

Biological Flora of the British Isles: *Ambrosia artemisiifolia*

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

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, history, and conservation, impacts and management.

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 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 N. 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 consensus among models that climate change will allow its northward and up-hill spread in Europe.

Key-words: agriculture, biogeography, climate change, ecophysiology, germination, geographical and altitudinal distribution, 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 4-angled, ridged and leafy, with several branches; leaves mostly opposite, alternate above, deltate to lanceolata or elliptic in outline, 25-55(90) x

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, 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 x 1.8-2.5 mm, enclosed in woody achenes. Fruit yellowish to reddish-brown, \pm 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 three others native to North America (*A. psilostachya*, *A. tenuifolia*, *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 widely, 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 *et al.* 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.

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; EPPO 2013), Japan (widespread; Nakayama 1998; Watanabe *et al.* 2002; EPPO 2013), South Korea (EPPO 2013), South Africa (established; L. Henderson unpublished data) Australia (Lazarides *et al.* 1997), and New Zealand (Webb 1987; EPPO 2013). In the Americas, the species has spread to Argentina (Anton & Zuloaga 2014), Chile (established; N. Fuentes unpublished 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 naturalised populations or transient and repeated colonisations (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 difficult to reconstruct. In Canada and the USA, the species is present in all provinces, states and territories, with the exception of Yukon and Nunavut (FNA Editorial Committee 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 soybean 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 *et al.* 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 infested 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 e.g. 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 **XI. Nature Conservation**). 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*, *Conyza 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 *Elymus 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 VI. F). In contrast, Kazinczi *et al.* (2008d) found that aqueous extracts from leaves of sunflower - and other donor plants - 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 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 soybean (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, i.e. 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; Bazzaz 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 & Lösch 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 & Lösch 2011), it does not occur in waterlogged sites under field conditions. *Ambrosia artemisiifolia* has the highest net photosynthesis rates under moist soil conditions in the absence of other plant species (Leiblein & Lösch 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 mass allocation, followed by 27% to roots and 18% to stems (Nitzsche 2010).

Leaves are opposite toward the stem base, but alternate toward 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 5 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, riverbanks, 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 etinicum* 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 (1976) and Martin *et al.* (2014) the diploid state is frequent, but sometimes triploid and tetraploid individuals are found in North American populations. 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 to 183 days (Bassett & Crompton 1975; Beres 1994; Kazinczi *et al.* 2008b). Photoperiod and temperature (see 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 & L sch 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 five-fold higher rates of photosynthesis (Bazzaz 1973). In a further experiment, field-grown, mature *A. artemisiifolia* plants did not saturate at a PAR c. $1450 \mu\text{mol m}^{-2} \text{s}^{-1}$; the photosynthetic rate at optimal light flux, temperature, water potential and 300 ppm CO_2 was c. $35 \text{ mg dm}^{-2} \text{ hr}^{-1}$ (Bazzaz 1974). Their optimal temperature for photosynthesis was 20°C and the high rate of photosynthesis was accompanied by a high transpiration rate ($3 \text{ g H}_2\text{O dm}^{-2} \text{ h}^{-1}$) (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) 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 CO_2 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 CO_2 concentration stimulated pollen production by 61% (Wayne *et al.* 2002).

(F) BIOCHEMICAL DATA

A. artemisiifolia contains various secondary metabolites with antibiotic properties, such as sesquiterpene lactones, including ambrosin, isabelin, psilostachyn, cumarin and peruvic acid, 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 1984; Wang & Zhu 1996; Brückner, Lepossa & Herpai 2003; Lehoczy *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 *et al.* 1998b). Germination in Europe occurs in early to mid-spring (late March and April), although a small proportion germinates later (Baskin & Baskin 1977; Bassett & Crompton 1975). Following seedling emergence, the rate of vegetative growth depends on temperature (Deen *et al.* 1998b), but development occurs over a wide thermal range (8 - 30°C) (Deen *et al.* 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 late July to 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 hours (Deen *et al.* 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 *et al.* 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 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

& Tackenberg 2014). For instance, late growth and flowering phenology in a common garden experiment were highly correlated with latitude, i.e. individuals from northern populations grew smaller and flowered and dispersed pollen and seeds up to five weeks earlier than individuals from southern populations (Leiblein & Tackenberg 2014). This may be responsible for the remarkable level of synchronisation 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, unpublished 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), i.e. usually in the morning after sunrise, and pollen release from a flower lasts only up to 6 hours. Although *Ambrosia 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 (Tamarcaz *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; Karrer *et al.* 2011; Gaudeul *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; FNA Editorial Committee 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 2,518 (± 271 SD) seeds per plant (Fumanal, Chauvel & Bretagnolle 2007). Planted individuals in the native range had higher seed production, ranging from 3,135–32,485 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, unpublished data) and Russia (62,000 seeds; Fisjunov 1984). Individuals from ruderal habitats had lower average seed production (between c. 300–2,500 seeds/plant) than individuals from arable fields (c. 2,300–6,000 seeds/plant; Fumanal, Chauvel & Bretagnolle 2007). Seed production in populations on arable fields is negatively affected by the density of crops (Chikoye, Weise & Swanton 2005; 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 (unpublished 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 unpublished data). Seeds tend to stay on the plants for one or two 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, unpublished 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 seedbank 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; Willemsen & Rice 1972; Willemsen 1975; Bazzaz 1979; 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 two-fold to twelve-fold higher when soil surface was disturbed. Furthermore, Fenesi *et al.* (2013) 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 two 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 germinated did so after 39 years (Toole & Brown 1946). Unburied seeds quickly lose their viability over four years (Béres 2003). Viability decreased by 73% within five years for seeds stored in paper bags at room temperature (Kazinczi *et al.* 2012).

Seed-bank densities of *A. artemisiifolia* in field-crop habitats have been analyzed 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 m² in the upper 20 cm of soil. Seed banks in crop

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fields were larger than in ruderal and set-aside habitats. The number of extant seeds in the upper soil layer (0–5cm) was lower (mean = 592, $n = 240$) than in the deeper layer (5–15cm) (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; Sang *et al.* 2001; Nitzsche 2010). 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 (Pickett & Baskin 1973; Willemsen 1975; 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 (Sartorato & Pignata 2008; Shrestha *et al.* 1999; Guillemain *et al.* 2013). However, according to Sang *et al.* (2011) the germination of seeds decreases near-linearly with increased osmotic potential until -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 to 8 and a maximum germination rate of 98.2% at pH 5.57 (Sang *et al.* 2011). It is also able to maintain high germination rates (70–80%) under moderate salinity of about 200 mmol L⁻¹ of NaCl (Sang *et al.* 2011; Eom, DiTommaso & Weston 2013) and can germinate (from 5–12%) 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 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 weight 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 Switzerland (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 infested area suggest that this species, which was accidentally introduced into China and now used there as a most

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 *Zygogramma suturalis* (see **XI. Biological management**) 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.* 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, i.e. 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 unpublished 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 *Plasmopara 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), Austria (1883; Essl, Dullinger & Kleinbauer 2009), Czech Republic (1883; Pyšek, Sádlo & Mandák 2002), Hungary (1888; Kazinczi *et al.* 2008a), Switzerland (1865; <http://www.ambrosia.ch/vorkommen-pflanze/vorkommen-von-ambrosia/>), Italy (1902; Mandrioli, Di Cecco & Andina 1998), Russia (1918; CABI 2014), Romania (1907; Csontos *et al.* 2010).

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, e.g. 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):

I) 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).

II. 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.

III. 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.

IV. 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, e.g. 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 (Rybnicek *et al.* 2000; Brandes & Nitzsche 2006; Tokarska-Gudzik *et al.* 2011). In Europe, the saturation phase of the invasion – i.e. 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- 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 *Seed Production and Dispersal*). 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 e.g. in Austria (Essl, Dullinger & Kleinbauer 2009) and France (Chauvel *et al.* 2006). However, experimental quantification of dispersal by vehicles suggest 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 meter 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 (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 soybean 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 *et al.* 2013; Chapman *et al.* 2014; Storkey *et al.* 2014). In contrast, parts of the currently southernmost distribution range in Europe will become 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 infested (e.g. southern Russia and Ukraine). With regards to Britain, cool summers and common ragweed's preference for a continental climate may remain limiting factors in all but southeast 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. 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 of 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 on 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 constriction), 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, 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, 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 (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 fertiliser use in northwest Europe have yet to be included in the models. Finally, in countries 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 (Gentilini 2011; Bullock *et al.* 2012).

Finally, all the models assume temporal and spatial conservatism of the ecological niche, i.e. 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 *et al.* 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 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 & Riesberg (2011) by comparing the expression of more than 45,000 genes between native and introduced populations subjected to light or nutrient stress. This genome-wide 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 & Riesberg 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 *et al.* (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) to 1st (1996-97; 2007-08) 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 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 soybean 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 *et al.* 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.* 2007; Nitzsche 2010; Bullock *et al.* 2012). For example, Kazinczi *et al.* (2007) demonstrated that *A. artemisiifolia* at densities of 5 and 10 plants m⁻² caused 21 and 33% yield reduction in sunflower and almost 30% in maize at both densities. In sugar beet, plots infested with *A. artemisiifolia* at a density of 2 to 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 European situation because of differing climatic conditions and cropping practices. Coble, Williams & Ritter (1981) calculated soybean yield losses of 8% at an *A. artemisiifolia* density of four plants per 10 m of row. Weaver *et al.* (2001) also found *A. artemisiifolia* was highly competitive with maize and soybean crops in Ontario (Canada). For high *A. artemisiifolia* density, the maximum yield loss in soybean 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 (Tamaracaz *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 sensitisation to *Ambrosia* pollen allergen determined in 14 European countries (3034 patients), showed that the clinically relevant sensitisation 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), e.g. 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 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, e.g. 1–3 pollen grains m⁻³ d⁻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, unpublished 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; EU 2011) and in animal feed material (since 1 January 2013; 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

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cutting machines (Vitalos & Karrer 2009) and crop harvesting machinery (G. Karrer unpublished data) 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 (U. Starfinger *et al.* unpublished data). 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; Buttenschøn, Waldispühl & 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; Simard & Benoit 2010; Nitzsche 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; Bohren, Mermillod & Delabays 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, Milakovic, Fiedler & Karrer 2014a; Kazinczi *et al.* 2008c) 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 prevent 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, Waldspühl & 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, Waldspühl & Bohren 2009; U. Starfinger *et al.* unpublished 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 outcompeted (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* outcompeted *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* e.g. 2,4-D in the 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; Schröder & Meinschmid 2009; Buttenschön, Waldspühl & Bohren 2009; Gauvrit & Chauvel 2010).

Yield losses are most important in certain spring crops (sorghum, soybean) 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 (Buttenschøn, Waldspühl & 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 (2012) 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 the USA. At first, some resistance to herbicides inhibiting photosynthesis was observed in ragweed infesting maize in the 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 if 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 2010) 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 *et al.* 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 5,000 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 defoliate 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).

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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.

Tables

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	Plantaginea, Polygono-Poetea
<i>Achillea millefolium</i> agg.			x	
<i>Artemisia vulgaris</i>		x		
<i>Chenopodium album</i>	x			
<i>Convolvulus arvensis</i>		x		
<i>Coryza canadensis</i>	x			
<i>Daucus carota</i>		x		
<i>Echinochloa crus-galli</i>	x			
<i>Elymus repens</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			

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 to 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 communa</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 flinata</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		
<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>Hypena 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>Frankliniella 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
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	China	15
(<i>Alternaria tenuis</i> Nees)		
Incertae sedis		
<i>Phoma</i> sp.	Hungary	3
LEOTIOMYCETES		
HELOTIALES		
Sclerotiniaceae		
<i>Botrytis cinerae</i> Pers.	Hungary	6
<i>Sclerotinia sclerotium</i> (Lib.) de Bary	Hungary	4
ERYSIPHALES		
Erysiphaceae		
<i>Golovinomyces cichoracearum</i> (DC.) V.P.	Korea, Mauritius	19, 22
<i>Heluta</i> (<i>Erysiphe cichoracearum</i> DC.)		
<i>Golovinomyces cichoracearum</i> var.	Germany	7
<i>latisporus</i> (U. Braun) U. Braun		
(<i>Erysiphe cichoracearum</i> var.		
<i>latispora</i> U. Braun)		
<i>Leveillula taurica</i> (Lév.) G. Arnaud	former USSR	1
SORDARIOMYCETES		
HYPOCREALES		
Netriaceae		
<i>Fusarium avenaceum</i> (Fr.). Sacc.	China	15
INCERTAE SEDIS		
Plectosphaerellaceae		

<i>Verticillium dahliae</i> Kleb.	Hungary	6
PHYLLACHORALES		
Phyllachoraceae		
<i>Phyllachora ambrosiae</i> (Berk. & M.A. Curtis)	Hungary	24
Sacc.		
AGARICOMYCETES		
CANTHARELLALES		
Ceratobasidiaceae		
<i>Thanatephorus cucumeris</i> (A.B. Frank) Donk (<i>Rhizoctonia solani</i> J.G. Kühn)	Hungary	6
EXOBASIDIOMYCETES		
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 (unpublished data); (28) Stephan *et al.* (unpublished data); (29) Petanović & Vidović (unpublished data).

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 the 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	↘	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)

Table 4. Summary of models predicting the effect 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 <i>et al.</i> (2013)	Europe (5'x5')	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)	Worldwide (50x50 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 northeastern Europe and Siberia.
Chapman <i>et al.</i> (2014)	Europe (5x5 km)	Mechanistic phenology model driven by temperature and photoperiod. Range predicted as region where ragweed completes lifecycle 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 seedbank 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.
Vogl <i>et al.</i> (2008), Richter <i>et al.</i> (2013a,b)	Central Europe (3'x5')	'Hybrid model' coupling species niche with dispersal kernel to simulate spread	Mean annual temperature, mean annual precipitation.	Crop and urban land cover, length of roads.	2050	IPCC A1b (lower & upper range:	Spread by infilling from multiple current occurrences

		dynamics. Fitted to data on spread in study region.				+1.5 °C, +2.4 °C)	is ~25% (lower range) and ~50% (upper range) worse under climate change.
Bullock <i>et al.</i> (2012)	Europe (5x5 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.

Figures

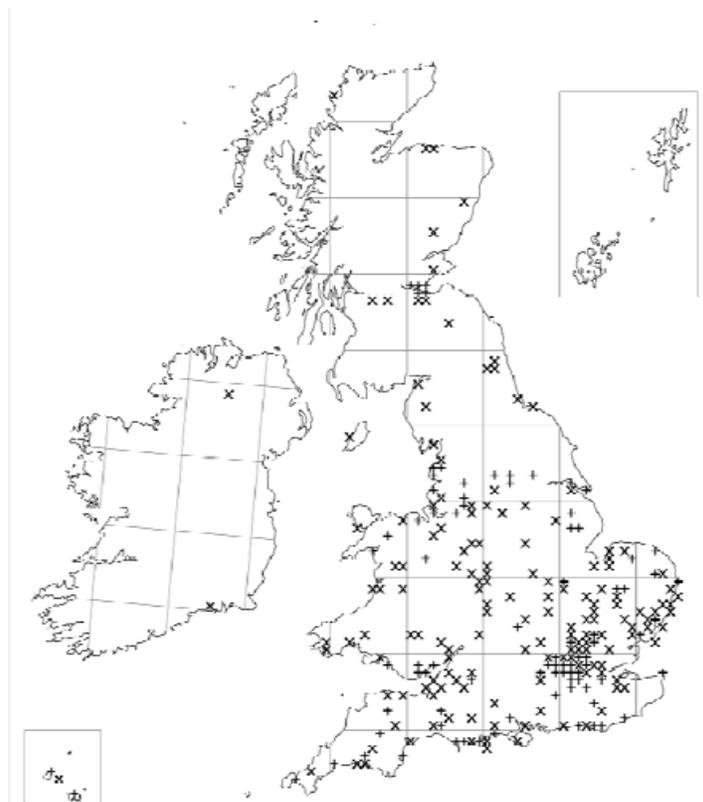


Fig. 1. The distribution of *Ambrosia artemisiifolia* in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (+) non-native 1970 onwards; (x) non-native pre-1970. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology, mainly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

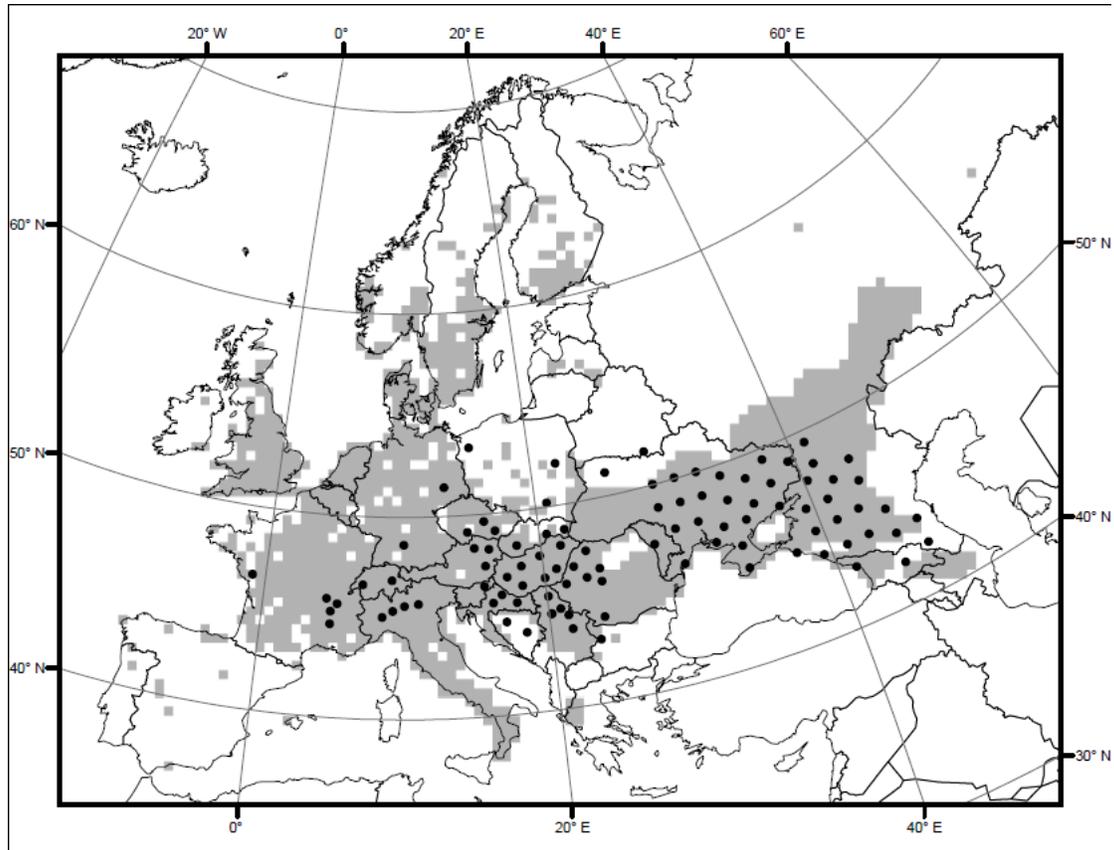


Fig. 2. The distribution (colonized grid cells of 50 x 50 km size are shown in grey) of *Ambrosia artemisiifolia* in Europe. Distribution data are based on Bullock *et al.* (2012), with additional records (D.S. Chapman, unpublished data). Black points indicate heavily infested areas with high level of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

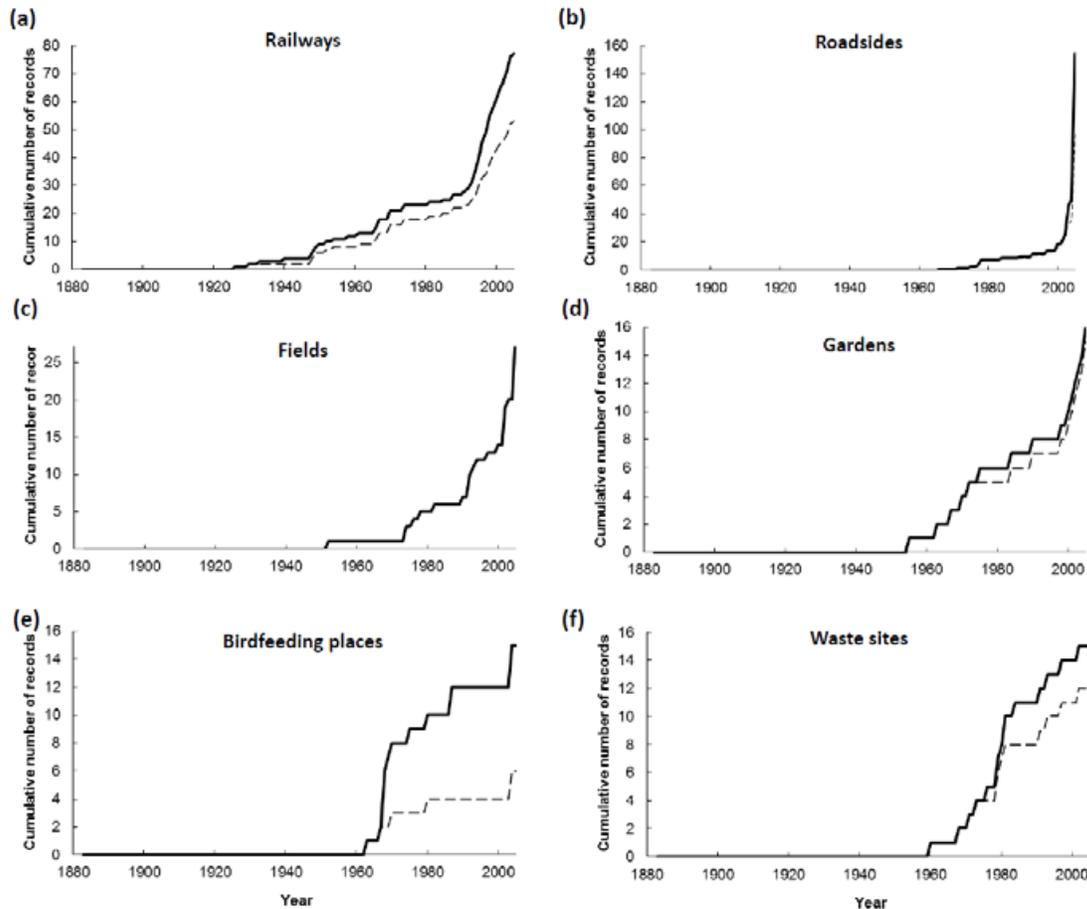


Fig. 3. Time course of invasion by *Ambrosia artemisiifolia* in six different habitats (a-f) in Austria. Results are shown as the cumulative number of records (solid line) and as cumulative number of colonised grid cells (dashed line) of the project 'Floristic Mapping of Austria' (5 x 3', c. 35 km²). The two lines coincide for (c) fields (Essl, Dullinger & Kleinbauer (2009, modified).



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 (4x), B. Fumanal (1x), M. Smith (1x).

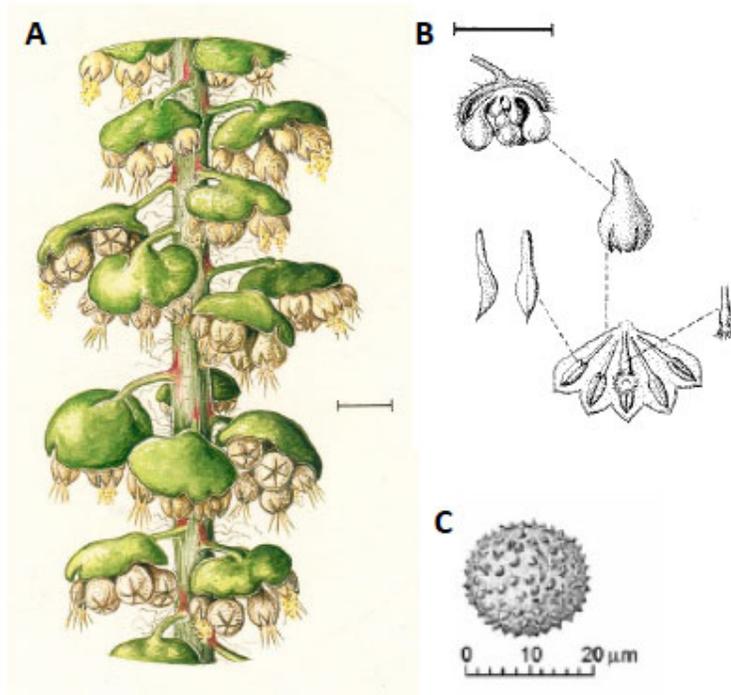


Fig. 5. Male capitula of *Ambrosia artemisiifolia*: (a) synflorescence; (b) single male flower; and(c) pollen. Drawings by Krisztina Bíró ©.

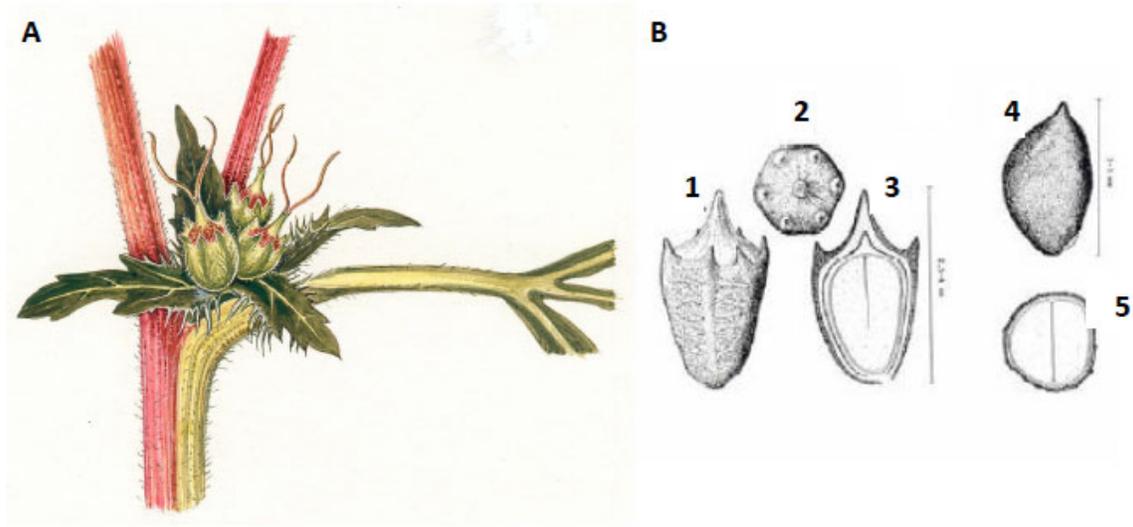


Fig. 6. Female capitula of *Ambrosia artemisiifolia*: (a) racemes with achenes; (b) 1, one-seeded syconium viewed from the side; 2, syconium viewed from above; 3, syconium in longitudinal section; 4, achene; 5, syconium cross-section. Drawings by Krisztina Bíró ©.



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



Fig. 8. *Ophraella communis* 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).

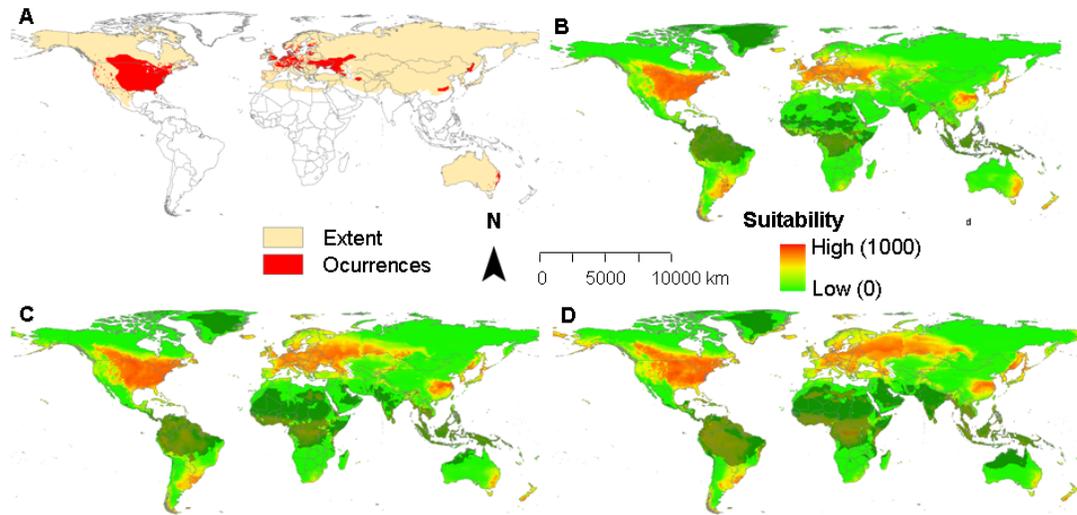


Fig. 9. World-wide potential distribution of *Ambrosia artemisiifolia*. Information about species occurrences in North America and for the non-native distribution in Eurasia and Australia (a) were used to calibrate SDMs providing potential distribution under current (b) and warmer (c and d) climates. 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-analog climate where predictions are not reliable. For details, see Appendix S1.

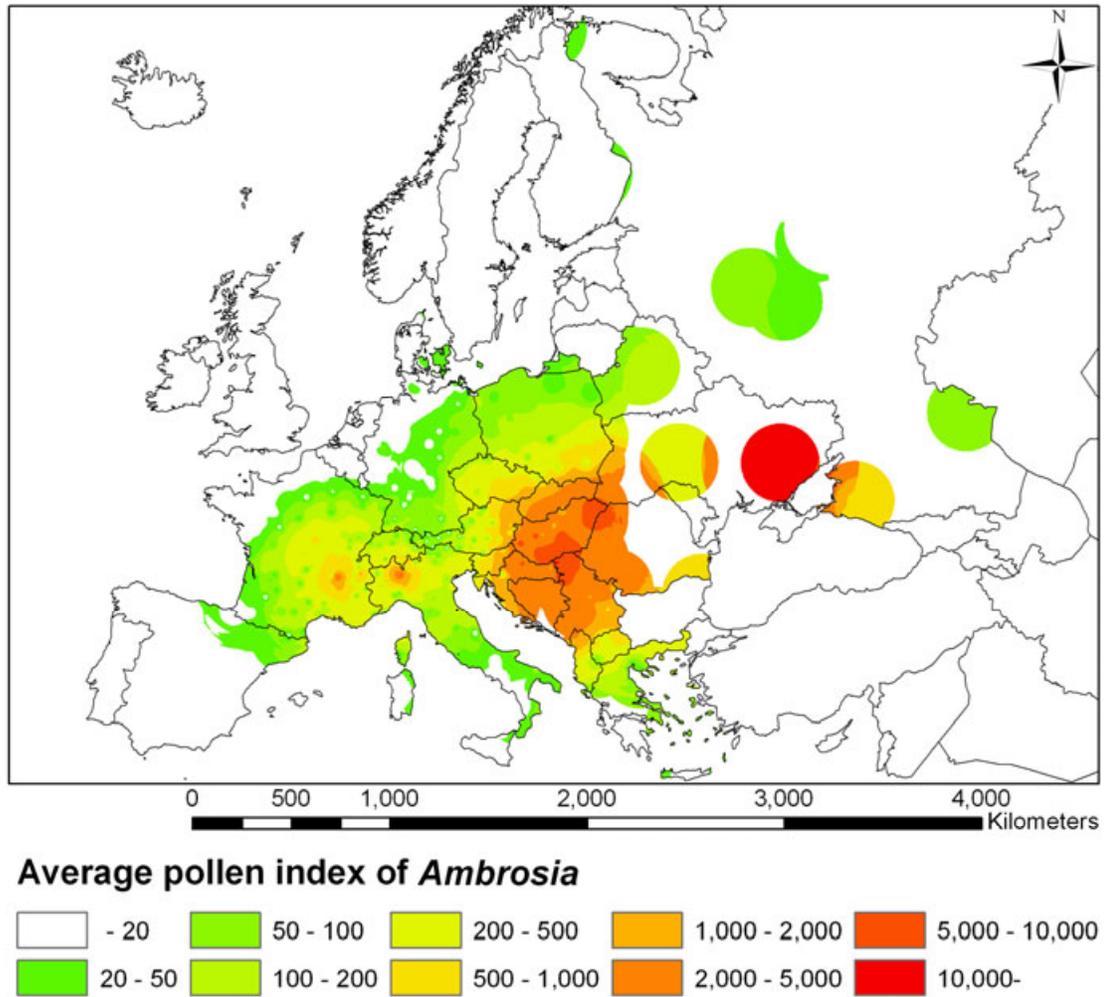


Fig. 10. A spatial assessment of the density of naturalised *Ambrosia artemisiifolia* populations with flowering potential for the years 2000-09. The map is based on the mean annual pollen index of *Ambrosia artemisiifolia* from 368 stations in Europe, simple interpolation, buffer zones of 200 km and presence/absence information in Flora Europea. The map is based on data stored in the European Aeroallergen Network database (<https://ean.polleninfo.eu/Ean/>). In Eastern Europe; there are gaps resulting from a lack of pollen stations (Smith *et al.* 2013, modified).