in southern Russia and destroyed all *A. artemisiifolia* plants, thereby increasing crop-yield two- to threefold (Goeden & Andres 1999). However, population outbreaks and destruction of host plant populations can only occur during the short period in spring when adults emerge and lay eggs, since damage of *A. artemisiifolia* plants over large areas (e.g. due to herbivory of *Zygogramma suturalis* larvae) provokes oviposition inhibition and can result in summer diapause in female *Z. suturalis* (Reznik 1991). Data from field surveys conducted between 2005 and 2006 indicated that average population densities in Russia were very low and, consequently, the impact on the target weed was negligible (Reznik *et al.* 2007).

In addition to these deliberate releases of biological control agents, two exotic organisms used as biological control agents elsewhere have been accidentally introduced into Europe. In the early 1960s, the pathogen *Pustula tragopogonis* (Pers.) Thines (synonym *Albugo tragopogonis* (D.C.) Gray) (Oomycota: Albuginaceae) was accidentally introduced from Canada into the former USSR (Julien & Griffiths 1998). Attack by *P. tragopogonis* can be very damaging and significantly reduces pollen and seed production if systemic infection is achieved (Hartmann & Watson 1980). In Russia, *P. tragopogonis* initially caused heavy infection of *A. artemisiifolia* and reduction in biomass and seed production, but levels of damage have declined strongly since (Julien & Griffiths 1998).

In 2013, the leaf beetle *Ophraella communa* Le Sage (Chrysomelidae; Fig. 8) was found in northern Italy and southern Switzerland (Müller-Schärer *et al.* 2014). This beetle is used as a successful biological control agent against *A. artemisiifolia* in China (Guo *et al.* 2011). First observations of *O. communa* in Italy were made in the area of Milano Malpensa International Airport, suggesting that *O. communa* may have been introduced by air traffic. By the end of 2013, *O. communa* had already colonized an area of c. 20 000 km² (Fig. S2), with populations high enough to completely defoli-

ate and prevent flowering and seed set of most *A. artemisiifolia* plants (Müller-Schärer *et al.* 2014). Population build-up due to multiple generations during the growing season results in repeated and extended attack of single plants. Thus, this biological control agent may be able to reduce common ragweed infestations in Europe significantly, but due to its climatic preferences, *O. communa* may remain restricted to areas in Europe with warm summer temperatures (Zhou *et al.* 2010).

Acknowledgements

We are obliged to numerous colleagues who shared their knowledge on *A. artemisiifolia* distribution, ecology and morphology. FE acknowledges support from EU COST Actions FA1209 'Alien Challenge' and FA1203 'Sustainable management of *Ambrosia artemisiifolia* in Europe' (SMARTER). This article also benefited from collaboration with the EU FP7 ATOPICA project (Grant # 282687). The work of several authors has benefited from the EC DG ENV project 'Complex research on methods to halt the *Ambrosia* invasion in Europe – HALT AMBROSIA' (07.0322/2010/586340/SUB/B2). G. Kazinczi was supported by the European Union and the State of Hungary and co-financed by the European Social Fund in the framework of TÁMOP-4.2.4.A/2-11/1-2012-0001 'National Excellence Program'. For the permission to reproduce drawings of *A. artemisiifolia*, we are obliged to Wiley (Weed Research) for reproducing Figs 8 and S2. This publication has greatly benefited from comments of M.C.F. Proctor, D.T. Streeter, P.A. Thomas, M. Usher and the Editor, A.J. Davy.

References

- Acevedo-Rodríguez, P. & Strong, M.T. (2007) Catalogue of the seed plants of the West Indies. URL <http://botany.si.edu/antilles/WestIndies/catalog.htm> (accessed 13 January 2014).
- Adolphson, C., Goodfriend, L. & Gleich, G.J. (1978) Reactivity of ragweed allergens with IgE antibodies: analyses by leukocyte histamine release and the radioallergosorbent test and determination of cross-reactivity. *Journal of Allergy and Clinical Immunology*, **62**, 197–210.
- Alberternst, B., Nawrath, S. & Klingenstein, F. (2006) Biologie, Verbreitung und Einschleppungswege von *Ambrosia artemisiifolia* in Deutschland und Bewertung aus Naturschutzsicht. *Nachrichtenblatt des Deutschen Pflanzenschutzdienstes*, **58**, 279–285.
- Allard, H.A. (1943) The North American ragweeds and their occurrence in other parts of the world. *Science*, **98**, 292–294.
- Almádi, L. (1976) Data to the water relations of *Ambrosia elatior* (Adatok az *Ambrosia elatior* vízértartásához). *Botanikai Közlemények*, **66**, 199–204.
- Amano, K. (1986) *Host Range and Geographical Distribution of the Powdery Mildew Fungi*. Japan Science Society Press, Tokyo, Japan.
- Anton, A.M. & Zuloaga, F.O. (2014) Flora Argentina. Plantas vasculares de la Republica Argentina. URL <http://www.floraargentina.edu.ar> (accessed 13 January 2014).
- Ascherson, P. (1874) *Ambrosia artemisiifolia*, ein bisher nicht beachteter Einwanderer in Europa. *Botanische Zeitung*, **48**, 770–773.
- Asero, R. (2007) The changing pattern of ragweed allergy in the area of Milan, Italy. *Allergy*, **62**, 1097–1099.
- Barbour, B. & Meade, J.A. (1981) The effect of cutting date and height on anthesis of common ragweed *Ambrosia artemisiifolia* (Asteraceae). *Proceedings of the Northeastern Weed Science Society*, **85**, 82–86.
- Baskin, J.M. & Baskin, C.C. (1987) Temperature requirements for after-ripening in buried seeds of four summer annual weeds. *Weed Research*, **27**, 385–389.
- Baskin, C.C. & Baskin, J.M. (1985) The annual dormancy cycle in buried weed seeds: a continuum. *BioScience*, **35**, 492–498.
- Baskin, J.M. & Baskin, C.C. (1980) Ecophysiology of secondary dormancy in seeds of *Ambrosia artemisiifolia*. *Ecology*, **61**, 475–480.
- Baskin, J.M. & Baskin, C.C. (1977) Role of temperature in the germination ecology of three summer annual weeds. *Oecologia*, **30**, 377–382.
- Basky, Z. (2009) Effect of native aphid species on the development of invasive ragweed *Ambrosia artemisiifolia* (L.) in Hungary. *Redia*, **XCII**, 211–213.
- Bassett, L.J. & Crompton, C.W. (1975) The biology of Canadian Weeds. 11. *Ambrosia artemisiifolia* L. and *A. psilostachya* DC. *Canadian Journal of Plant Science*, **55**, 463–476.

- Bazzaz, F.A. (1968) Succession on abandoned fields in the Shawnee Hills, Southern Illinois. *Ecology*, **49**, 924–936.
- Bazzaz, F.A. (1970) Secondary dormancy in the seeds of the common ragweed *Ambrosia artemisiifolia*. *Bulletin of the Torrey Botanical Club*, **97**, 302–305.
- Bazzaz, F.A. (1973) Photosynthesis of *Ambrosia artemisiifolia* L. plants grown in greenhouse and in the field. *American Midland Naturalist*, **90**, 186–190.
- Bazzaz, F.A. (1974) Ecophysiology of *Ambrosia artemisiifolia*: a successional dominant. *Ecology*, **55**, 112–119.
- Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351–371.
- Belcher, E. (1985) *Handbook on Seeds of Browse-Shrubs and Forbs*. USA Forest Service, Atlanta, GA, USA.
- Béres, I. (2004) Integrated weed management strategies of *Ambrosia artemisiifolia* (Az ürömlevelű parlagfű (*Ambrosia artemisiifolia* L.) elleni integrált gyomszabályozási stratégiák). *Magyar Gyomkutatás és Technológia*, **1**, 3–14.
- Béres, I. (2003) Distribution, importance and biology of common ragweed (*Ambrosia artemisiifolia* L.). *Növényvédelem*, **39**, 293–302.
- Béres, I. (1994) New investigations on the biology of *Ambrosia artemisiifolia* L. Mededelingen Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen. *Universiteit Gent*, **59**, 1295–1297.
- Béres, I. (1981) *Distribution, biology of Ambrosia elatior in Hungary and protection possibilities (in Hungarian)*. PhD thesis, Keszthely University, Keszthely.
- Béres, I. & Hunyadi, K. (1984) Dormancy and germination of common ragweed (*Ambrosia elatior* L.) seeds in the field in Hungary. *Acta Agronomica Academiae Scientiarum Hungaricae*, **33**, 383–387.
- Bigwood, D.W. & Inouye, D.W. (1988) Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology*, **69**, 497–507.
- Blackburn, T.M., Essl, F., Evans, T., Hulme, P.E., Jeschke, J.M., Kühn, I. et al. (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biology*, **12**, e1001850.
- Bohár, G., Bohár, K.V., Pintye, A. & Kiss, L. (2009) First European report of a leaf spot of common ragweed (*Ambrosia artemisiifolia*) caused by a *Phoma* sp. *Plant Disease*, **93**, 763.
- Bohár, G. & Kiss, L. (1999) First report of *Septoria sclerotiorum* on common ragweed (*Ambrosia artemisiifolia*) in Europe. *Plant Disease*, **83**, 302.
- Bohár, G. & Schwarzingler, I. (1999) First report of *Septoria* sp. on common ragweed (*Ambrosia artemisiifolia*) in Europe. *Plant Disease*, **83**, 696.
- Bohár, G. & Vajna, L. (1996) Occurrence of some pathogenic fungi of common ragweed (*Ambrosia artemisiifolia* var. *elatior*) in Hungary. *Növényvédelem*, **32**, 527–528.
- Bohren, C., Mermillod, G. & Delabays, N. (2008) *Ambrosia artemisiifolia* L. – control measures and their effects on its capacity of reproduction. *Journal of Plant Diseases and Protection*, **21**, 311–316.
- Bohren, C., Mermillod, N. & Delabays, N. (2006) Common ragweed (*Ambrosia artemisiifolia* L.) in Switzerland: development of a nationwide concerted action. *Journal of Plant Diseases and Protection*, **113**, 497–503.
- BOKU (2014) Ökologische Zeigerwerte. URL <http://statedv.boku.ac.at/zeigerwerte/> (accessed 27 February 2014).
- Bonnot, E.J. (1967) *Ambrosia artemisiifolia* L. *Bulletin Mensuel de la Société Linnéenne de Lyon*, **36**, 348–359.
- Bosak, P. & Mod, S. (2000) Influence of different weed species on sugar beet yield. *Növénytermelés*, **49**, 571–580.
- Brandes, D. & Nitzsche, J. (2006) Biology, introduction, dispersal and distribution of ragweed *Ambrosia artemisiifolia* with special reference to Germany. *Nachrichtenblatt des Deutschen Pflanzenschutzdiensts*, **58**, 286–291.
- Brandes, D. & Nitzsche, J. (2007) Verbreitung, Ökologie und Soziologie von *Ambrosia artemisiifolia* L. in Mitteleuropa. *Tuexenia*, **27**, 167–194.
- Braun, U. (1995) *The Powdery mildews (Erysiphales) of Europe*. Gustav Fischer Verlag, Jena, Germany.
- Brewer, C.E. & Oliver, L.R. (2009) Confirmation and resistance mechanisms in glyphosate-resistant common ragweed (*Ambrosia artemisiifolia*) in Arkansas. *Weed Science*, **57**, 567–573.
- Brouillet, L., Coursol, F., Meades, S.J., Favreau, M., Anions, M., Bélisle, P. & Desmet, P. (2014) VASCAN, la base de données des plantes vasculaires du Canada. URL <http://data.canadensys.net/vascan> (accessed 13 January 2014).
- Brückner, D.J., Lepossa, A. & Herpat, Z. (2003) Inhibitory effect of ragweed (*Ambrosia artemisiifolia* L.)-inflorescence extract on the germination of *Amaranthus hypochondriacus* L. and growth of two soil algae. *Chemosphere*, **51**, 515–519.
- Bullock, J., Chapman, D., Schaffer, S., Roy, D., Girardello, M., Haynes, T. et al. (2012) Assessing and controlling the spread and the effects of common ragweed in Europe (ENV.B2/ETU/2010/0037). European Commission, Final Report.
- Burbach, G.J., Heinzerling, L.M., Edenharter, G., Bachert, C., Bindslev-Jensen, C., Bonini, S. et al. (2009a) GA2LEN skin test study II: clinical relevance of inhalant allergen sensitizations in Europe. *Allergy*, **64**, 1507–1515.
- Burbach, G.J., Heinzerling, L.M., Rohnelt, C., Bergmann, K.C., Behrendt, H. & Zuberbier, T. (2009b) Ragweed sensitization in Europe - GA(2)LEN study suggests increasing prevalence. *Allergy*, **64**, 664–665.
- Buttenschön, R.M., Waldspühl, S. & Bohren, C. (2009) Guidelines for management of common ragweed, *Ambrosia artemisiifolia*. EUPHRESKO project AMBROSIA 2008-09. URL <http://www.euphresco.org> (accessed 13 January 2014).
- Centre for Agricultural Bioscience International (CABI) (2014) Invasive Species Compendium: *Ambrosia artemisiifolia* factsheet. URL <http://www.cabi.org/iscf/?compid=5&dsid=4691&loadmodule=data-sheet&page=481&site=144> (accessed 13 January 2014).
- Cartwright, R.D. & Templeton, G.E. (1988) Biological limitations of *Protomyces gravidus* as a mycoherbicide for giant ragweed, *Ambrosia trifida*. *Plant Disease*, **72**, 580–582.
- Cecchi, L., Testi, S., Campi, P. & Orlandini, S. (2010) Long-distance transport of ragweed pollen does not induce new sensitizations in the short term. *Aerobiologia*, **26**, 351–352.
- Chapman, D.S., Haynes, D., Beal, S., Essl, F. & Bullock, J. (2014) Phenology predicts the native and invasive range limits of common ragweed. *Global Change Biology*, **20**, 192–202.
- Chauvel, B., Vieren, E., Fumanal, B. & Bretagnolle, F. (2004) Possibilité de dissémination d'*Ambrosia artemisiifolia* L. via les semences de tournesol. *Proceedings of the XIIe Colloque International sur la biologie des Mauvaises Herbes*, pp. 445–452. Dijon, France.
- Chauvel, B., Dessaint, F., Cardinal-Legrand, C. & Bretagnolle, F. (2006) The historical spread of *Ambrosia artemisiifolia* L. in France from herbarium records. *Journal of Biogeography*, **33**, 665–673.
- Chauvel, B. & Gard, B. (2010) Gérer l'ambrosioïse à feuilles d'armoise. *Phytoma la Défense des Végétaux*, **633**, 12–16.
- Chikoye, D., Weise, S.F. & Swanton, C.J. (1995) Influence of common ragweed (*Ambrosia artemisiifolia*) time of emergence and density on white bean (*Phaseolus vulgaris*). *Weed Science*, **43**, 375–380.
- Chun, Y.J., Le Corre, V. & Bretagnolle, F. (2011) Adaptive divergence for a fitness-related trait among invasive *Ambrosia artemisiifolia* populations in France. *Molecular Ecology*, **20**, 1378–1388.
- Chun, Y.J., Fumanal, B., Laitung, B. & Bretagnolle, F. (2010) Gene flow and population admixture as the primary post-invasion processes in common ragweed (*Ambrosia artemisiifolia*) populations in France. *New Phytologist*, **185**, 1100–1107.
- Coble, H.D., Williams, F.M. & Ritter, R.L. (1981) Common ragweed (*Ambrosia artemisiifolia*) interference in soybean (*Glycine max*). *Weed Science*, **29**, 339–342.
- Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the Enemy Release Hypothesis? *Ecology Letters*, **7**, 721–732.
- Comtois, P. & Gagnon, L. (1988) Concentration pollinique et fréquence des symptômes de pollinose: une méthode pour déterminer les seuils cliniques. *Revue Française d'Allergologie et d'Immunologie Clinique*, **28**, 279–286.
- Cowbrough, M.J., Brown, R.B. & Tardif, F.J. (2003) Impact of common ragweed (*Ambrosia artemisiifolia*) aggregation on economic thresholds in soybean. *Weed Science*, **51**, 947–954.
- Crowell, H.F. & Boerner, R.E.J. (1988) Influences of mycorrhizae and phosphorus on belowground competition between two old-field annuals. *Environmental Experimental Botany*, **28**, 381–392.
- Cseh, A., Cernak, I. & Taller, J. (2009) Molecular characterization of atrazine resistance in common ragweed (*Ambrosia artemisiifolia* L.). *Journal of Applied Genetics*, **50**, 321–327.
- 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.
- Cunze, S., Leiblein, M.C. & Tackenberg, O. (2013) Range expansion of *Ambrosia artemisiifolia* in Europe is promoted by climate change. *ISRN Ecology*, **2013**, ID 610126.
- Dahl, A., Strandhede, S.-O. & Wihl, J.-A. (1999) Ragweed – An allergy risk in Sweden? *Aerobiologia*, **15**, 293–297.
- Darlington, H.T. (1922) Dr. W. J. Beal's seed-viability experiment. *American Journal of Botany*, **9**, 266–269.
- Déchamp, C., Méon, H. & Reznik, S. (2009) *Ambrosia artemisiifolia* L. an invasive weed in Europe and adjacent countries: the geographical distribution (except France) before 2009. *Ambrosioïse: The First International Ragweed Review* (eds C. Déchamp & H. Méon), pp. 24–26. AFEDA, Saint-Priest, France.
- Deen, W., Hunt, L.A. & Swanton, C.J. (1998a) Photothermal time describes common ragweed (*Ambrosia artemisiifolia* L.) phenological development and growth. *Weed Science*, **46**, 561–568.

- Deen, W., Hunt, T. & Swanton, C.J. (1998b) Influence of temperature, photoperiod, and irradiance on the phenological development of common ragweed (*Ambrosia artemisiifolia*). *Weed Science*, **46**, 555–560.
- Dickerson, C.T. (1968) *Studies on the germination, growth, development and control of Common Ragweed* (*Ambrosia artemisiifolia* L.). PhD thesis, Cornell University, Ann Arbor.
- Dickerson, C.T. & Sweet, R.D. (1971) Common ragweed ecotypes. *Weed Science*, **19**, 64–66.
- DiTommaso, A. (2004) Germination behavior of common ragweed (*Ambrosia artemisiifolia*) populations across a range of salinities. *Weed Science*, **52**, 1002–1009.
- Duan, H. & Chen, B. (2000) Biological characters, encroaching habit and control strategy of common ragweed in Shanghai area. *Acta Agriculturae Shanghai*, **16**, 73–77.
- Dudka, I.A. & Hayova, V.P. (2007) *Plasmopara angustiterminalis* on *Ambrosia artemisiifolia* in Ukraine. *Mikologiya i Fitopatologiya*, **41**, 12–19.
- European Food Safety Authority (EFSA) (2010) Scientific opinion on the effect on public or animal health or on the environment on the presence of seeds of *Ambrosia* spp. in animal feed. *ESFA Journal*, **8**, 1566.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1992) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–258.
- Eom, S.H., DiTommaso, A. & Weston, L.A. (2013) Effects of soil salinity in the growth of *Ambrosia artemisiifolia* biotypes collected from roadside and agricultural field. *Journal of Plant Nutrition*, **36**, 2191–2204.
- European and Mediterranean Plant Protection Organization (EPPO) (2013) PQR database Version 5.3.1. URL <http://www.eppo.int> (accessed 15 April 2013).
- Essl, F., Dullinger, S. & Kleinbauer, I. (2009) Changes in the spatio-temporal patterns and habitat preferences of *Ambrosia artemisiifolia* during its invasion in Austria. *Preslia*, **81**, 119–133.
- European Union (EU) (2012) Commission Regulation (EU) No 744/2012 of 16 August 2012 amending Annexes I and II to Directive 2002/32/EC of the European Parliament and of the Council as regards maximum levels for arsenic, fluorine, lead, mercury, endosulfan, dioxins, *Ambrosia* spp., diclazuril and lasalocid A sodium and action thresholds for dioxins. *Official Journal of the European Union*, **L219**, 5–12.
- Fenesi, A., Albert, Á.-J. & Ruprecht, E. (2014) Fine-tuned ability to predict future competitive environment in *Ambrosia artemisiifolia* seeds. *Weed Research*, **54**, 58–69.
- File, A.L., Klironomos, J., Maherali, H. & Dudley, S.A. (2012) Plant kin recognition enhances abundance of symbiotic microbial partner. *PLoS ONE*, **7**, e45648.
- Fisher, N.H. & Quijano, L. (1985) Allelopathic agents from common weeds. *Amaranthus palmeri*, *Ambrosia artemisiifolia*, and related weeds. *The Chemistry of Allelopathy – Biochemical Interactions between Plants* (ed. A.C. Thompson), pp. 133–147. ACS Symposium Series, Washington, DC, USA.
- Fisjunov, A.B. (1984) *Sornie rastenija*. Kolos, Moskva, 320 pp.
- Flora North America (FNA) (2006) *Volume 21: Magnoliophyta: Asteridae (in part): Asteraceae, part 3*. Oxford University Press, New York, NY, USA.
- Follak, S., Dullinger, S., Kleinbauer, S., Moser, D. & Essl, F. (2013) Invasion dynamics of three allergenic invasive Asteraceae (*Ambrosia trifida*, *Artemisia annua*, *Iva xanthiifolia*) in central and eastern Europe. *Preslia*, **85**, 41–61.
- Follak, S. & Fertsak, S. (2012) Befragung zur Verbreitung und zur Bekämpfung der *Ambrosia artemisiifolia* in der Landwirtschaft in Österreich. *Proceedings of the 67th ALVA-Conference* (ed. G. Bedlan), pp. 347–349. Wien, Austria.
- Forcella, F., Wilson, R.G., Renner, K.A., Dekker, J., Harvey, R.G., Alm, D.A., Buhler, D.D. & Cardina, J. (1992) Weed seedbanks of the U.S. corn belt: magnitude, variation, emergence, and application. *Weed Science*, **40**, 636–644.
- Fried, G., Laitung, B., Pierre, C., Chagué, N. & Panetta, D. (2014) Impact of invasive plants in Mediterranean habitats: disentangling the effects of characteristics of invaders and recipient communities. *Biological Invasions*, **16**, 1639–1658.
- Friedman, J. & Barrett, S. (2011) Genetic and environmental control of temporal and size-dependent sex allocation in a wind-pollinated plant. *Evolution*, **65**, 2061–2074.
- Friedman, J. & Barrett, S. (2008) High outcrossing in the annual colonizing species *Ambrosia artemisiifolia* (Asteraceae). *Annals of Botany*, **101**, 1303–1309.
- Fumanal, B. (2007) *Biological traits and evolutive processes of an invasive plant species in France: Ambrosia artemisiifolia L.* PhD Thesis, University of Burgundy, Dijon, France.
- Fumanal, B., Gaudot, I. & Bretagnolle, F. (2008) Seed-bank dynamics in the invasive plant, *Ambrosia artemisiifolia* L. *Seed Science Research*, **18**, 101–114.
- 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.
- Fumanal, B., Chauvel, B. & Bretagnolle, F. (2007) 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. (2007) Variability and cryptic heteromorphism of *Ambrosia artemisiifolia* seeds: what consequences for its invasion in France? *Annals of Botany*, **100**, 305–313.
- Fumanal, B., Plenchette, C., Chauvel, B. & Bretagnolle, F. (2006) Which role can arbuscular mycorrhizal fungi play in the facilitation of *Ambrosia artemisiifolia* L. invasion in France? *Mycorrhiza*, **17**, 25–35.
- Gadermaier, G., Hauser, M. & Ferreira, F. (2013) Allergens of weed pollen: an overview on recombinant and natural molecules. *Methods*, **66**, 55–66.
- Gadermaier, G., Wopfner, N., Wallner, M., Egger, M., Didierlaurent, A., Regl, G., Aberger, F., Lang, R., Ferreira, F. & Hawranek, T. (2008) Array-based profiling of ragweed and mugwort pollen allergens. *Allergy*, **63**, 1543–1549.
- Gallien, L., Münkemüller, T., Albert, C.H., Boulangeat, I. & Thuiller, W. (2010) Predicting potential distributions of invasive species: where to go from here? *Diversity and Distributions*, **16**, 331–342.
- Galzina, N., Barić, K., Šćepanović, M., Gorić, M. & Ostojčić, Z. (2010) Distribution of invasive weed *Ambrosia artemisiifolia* L. in Croatia. *Agriculturae Conspectus Scientificus*, **75**, 75–81.
- Gard, B., Bretagnolle, F., Dessaint, F. & Laitung, B. (2013) Invasive and native populations of common ragweed exhibit strong tolerance to foliar damage. *Basic and Applied Ecology*, **14**, 28–35.
- Gaudeul, M., Giraud, T., Kiss, L. & Shykoff, J.A. (2011) Nuclear and chloroplast microsatellites show multiple introductions in the worldwide invasion history of common ragweed, *Ambrosia artemisiifolia*. *PLoS ONE*, **6**, e17658.
- Gauvrit, C. & Chauvel, B. (2010) Sensitivity of *Ambrosia artemisiifolia* to glufosinate and glyphosate at various developmental stages. *Weed Research*, **50**, 503–510.
- Gebben, A.I. (1965) *The ecology of common ragweed* (*Ambrosia artemisiifolia* L.) in south-eastern Michigan. PhD thesis, University of Michigan, Ann Arbor, MI, USA.
- Genton, B.J., Shykoff, J.A. & 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.
- Genton, B.J., Kotanen, P.M., Cheptou, P.O., Adolphe, C. & Shykoff, J.A. (2005) Enemy release but no evolutionary loss of defence in a plant invasion: an inter-continental reciprocal transplant experiment. *Oecologia*, **146**, 404–414.
- Gerber, E., Schaffner, U., Gassmann, A., Hinz, H.L., Seier, M. & Müller-Schärer, H. (2011) Prospects for biological control of *Ambrosia artemisiifolia* in Europe: learning from the past. *Weed Research*, **51**, 559–573.
- Gilles, V., Lauzer, D. & Cappadocia, M. (1988) Characterization of reciprocal hybrids of Common Ragweed, *Ambrosia artemisiifolia*, and Giant Ragweed, *A. trifida*. *Weed Science*, **26**, 574–576.
- Gladieux, P., Giraud, T., Kiss, L. & Genton, B. (2011) Distinct invasion sources of common ragweed (*Ambrosia artemisiifolia*) in Eastern and Western Europe. *Biological Invasions*, **13**, 933–944.
- Goeden, R.D. & Andres, L.A. (1999) Three recent successes outside of North America. In: *Handbook of Biological Control* (ed. T.W. Fisher), pp. 884–885. Academic Press, San Diego, CA, USA.
- Goeden, R.D. & Palmer, W.A. (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. *8th International Symposium on Biological Control of Weeds, Canterbury, New Zealand* (ed. R.R. Scott), pp. 565–573. CSIRO, Melbourne, Australia.
- Grangeot, M., Chauvel, B. & Gauvrit, C. (2006) Spray retention, foliar uptake and translocation of glufosinate and glyphosate in *Ambrosia artemisiifolia*. *Weed Research*, **46**, 152–162.
- Grewling, L., Nowak, M., Jenerowicz, D., Szymanska, A., Czarnecka-Operacz, M., Kostecki, L., Bogawski, P., Sikoparija, B., Skjøth, C.A. & Smith, M. (2013) Atmospheric concentrations of ragweed pollen and Amb a 1 recorded in Poznan (Poland), 2010–2012. EAACI-WAO World Allergy Congress 2013, Milan, Italy, pp. 686.
- Gross, K.L. (1990) A comparison of methods for estimating seeds numbers in the soil. *Journal of Ecology*, **78**, 1079–1093.
- Guillemain, J.-P. & Chauvel, B. (2011) Effects of the seed weight and burial depth on the seed behavior of common ragweed (*Ambrosia artemisiifolia*). *Weed Biology and Management*, **11**, 217–223.

- Guillemin, J.P., Gardarin, A., Granger, S., Reibel, C., Munier-Jolain, N. & Colbach, N. (2013) Assessing potential germination period of weeds with base temperatures and base water potentials. *Weed Research*, **53**, 76–87.
- Guisan, A., Petitpierre, B., Broennimann, B., Daehler, C. & Kueffer, C. (2014) Unifying niche shift studies: insights from biological invasions. *Trends in Ecology and Evolution*, **29**, 260–269.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guo, J.-Y., Zhou, Z.-S., Zheng, X.-W., Chen, H.-S., Wan, F.-H. & Luo, Y.-H. (2011) Control efficiency of leaf beetle, *Ophraella communa*, on the invasive common ragweed, *Ambrosia artemisiifolia*, at different growing stages. *Bio-control Science and Technology*, **21**, 1049–1063.
- Hartmann, H. & Watson, A.K. (1980) Damage to common ragweed (*Ambrosia artemisiifolia*) caused by the white rust fungus (*Albugo tragopogi*). *Weed Science*, **28**, 632–635.
- Heap, I. (2014) The international survey of herbicide resistant weeds. URL <http://www.weedscience.com> (accessed 22 February 2014).
- Hill, M.O., Mountford, J.O., Roy, D.B. & Bunce, R.G.H. (1999) *Ellenberg's Indicator Values for British Plants ECOFACT*, Vol. 2. Technical Annex. Department for Environment, Transport and the Regions, HMSO, London, UK.
- Hodgins, K.A. & Rieseberg, L. (2011) Genetic differentiation in life-history traits of introduced and native common ragweed (*Ambrosia artemisiifolia*) populations. *Journal of Evolutionary Biology*, **24**, 2731–2749.
- Horváth, D., Kazinczi, G. & Keszthelyi, S. (2014) A karcú rébabarkó (*Conioleonus nigrosaturatus*, Geoeze, 1777), a parlagfű természetes ellensége. *Növényvédelem*, **50**, 371–374.
- Igrc, J., DeLoach, C.J. & Zlof, F.V. (1995) Release and establishment of *Zygotogramma suturalis* F. (Coleoptera: Chrysomelidae) in Croatia for control of common ragweed (*Ambrosia artemisiifolia* L.). *Biological Control*, **5**, 203–208.
- Irwin, D.L. & Aarssen, L.W. (1996) Testing for cost of apical dominance in vegetation: a field study of three species. *Annales Botanici Fennici*, **33**, 123–128.
- Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O., Bouwer, L. et al. (2013) EURO-CORDEX: new high-resolution climate change projections for European impact research. *Regional Environmental Change*, **14**, 563–578.
- Jenser, G., Kiss, B. & Takács, A. (2009) *Ambrosia artemisiifolia* is a joint host of tomato spotted wilt virus (TSWV) and its vectors, *Thrips tabaci* Lindeman and *Frankliniella occidentalis* (Pergande) in Hungary (A parlagfű? (*Ambrosia artemisiifolia* Linnaeus) a paradicsom bronzfoltosság vírus (TSWV) és vektorainak közös gazdanövénye Magyarországon). *Növényvédelem*, **45**, 435–437.
- Joly, M., Bertrand, P., Gbangou, R.Y., White, M.-C., Dubé, J. & Lavoie, C. (2011) Paving the way for invasive species: road types and the spread of common ragweed (*Ambrosia artemisiifolia*). *Environmental Management*, **48**, 514–522.
- Julien, M.H. & Griffiths, M.W. (1998) *Biological Control of Weeds – A Catalogue of Agents and their Target Weeds*, 4th edn. CABI Publishing, Wallingford, UK.
- Karrer, G., Milakovic, M., Kropf, M., Hackl, G., Essl, F., Hauser, M. et al. (2011) Ausbreitungsbiologie und Management einer extrem allergenen, eingeschleppten Pflanze – Wege und Ursachen der Ausbreitung von Ragweed (*Ambrosia artemisiifolia*) sowie Möglichkeiten seiner Bekämpfung, Final Report, BMLFUW, Wien, Austria.
- Karrer, G. & Pixner, T. (2012) The contribution of post-harvest ripened ragweed seeds after cut for control. *NEOBIOTA: Halting Biological Invasions in Europe: from Data to Decisions*, 7th European Conference on Biological Invasions (ed. GEIB), p. 229. GEIB, León, Spain.
- Kazinczi, G., Béres, I., Novák, R., Biró, K. & Pathy, Z. (2008a) Common Ragweed (*Ambrosia artemisiifolia*) A review with special regards to the results in Hungary. I. Taxonomy, origin and distribution, morphology, life cycle and reproduction strategy. *Herbologia*, **9**, 55–91.
- Kazinczi, G., Béres, I., Novák, R., Biró, K. & Pathy, Z. (2008b) Common Ragweed (*Ambrosia artemisiifolia*). 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.
- Kazinczi, G., Béres, I., Novák, R., Biró, K. & Pathy, Z. (2008c) Common Ragweed (*Ambrosia artemisiifolia*). A review with special regards to the results in Hungary. III. Resistant biotopy, control methods and authority arrangements. *Herbologia*, **9**, 119–144.
- Kazinczi, G., Béres, I., Onofri, A., Nádas, E., Takács, A., Horváth, J. & Torma, M. (2008d) Allelopathic effects of plant extracts on common ragweed (*Ambrosia artemisiifolia* L.). *Journal of Plant Diseases and Plant Protection*, **21**, 335–340.
- Kazinczi, G., Béres, I., Novák, R. & Karamán, J. (2009) Újra fókuszban az ürömlévelvű parlagfű (*Ambrosia artemisiifolia* L.). (Focusing again on common ragweed (*Ambrosia artemisiifolia* L.). *Növényvédelem*, **45**, 389–403.
- Kazinczi, G. & Novák, R. (eds) (2012) *A Parlagfű visszaszorításának integrált módszerei (Integrated methods for suppression of ragweed)*. National Food Chain Safety Office, Directorate of Plant Protection, Soil Conservation and Agri-Environment, Budapest, Hungary, 223 pp.
- Kazinczi, G. & Novák, R. (eds) (2014) *Integrated Methods for Suppression of Common Ragweed*. National Food Chain Safety Office, Directorate of Plant Protection, Soil Conservation and Agri-Environment, Budapest, Hungary.
- Kiss, B. (2009) Hazai parlagfűfogyasztó rovarok. *Növényvédelem*, **45**, 419–424.
- Kiss, B., Rédei, D. & Koczor, S. (2008) Occurrence and feeding of hemipterans on common ragweed (*Ambrosia artemisiifolia*) in Hungary. *Bulletin of Insectology*, **61**, 195–196.
- Kiss, L. & Beres, I. (2006) Anthropogenic factors behind the recent population expansion of common ragweed (*Ambrosia artemisiifolia* L.) in Eastern Europe: is there a correlation with political transitions? *Journal of Biogeography*, **33**, 2156–2157.
- Kiss, L., Vajna, L., Bohár, G., Varga, K., Paksiri, U., Takamatsu, S. & Magyar, D. (2003) *Phyllachora* epidemic on common ragweed (*Ambrosia artemisiifolia*): a unique natural control phenomenon in Hungary in 1999. *Workshop on Biocontrol of Weeds with Pathogens, Lincoln, New Zealand* (eds G. Bourdet & S. Lamoureaux), pp. 17–18. AgResearch, Lincoln, New Zealand.
- Koide, R.T. & Li, M.G. (1991) Mycorrhizal fungi and the nutrient ecology of three old field annual plant species. *Oecologia*, **85**, 403–412.
- Kovalev, O.V. (1971a) Modern outlooks of biological control of weed plants in the U.S.S.R. and the international phytophagous exchange. In: *Second International Symposium on Biological Control of Weeds, Rome, Italy* (ed. P.H. Dunn), pp. 166–172. Commonwealth Agricultural Bureaux, Farnham Royal, Slough, UK.
- Kovalev, O.V. (1971b) Phytophagas of ragweeds (*Ambrosia* L.) in North America and their application in biological control in the USSR. *Zoologicheskii Zhurnal*, **50**, 199–209.
- Krumbiegel, A. (2007) Wirtsspektrum, Soziologie und Standortansprüche der Amerikanischen Grob-Seide (*Cuscuta campestris* Yuncker) an der mittleren Elbe. *Berichte des Botanischen Vereins zu Hamburg*, **23**, 27–51.
- Kukorelli, G., Reisinger, P., Torma, M. & Adamszki, T. (2011) Experiments with the control of common ragweed in imidazolinone-resistant and tribenuron-methyl-resistant sunflower. *Herbologia*, **12**, 15–22.
- Landolt, E. (2010) *Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Haupt Verlag, Bern, Switzerland.
- Lavoie, C., Jodoin, Y. & Goursaud de Merlis, A. (2007) How did common ragweed (*Ambrosia artemisiifolia* L.) spread in Québec? A historical analysis using herbarium records. *Journal of Biogeography*, **34**, 1751–1761.
- Lazarides, M., Cowley, K. & Hohnen, P. (1997) *CSIRO Handbook of Australian Weeds*. CSIRO Publishing, Collingwood, Australia.
- Lehoczky, E., Szabó, R., Nelima, M.O., Nagy, P. & Béres, I. (2011) Allelopathic effects of ragweed (*Ambrosia artemisiifolia* L.) on cultivated plants. *Communications in Agricultural and Applied Biological Sciences*, **7**, 545–549.
- Leiblein, M.C. & Lösch, R. (2011) Biomass development and CO₂ gas exchange of *Ambrosia artemisiifolia* L. under different soil moisture conditions. *Flora*, **206**, 511–516.
- Leiblein-Wild, M.C. & Tackenberg, O. (2014) Phenotypic variation of 38 European *Ambrosia artemisiifolia* populations measured in a common garden experiment. *Biological Invasions*, **16**, 2003–2015.
- Leiblein-Wild, M.C., Kaviani, R. & Tackenberg, O. (2014) Germination and seedling frost tolerance differ between the native and invasive range in common ragweed. *Oecologia*, **174**, 739–750.
- Leskovšek, R., Datta, A., Knezevic, S.Z. & Simončič, A. (2012a) Common ragweed (*Ambrosia artemisiifolia*) dry matter allocation and partitioning under different nitrogen and density levels. *Weed Biology and Management*, **12**, 98–108.
- Leskovšek, R., Eler, K., Batič, F. & Simončič, A. (2012b) The influence of nitrogen, water and competition on the vegetative and reproductive growth of common ragweed (*Ambrosia artemisiifolia* L.). *Plant Ecology*, **213**, 769–781.
- Li, H.K. & Li, Y.N. (1993) Survey of pathogens as potential biological control agent to control the ragweed, *Ambrosia artemisiifolia*. *Chinese Journal of Biological Control*, **9**, 45–46.
- Li, X.M., Liao, W.J., Wolfe, L.M. & Zhang, D.Y. (2012) No evolutionary shift in the mating system of North American *Ambrosia artemisiifolia* (Asteraceae) following its introduction to China. *PLoS ONE*, **7**, e31935.
- Lockton, A.J. & Crocker, J. (2014) Species account: *Ambrosia artemisiifolia*. URL <http://www.bsbi.org.uk> (accessed 3 March 2014).

- MacDonald, A.A.M. & Kotanen, P.M. (2010) Leaf damage has weak effects on growth and fecundity of common ragweed (*Ambrosia artemisiifolia*). *Botany-Botanique*, **88**, 158–164.
- Maceljski, M. & Igrc, J. (1989) The phytophagous insect fauna of *Ambrosia artemisiifolia* in Yugoslavia. *Proceedings of the VII International Symposium on Biological Control of Weeds* (ed. E. Delfosse), pp. 639–643. Ministero dell'Agricoltura e delle Foreste, Rome, Italy.
- MacKay, J. & Kotanen, P.M. (2008) Local escape of an invasive plant, common ragweed (*Ambrosia artemisiifolia* L.), from aboveground and below-ground enemies in its native area. *Journal of Ecology*, **96**, 1152–1161.
- Mandrioli, P., Di Cecco, M. & Andina, G. (1998) Ragweed pollen: the aeroallergen is spreading in Italy. *Aerobiologia*, **14**, 13–20.
- Martin, M.D., Zimmer, E.A., Olsen, M.T., Foote, A.D., Gilbert, M.T.B. & Brush, G.S. (2014) Herbarium specimens reveal a historical shift in phylogeographic structure of common ragweed during native range disturbance. *Molecular Ecology*, **23**, 1701–1716.
- Martin, M.D., Chamecki, M. & Brush, G.S. (2010) Anthesis synchronization and floral morphology determine diurnal patterns of ragweed pollen dispersal. *Agriculture, Forest and Meteorology*, **150**, 1307–1317.
- Martínez, M.L., Vázquez, G., White, D.A., Tivet, G. & Brengues, M. (2002) Effect of burial by sand and inundation by fresh- and seawater on seed germination of five tropical beach species. *Canadian Journal of Botany*, **80**, 416–424.
- Meiss, H. (2010) *Diversifying crop rotations with temporary grasslands: potentials for weed management and farmland biodiversity*. PhD thesis, University of Giessen, Giessen, Germany.
- Meiss, H., Munier-Jolain, N., Henriot, F. & Caneil, J. (2008) Effects of biomass, age and functional traits on regrowth of arable weeds after cutting. *Journal of Plant Diseases and Protection*, **21**, 493–500.
- Mihály, B. & Botta-Dukát, Z. (2004) *Özönnyövények – Biológiai Inváziók Magyarországon*. Természettudományi Alapítvány Kiadó, Budapest, Hungary.
- Milakovic, I., Fiedler, K. & Karrer, G. (2014a) Management of roadside populations of invasive *Ambrosia artemisiifolia* by mowing. *Weed Research*, **54**, 256–264.
- Milakovic, I., Fiedler, K. & Karrer, G. (2014b) Fine tuning of mowing regime, a method for the management of the invasive plant *Ambrosia artemisiifolia* L. at different population densities. *Weed Biology and Management*, **14**, 232–241.
- Milanova, S., Vladimirov, V. & Maneva, S. (2010) Suppressive effect of some forage plants on the growth of *Ambrosia artemisiifolia* and *Iva xanthiifolia*. *Pesticides and Phytomedicine*, **25**, 171–176.
- Mondin, C.A. & Nakajima, J. (2014) Lista de espécies da flora do Brasil. URL <http://reflora.jbrj.gov.br/jabot/floradobrasil/FB103255> (accessed 13 January 2014).
- Moskalenko, G.P. (2001) *Quarantine Weeds of Russia*. Plant Quarantine Inspectorate, Moscow, Russia.
- Müller-Schärer, H., Lommen, S.T.E., Rossinelli, M., Bonini, M., Boriani, M., Bosio, G. & Schaffner, U. (2014) *Ophraella communa*, the ragweed leaf beetle, has successfully landed in Europe: fortunate coincidence or threat? *Weed Research*, **54**, 109–119.
- Murphy, S.D., Clements, D.R., Belaussoff, S., Kevan, P.G. & Swanton, C.J. (2006) Promotion of weed species diversity and reduction of weed seedbanks with conservation tillage and crop rotation. *Weed Science*, **54**, 69–77.
- Naito, N. (1940) Studies on Septorioses of plants. VII New or noteworthy species of Septoria found in Japan. *Memoirs of the College of Agriculture, Kyoto Imperial University*, **47**, 31–43.
- Nakayama, T. (1998) Positive rates of specific IgE antibody in cases with pollinosis in the south districts of Tokushima prefecture. *Shikoku Acta Medica*, **54**, 393–397.
- Ngom, R. & Gosselein, P. (2014) Development of a remote sensing-based method to map likelihood of common ragweed (*Ambrosia artemisiifolia*) presence in urban areas. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, **7**, 126–139.
- Nitzsche, J. (2010) *Ambrosia artemisiifolia* L. (Beifuß-Ambrosie) in Deutschland. *Biologie der Art, Konkurrenzverhalten und Monitoring*. PhD thesis, University of Braunschweig, Braunschweig, Germany.
- Novák, R., Dancza, I., Szentey, L. & Karáman, J. (2009) *Arable Weeds of Hungary. The 5th National Weed Survey (2007–2008)*. Ministry of Agriculture and Rural Development, Budapest, Hungary.
- Orieux, L. & Felix, S. (1968) List of plant diseases in Mauritius. *Phytopathological Papers*, **7**, 1–48.
- Páldy, A., Bobvos, J., Magyar, D., Nékám, K., Bitay, Z., Csajbók, V. & Kelemen, A. (2010) *Ambrosia* sensitization any triggering effect on non-ragweed allergies? *Egészségtudomány*, **54**, 10–12.
- Palmer, W.A., Heard, T. & Sheppard, A.W. (2010) A review of Australian classical biological control of weeds programs and research activities over the past 12 years. *Biological Control*, **52**, 271–287.
- Patracchini, C., Vidotto, F. & Ferrero, A. (2011) Common ragweed (*Ambrosia artemisiifolia*) growth as affected by plant density and clipping. *Weed Technology*, **25**, 268–276.
- Patzoldt, W.L., Tranel, P.J., Alexander, A.L. & Schmitzer, P.R. (2001) A common ragweed population resistant to cloransulam-methyl. *Weed Science*, **49**, 485–490.
- Payne, W.W. (1964) A re-evaluation of the genus *Ambrosia* (Compositae). *Journal of the Arnold Arboretum*, **65**, 401–438.
- Petitpierre, B. (2014) *Using environmental niche modelling to understand biological invasions in a changing world*. PhD thesis, University of Lausanne, Lausanne, Switzerland.
- Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. & Guisan, A. (2012) Climatic niche shifts are rare among terrestrial plant invaders. *Science*, **335**, 1344–1348.
- Pickett, S.T. & Baskin, J.M. (1973) The role of temperature and light in the germination behavior of *Ambrosia artemisiifolia*. *Bulletin of the Torrey Botanical Club*, **100**, 165–170.
- Pinke, G., Karácsóny, P., Botta-Dukát, Z. & Czúcz, B. (2013) Relating *Ambrosia artemisiifolia* and other weeds to the management of Hungarian sunflower crops. *Journal of Pest Science*, **86**, 621–631.
- Poltavsky, A.N. & Artokhin, K.R. (2006) *Tarachidia candefacta* (Lepidoptera, Noctuidae) in the south of European Russia. *Phega*, **34**, 41–43.
- Poppendieck, H.H. (2007) Die Gattungen *Ambrosia* und *Iva* (Compositae) in Hamburg, mit einem Hinweis zur Problematik der *Ambrosia*-Bekämpfung. *Berichte des Botanischen Vereins zu Hamburg*, **23**, 53–70.
- Prank, M., Chapman, D.S., Bullock, J.M., Belmonte, J., Berger, U., Dahl, A. et al. (2013) An operational model for forecasting ragweed pollen release and dispersion in Europe. *Agricultural and Forest Meteorology*, **182–183**, 43–53.
- Protopopova, V.V., Shevera, M.V. & Mosyakin, S.L. (2006) Deliberate and unintentional introduction of invasive weeds: a case study of the alien flora of Ukraine. *Euphytica*, **148**, 17–33.
- Pyšek, P. & Hulme, P. (2005) Spatio-temporal dynamics of plant-invasions: linking pattern to process. *Ecoscience*, **12**, 302–315.
- Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.
- Raynal, D.J. & Bazzaz, F.A. (1975) Interference of winter annuals with *Ambrosia artemisiifolia* in early successional fields. *Ecology*, **56**, 35–49.
- Raynal, D.J. & Bazzaz, F.A. (1973) Establishment of early successional plant populations on forest and prairie soil. *Ecology*, **54**, 1335–1341.
- Reinhardt, F., Herle, M., Bastiansen, F. & Streit, B. (2003) Economic Impact of the Spread of Alien Species in Germany. J.W. Goethe University Frankfurt/Main, <http://www.nobanis.org/files/EconImpactNeobiota.pdf>.
- Reznik, S.Y. (1991) The effects of feeding damage in ragweed *Ambrosia artemisiifolia* (Asteraceae) on populations of *Zygogramma suturalis* (Coleoptera, Chrysomelidae). *Oecologia*, **88**, 204–210.
- Reznik, S.Y., Spasskaya, I.A., Dolgovskaya, M.Y., Volkovitch, M.G. & Zaitzev, V.F. (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 *7th International Symposium on Biological Control of Weeds* (eds M.H. Julien, R. Sforza, M.C. Bon, H.C. Evans, P.E. Hatcher, H.E. Hinz & B.G. Rector), pp. 614–619. CAB International, Wallingford, UK.
- Rich, T.C.G. (1994) Ragweeds (*Ambrosia* L.) in Britain. *Grana*, **33**, 38–43.
- Richter, R., Dullinger, S., Essl, F., Leitner, M. & Vogl, G. (2013a) How to account for habitat suitability in weed management programs. *Biological Invasions*, **15**, 657–669.
- Richter, R., Berger, U., Dullinger, S., Essl, F. & Vogl, G. (2013b) Spread of invasive ragweed: climate change, management and how to reduce allergy costs. *Journal of Applied Ecology*, **50**, 1422–1430.
- Rodwell, J.S., ed. (2000) *British Plant Communities, Vol. 5: Maritime Communities and Vegetation of Open Habitats*. Cambridge University Press, Cambridge, UK.
- Rosas, C.A., Engle, D.M., Shaw, J.H. & Palmer, M.W. (2008) Seed dispersal by bison in a tallgrass prairie. *Journal of Vegetation Science*, **19**, 769–778.
- Rothrock, P.E., Squiers, E.R. & Sheeley, S. (1993) Heterogeneity and size of a persistent seedbank of *Ambrosia artemisiifolia* L. and *Setaria faberii* Herrm. *Bulletin of the Torrey Botanical Club*, **120**, 417–422.
- Rybníček, O., Novotná, B., Rybníčková, E. & Rybníček, K. (2000) Ragweed in the Czech Republic. *Aerobiologia*, **16**, 287–290.
- Saint-Louis, S., DiTommaso, A. & Watson, A.K. (2005) A common ragweed (*Ambrosia artemisiifolia*) biotype in southwestern Québec resistant to linuron. *Weed Technology*, **19**, 737–743.
- Sang, W., Liu, X. & Axmacher, J.C. (2011) Germination and emergence of *Ambrosia artemisiifolia* L. under changing environmental conditions in China. *Plant Species Biology*, **26**, 125–133.

- Sartorato, I. & Pignata, G. (2008) Base temperature estimation of 21 weed and crop species. *Proceedings of the 5th International Weed Science Congress* (ed. International Weed Science Society), p. 274. International Weed Science Society, Vancouver, Canada.
- Schreiner, R.P. & Koide, R.T. (1993) Mustards, mustard oils and mycorrhizas. *New Phytologist*, **123**, 107–113.
- Schröder, G. & Meinschmid, E. (2009) Untersuchungen zur Bekämpfung von Beifußblättriger Ambrosie (*Ambrosia artemisiifolia* L.) mit herbiziden Wirkstoffen. *Gesunde Pflanzen*, **61**, 135–150.
- Sheppard, A.W., Shaw, R.H. & Sforza, R. (2006) Top 20 environmental weeds for classical control in Europe: a review of opportunities, regulations and other barriers to adoption. *Weed Research*, **46**, 93–117.
- Shin, H.D. (2000) *Erysiphaceae of Korea*. National Institute of Agricultural Science and Technology, Suwon, Korea.
- Shrestha, A., Erivelton, S.R., Thomas, A.G. & Swanton, C.J. (1999) Modeling germination and shoot-radicle elongation of *Ambrosia artemisiifolia*. *Weed Science*, **47**, 557–562.
- Šikoparija, B., Skjøth, C.A., Alm Kübler, K., Dahl, A., Sommer, J., Grewling, L., Radišić, P. & Smith, M. (2013) A mechanism for long distance transport of *Ambrosia* pollen from the Pannonian Plain. *Agricultural and Forest Meteorology*, **180**, 112–117.
- Šikoparija, B., Smith, M., Skjøth, C.A., Radišić, P., Milkovska, S., Šimić, S. & Brandt, J. (2009) The Pannonian Plain as a source of *Ambrosia* pollen in the Balkans. *International Journal of Biometeorology*, **53**, 263–272.
- Simard, M.J. & Benoit, D.L. (2010) Distribution and abundance of an allergenic weed, common ragweed (*Ambrosia artemisiifolia* L.), in rural settings of southern Québec, Canada. *Canadian Journal of Plant Science*, **90**, 549–557.
- Singer, B.D., Ziska, L.H., Frenz, D.A., Gebhard, D.E. & Straka, J.G. (2005) Increasing Amb a 1 content in common ragweed (*Ambrosia artemisiifolia*) pollen as a function of rising atmospheric CO₂ concentration. *Functional Plant Biology*, **32**, 667–670.
- Smith, M., Cecchi, L., Skjøth, C.A., Karrer, G. & Šikoparija, B. (2013) Common ragweed: a threat to environmental health in Europe. *Environment International*, **61**, 115–126.
- Smith, M., Skjøth, C.A., Myszkowska, D., Puc, M., Stach, A., Balwierc, Z., Chlopek, K., Piotrowska, K., Kasprzyk, I. & Brandt, J. (2008) Long-range transport of *Ambrosia* pollen to Poland. *Agricultural and Forest Meteorology*, **148**, 1402–1411.
- Smolik, M.G., Dullinger, S., Essl, F., Kleinbauer, I., Leitner, M., Peterseil, J., Stadler, L.-M. & Vogl, G. (2010) Integrating species distribution models and interacting particle systems to predict the spread of an invasive alien plant. *Journal of Biogeography*, **37**, 411–422.
- Stoller, E.W. & Wax, L.M. (1974) Dormancy changes and the fate of some annual weed seeds in the soil. *Weed Science*, **22**, 151–155.
- Solujić, L., Sukdolac, S., Vuković, N., Nićiforović, N. & Stanić, S. (2008) Chemical composition and biological activity of the acetone extract of *Ambrosia artemisiifolia* L. pollen. *Journal of the Serbian Chemical Society*, **73**, 1039–1049.
- Song, J.S. & Prots, B. (1998) Invasion of *Ambrosia artemisiifolia* L. (Compositae) in the Ukrainian Carpathians Mts. and the Transcarpathian plain (Central Europe). *Korean Journal of Biological Sciences*, **2**, 209–216.
- Spangenberg, J.H., Bondeau, A., Carter, T.R., Fronzek, S., Jaeger, J., Jylhä, K. et al. (2012) Scenarios for investigating risks to biodiversity. *Global Ecology and Biogeography*, **21**, 5–18.
- Stace, C. (2010) *New Flora of the British Isles*, 3rd edn. Cambridge University Press, Cambridge, UK.
- Stach, A., Smith, M., Skjøth, C.A. & Brandt, J. (2007) Examining *Ambrosia* pollen episodes at Poznan (Poland) using back-trajectory analysis. *International Journal of Biometeorology*, **51**, 275–286.
- Stephenson, G.R., Dykstra, M.D., McLaren, R.D. & Hamill, A.S. (1990) Agro-nomic practices influencing Triazine-resistant weed distribution in Ontario. *Weed Technology*, **4**, 199–207.
- Steyermark, J.A. (1963) *Flora of Missouri*. Iowa State University Press, St. Louis, MI, USA.
- Stojanović, D.V., Đurčić, S.B., Orlović, S., Kereši, T. & Galić, Z. (2011) Prvi nalaz sovice *Ponometia candefacta* (Hübner, 1831) (Lepidoptera, Noctuidae) u Srbiji. *Biljni lekar*, **39**, 31–36.
- Storkey, J., Stratonovitch, P., Chapman, D.S., Vidotto, F. & Semenov, M.A. (2014) A process-based approach to predicting the effect of climate change on the distribution of an invasive allergenic plant in Europe. *PLoS ONE*, **9**, e88156.
- Swanton, C.J., Shrestha, A., Knezevic, S.Z., Roy, R.C. & Ball-Coelho, B.R. (2000) Influence of tillage type on vertical weed seedbank distribution in a sandy soil. *Canadian Journal of Plant Science*, **80**, 455–457.
- Taramarcz, P., Lambelet, C., Clot, B., Keimer, C. & Hauser, C. (2005) Ragweed (*Ambrosia*) progression and its health risks: will Switzerland resist this invasion? *Swiss Medical Weekly*, **135**, 538–548.
- Taylor, J.B., Loux, M.M., Harrison, S.K. & Regnier, E. (2002) Response of ALS-Resistant common ragweed (*Ambrosia artemisiifolia*) and giant ragweed (*Ambrosia trifida*) to ALS-Inhibiting and alternative herbicides. *Weed Technology*, **16**, 815–825.
- Teshler, M.P., DiTommasso, A., Gagnon, J.A. & Watson, A.K. (2002) *Ambrosia artemisiifolia* L., common ragweed (Asteraceae). *Biological Control Programmes in Canada* (ed. J.T. Huber), pp. 290–294. CABI Publishing, New York, NY, USA.
- Thompson, K., Bakker, J.P. & Bekker, R.M. (1997) *The Soil Seed Banks of Northwest Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge, UK.
- Tokarska-Gudzik, B., Bzdega, K., Koszela, K., Zabinska, I., Krzus, B., Sajan, M. & Sendek, A. (2011) Allergenic invasive plant *Ambrosia artemisiifolia* L. in Poland: threat and selected aspects of biology. *Biodiversity Research and Conservation*, **21**, 39–48.
- Toole, H.E. & Brown, E. (1946) Final results of the Durvel buried seed experiment. *Journal of Agricultural Research*, **72**, 201–210.
- Tosi, A., Wüthrich, B., Bonini, M. & Pietragalla-Köhler, B. (2011) Time lag between *Ambrosia* sensitisation and *Ambrosia* allergy: A 20-year study (1989–2008) in Legnano, northern Italy. *Swiss Medical Weekly*, **141**, w13253.
- Tropicos (2014) Missouri Botanical Garden. URL: <http://www.tropicos.org/Name/2701648> (accessed 26 February 2014).
- Týr, Š., Vereš, T. & Lacko-Bartošová, M. (2009) Occurrence of common ragweed (*Ambrosia artemisiifolia* L.) in field crops in the Slovak Republic. *Herbolgia*, **10**, 1–9.
- Vajna, L. (2002) Downy mildew epidemic on common ragweed in Hungary caused by *Plasmopara halstedii*. *Plant Pathology*, **51**, 809.
- Vajna, L., Bohár, G. & Kiss, L. (2000) First report of *Phyllachora ambrosiae* in Europe causing epidemics on common ragweed. *Plant Disease*, **84**, 489.
- Vanky, K., Toth, S., Gonczol, J. & Revay, A. (1988) Further six species of Ustilaginales, new to Hungary. *Acta Botanica Hungarica*, **34**, 193–208.
- Varga, P., Kazinczi, G., Beres, I. & Kovacs, I. (2006) Competition between sunflower and *Ambrosia artemisiifolia* in additive experiments. *Cereal Research Communications*, **34**, 701–704.
- Varga, P., Beres, I. & Reisinger, P. (2002) The competitive effect of three dangerous weeds on the yields of maize in different years. *Növényvédelem*, **38**, 219–226.
- Vidotto, F., Tesio, F. & Vidotto, A.F. (2013) Allelopathic effects of *Ambrosia artemisiifolia* L. in the invasive process. *Crop Protection*, **54**, 161–167.
- Vincent, G. & Cappadocia, M. (1988) Characterization of reciprocal hybrids of common ragweed, *Ambrosia artemisiifolia*, and giant ragweed, *A. trifida*. *Weed Science*, **36**, 574–576.
- Vitalos, M. & Karrer, G. (2009) Dispersal of *Ambrosia artemisiifolia* seeds along roads: contribution of traffic and mowing machines. *Neobiota*, **8**, 53–60.
- Vogl, G., Smolik, M., Stadler, L.-M., Leitner, M., Essl, F., Dullinger, S., Kleinbauer, I. & Peterseil, J. (2008) Modelling the spread of ragweed: effects of habitat, climate change and diffusion. *European Journal of Physics*, **161**, 167–173.
- Voglmayr, H. & Riethmüller, A. (2006) Phylogenetic relationships of *Albugo* species (white blister rusts) based on LSU rDNA sequence and oospore data. *Mycological Research*, **110**, 75–85.
- von der Lippe, M., Bullock, J.M., Kowarik, I., Knopp, T. & Wichmann, M. (2013) Human-mediated dispersal of seeds by the airflow of vehicles. *PLoS ONE*, **8**, e52733.
- Wagner, W.H. & Beals, T.F. (1958) Perennial ragweeds (*Ambrosia*) in Michigan, with description of a new, intermediate taxon. *Rhodora*, **60**, 177–204.
- Wan, F.H., Ma, J., Gui, J.Y. & You, L.S. (2003) Integrated control effects of *Epilema strenuana* (Lepidoptera: Tortricidae) and *Ostrinia orientalis* (Lepidoptera: Pyralidae) against ragweed, *Ambrosia artemisiifolia* (Compositae). *Acta Entomologica Sinica*, **46**, 473–478.
- Wang, D. & Zhu, X. (1996) Research on allelopathy of *Ambrosia artemisiifolia*. *Acta Ecologica Sinica*, **16**, 11–19.
- Watanabe, O., Kurokawa, S., Sasaki, H., Nishida, T., Onoue, T. & Yoshimura, Y. (2002) Geographic scale distribution and occurrence pattern of invasive weeds. *Grassland Science*, **48**, 440–450.
- Wayne, P., Foster, S., Connolly, J., Bazzaz, F. & Epstein, P. (2002) Production of allergenic pollen by ragweed (*Ambrosia artemisiifolia* L.) is increased in CO₂-enriched atmospheres. *Annals of Allergy, Asthma and Immunology*, **8**, 279–282.
- Weaver, S.E. (2001) Impact of lamb's-quarters, common ragweed and green foxtail on yield of maize and soybean in Ontario. *Canadian Journal of Plant Science*, **81**, 821–828.
- Webb, C.J. (1987) Checklist of dicotyledons naturalised in New Zealand. 18. Asteraceae (Compositae) subfamily Asteroideae. *New Zealand Journal of Botany*, **25**, 489–501.

Webster, T.M. & Nichols, R.L. (2012) Changes in the prevalence of weed species in the major agronomic crops of the southern United States: 1994/1995 to 2008/2009. *Weed Science*, **60**, 145–157.

Webster, T.M., Cardina, J. & White, A.D. (2003) Weed seed rain, soil seed-banks, and seedling recruitment in no-tillage crop rotations. *Weed Science*, **51**, 569–575.

White, J.F. & Bernstein, D.I. (2003) Key pollen allergens in North America. *Annals of Allergy Asthma and Immunology*, **91**, 425–435.

Willemsen, R.W. (1975) Effect of stratification temperature and germination temperature on germination and the induction of secondary dormancy in common ragweed seeds. *American Journal of Botany*, **62**, 1–5.

Willemsen, R.W. & Rice, E.L. (1972) Mechanism of seed dormancy in *Ambrosia artemisiifolia*. *American Journal of Botany*, **59**, 248–257.

Wopfner, N., Gadermaier, G., Egger, M., Asero, R., Ebner, C., Jahn-Schmid, B. & Ferreira, F. (2005) The spectrum of allergens in ragweed and mugwort Pollen. *International Archives of Allergy and Immunology*, **138**, 337–346.

Zhou, Z.S., Guo, J.Y., Chen, H.S. & Wan, F.H. (2010) Effects of temperature on survival, development, longevity, and fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae), a potential biological control agent against *Ambrosia artemisiifolia* (Asterales: Asteraceae). *Physiological Ecology*, **39**, 1021–1027.

Ziska, L.H., Knowlton, K., Rogers, C., Dalan, D., Tierney, N., Elder, M.A. et al. (2011) Recent warming by latitude associated with increased length of ragweed pollen season in central North America. *Proceedings of the National Academy of Sciences*, **108**, 4248–4251.

Ziska, L.H., Gebhard, D.E., Frenz, D.A., Faulkner, S., Singer, B.D. & Straka, J.G. (2003) Cities as harbingers of climate change: common ragweed, urbanization, and public health. *Journal of Allergy and Clinical Immunology*, **111**, 290–295.

zation, and public health. *Journal of Allergy and Clinical Immunology*, **111**, 290–295.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Modelling the spread of *Ambrosia artemisiifolia*.

Figure S1. Appearance of *Ambrosia artemisiifolia* populations in habitats that are most invaded in Europe.

Figure S2. Occurrence of *Ophraella communa* in Europe in 2013.

Figure S3. The spread of *Ambrosia artemisiifolia* in Central and Eastern Europe.

Figure S4. The relative importance of variables used as predictors in SDMs.

Figure S5. The potential binarized distribution of *A. artemisiifolia* under current and future climate, as predicted by SDMs.