The worldwide spread, success and impact of ragweed (Ambrosia spp.)

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Abstract

Ambrosia species represent one of the most problematic groups of invasive weeds around the world. The ease they are introduced and spread in new countries, their generalist ecological requirements and functional traits facilitate their invasion and subsequent naturalization in new areas. All of these aspects contribute to increasing their global social and economic impact, which is mostly related to pollen allergy. Here we analyse available scientific publications about *Ambrosia artemisiifolia*, *A. psilostachya*, *A. tenuifolia* and *A. trifida*, with the aim of defining the current level of knowledge and summarizing important data that is currently scattered throughout the literature. Specifically, we analysed the following: (1) their current global distribution and current stage of invasion; (2) traits and requirements promoting their introduction, reproductive success and adaptation to climate and environment in the non-native range; as well as (3) current knowledge about allergens and elements increasing their impact.

Key words: *Ambrosia artemisiifolia*, *A. psilostachya*, *A. tenuifolia*, *A. trifida*, invasive alien plants, pollen allergy.

Contents

I. Introduction

There are over 40 species in the genus *Ambrosia* L. (Asteraceae) (Rich, 1994; Makra *et al.*, 2015; www.theplantlist.org), most of which are native to the Americas. Over the last 200 years, human impacts on land use (i.e. urbanization, the intensification of farming practices and increased transportation networks) have had serious effects on the distribution and ecology of several *Ambrosia* species. In particular, the introduction of the following species in non-native continents: *A. artemisiifolia* L. (common or short ragweed), *A. trifida* L. (giant ragweed), *A. tenuifolia* Spreng. (slender or slim-leaf burr ragweed) and *A. psilostachya* DC. (Western or perennial ragweed).

These *Ambrosia* (ragweed) species have been introduced into new countries since the 19th century, especially *A. artemisiifolia* which has quickly become an invasive species (Smith *et al.* (2013) and references therein) and is presently a species of concern for public health in both its native and invasive ranges because of its highly allergenic pollen. In North America, *Ambrosia* pollen is the second most important cause of seasonal allergic rhinitis and asthma, affecting more than 15 million people (about 20-25% of the United States population), with a prevalence of about 45% in atopic individuals (Wopfner *et al.*, 2005; Kats and Carey 2014). In Europe, *Ambrosia* has become a serious problem in the past decades, contributing to an evident increase in respiratory allergic reactions in areas where it is distributed (D’Amato, 1992; D’Amato, 2007). It is therefore recognized globally that *Ambrosia* species represent one of the most problematic groups of invasive weeds.

Biological invasions can be represented as a chronological series of decisive stages that can allow or halt the entry and establishment of an organism in a new range (Blackburn *et al.*, 2011; Richardson and Pysek, 2012). A non-native organism needs to overcome geographical, environmental and reproductive barriers to establish in a new area, and some factors and traits can be more meaningful than others in predicting or explaining its success or failure during the process of introduction, establishment and spread (Van Kleunen *et al.*, 2015). Expressing the invasion process formulaically as "introduction - naturalization - invasion *continuum*", Richardson and Pysek (2012) stressed the importance of focusing on "naturalization", which is the fundamental preliminary step before invasion. According to their review, this "naturalization" is understudied, but its predictors/mediators can be more robust than those formulated for the invasion phase as they depend on factors less unpredictable and highly context-dependent.

On this basis, our review examines the main predictors of introduction-naturalization of the most widespread *Ambrosia* species at a global level, considering the environmental requirements and traits discussed and reported in scientific literature. After starting with a brief description of the taxa considered, this review then follows the logical sequence of the *continuum* in order to examine factors and traits involved in overcoming:

- *Geographical barriers*. Mediators of the introduction of species into new areas: native extent of occurrence, pathways of introduction and their effectiveness in terms of space (extent of the invasive range) and time (protraction of invasion).
- *Environmental barriers*. Predictors of the likelihood of persistence of *Ambrosia* species: environmental and climatic (broad-scale) matching between native and invasive range, requirements and tolerance to the main environmental abiotic factors (temperature, soil, light) in sensitive phases of the life cycle, resilience (strategies) to disturbances and competition.
- *Reproductive and dispersal barriers*. Predictors of successful propagation and spread of species, such as: specific pollinators, reproduction and dispersal strategies, propagule pressure.

The review ends with an overview of the allergenic impact of ragweed and how environmental factors and plant traits influence the magnitude of pollinosis.

II. Literature screening

Google Scholar, Web of Science and Scopus databases were consulted to identify scientific literature about the *Ambrosia* genus. However, given the availability of interesting information also in additional web repositories, technical reports and online databases (national/regional floras, CABI, IUCN, EPPO, DAISIE, HEAR) were examined.

III. Species considered and their description

The *Ambrosia* species considered in this review are presently introduced in more than ten countries: *A. artemisiifolia, A. trifida, A. psilostachya* and *A. tenuifolia.* All *taxa* are herbaceous or slightly suffruticose species. *Ambrosia artemisiifolia* and *A. trifida* are annual plants, while *A. psilostachya* and *A. tenuifolia* are perennials. Besides the presence of different belowground organs, diagnostic elements are mainly leaves, whose shape and clefts, as well as the presence of petioles, are useful in identifying different species. Leaves are variously pubescent or glaborous. They are monoic species with inflorescences of unisexual heads. All *taxa* produce 1-seeded cypselae and its size and coat ornaments may differ: *A. trifida* produces the biggest seeds and, among others species, spines may differ in number and bluntness.

A. trifida is an easily identifiable *taxon*, whose height (up to 4 m) and shape of leaves are unmistakable. However, the determination of other *taxa* can often be hard owing to a high variability in leaf or seed shape. Furthermore, the taxonomy is complicated by the possible presence of hybrids between *A. artemisiifolia* and *A. psilostachya* (*A.* x *intergradiens*; Wagner and Beals, 1958) and *A. artemisiifolia* and *A. trifida* (*Ambrosia* × *helenae*; Wagner, 1958; Strother, 2006).

Recently, the SMARTER project (COST Action FA1203) brought together a European team of botanists from different countries who reviewed the discriminating characters among species to provide a proper key of identification; as the most recent and reliable source, their findings relevant for this section are summarized in Table 1 and they are also available at http://internationalragweedsociety.org/

IV. Geographical barriers

Geographical barriers are the first obstacle an organism has to overcome before reaching a new range (Richardson *et al.*, 2000; Blackburn *et al.*, 2011). All the *taxa* considered here are native to the Americas, where the highest number of species of the genus have occurred: the genus appears to have originated and diversified from arid and semi-arid regions in Southwestern North America (Payne, 1970; Gerber *et al.*, 2011).

From the current distribution of ragweed, it is clear that these species have often successfully crossed the natural borders of their broad native ranges (Fig. 1). Pathways of introduction are linked to involuntary human actions and the flux of propagules has been in operation for at least a century. Here the pathways of introduction from native to invasive ranges are explained and the present global distribution is discussed, starting from a description of the native environments of the single species.

A. Native range

Ambrosia artemisiifolia is native to North America and is presently widespread in the United States and Canada except for Yukon and Nunavut (Strother, 2006; Essl *et al.*, 2015). In its native area, it was first recorded before 1838 in the United States (Kazinczi *et al.*, 2008) and in 1822 in Canada (Bassett and Crompton, 1975; Mitich, 1996; Lavoie *et al.*, 2007). It is, however, difficult to understand its primitive range of distribution because its spread has been human-mediated for a long time (McAndrews, 1988). According to Basset and Crompton (1982) the species spread widely with the increase of settlements of white men in North America. As a consequence of this, and due to taxonomic disagreements, there are several incongruities among floras about the native or introduced status of *A. artemisiifolia* in a number of countries, above all regarding Central and South America (Fig. 1).

Like *A. artemisiifolia, A. trifida* is native to North America. According to Bazzaz (1979), it was found in repeatedly disturbed ground only in the Midwestern and Eastern United States. However, based on more recent sources, *A. trifida* occurs in a wider range, covering almost all the USA (except for Nevada) and Canada (except for the Northwest Territories, Nunavut, and Yukon (Strother, 2006); it moved into Canada from the South, following the retreat of the last glacial ice (Fig. 1) (Bassett and Crompton, 1982).

Ambrosia psilostachya is also native to Western North America. As with *A. trifida*, it migrated to Canada after the glacial retreat, colonizing the Eastern Canada, where it has been present for a considerable time (Fig. 1) (Mitich, 1996). Bovey (1966) confirmed that *A. psilostachya* is widely distributed from California, Texas, Mexico, Idaho and Saskatchewan eastward to Illinois and Louisiana, on pasture land in Nebraska but especially in the Rocky Mountain States (Bovey, 1966). According to Strother (2006), its native range in the United States includes almost all States (except for Maryland, Delaware, and New Jersey) and the Southern part of Canada (from Columbia to Nova Scotia and Newfoundland).

In contrast to the other three species, *A. tenuifolia* is native to temperate South American countries, particularly Brazil, Paraguay, Uruguay, Argentina, and probably Perù (Fig. 1) (Randall, 2012).

B. From native to invasive range: pathways of introduction

Due to their ethnobotanical value, *Ambrosia* spp. have been used in traditional medicine since ancient times. In North and Central America, *A. artemisiifolia, A. psilostachya* and *A. trifida* were medicinal plants for Native Americans (Chamberlin, 1911; Shemluck, 1982; Mamedov *et* *al.*, 2015) and today some of them are still used (i.e. *A. psilostachya*, see Gioanetto *et al.*, 2010). Moreover, *A. trifida* was domesticated by Indigenous North Americans, who collected and planted seeds mainly for alimentary purposes (Simon, 2009; Jurney, 2012), In South America, predominantly in the Southern Cone, *A. tenuifolia* has also been a traditional medicinal plant (Mongelli *et al.*, 1996; Del Vitto, 1997; Trillo *et al.*, 2014). Thus, owing to the long-lasting utilization of ragweed in traditional medicine and uses, it is likely that European colonizers carried seeds to their countries by growing plants in botanical gardens (Essl. *et al.*, 2015). However, the scientific or ethnobotanical interest was probably not the main root of introduction for these species, as the amounts of seeds or plants moved were small. Ragweed plants are not suitable for flower market trading or collection, and so it is likely that their massive expansion followed involuntary human pathways. Today, owing to the frequency and abundance of ragweeds in anthropic environments in their native range, it is widely accepted that seeds and/or propagules of plants have been unintentionally transported outside the Americas by human activities along trade routes.

The introduction of *A. artemisiifolia* into different parts of the world has been ascribed to contaminated seed lots of grain, vegetables (e.g. potatoes), seed for forage or oil-seeds (e.g. sunflower (Genton *et al.*, 2005; Chauvel *et al.*, 2006; Smith *et al.*, 2013; Essl *et al.*, 2015) and also in bird food (Brandes and Nitzsche, 2006; Frick *et al.*, 2011), fodder, ship ballasts, and military movements (Kazinczi *et al.*, 2008; Gaudeul *et al.*, 2011). During the 20th century, particularly during the World Wars, *A. artemisiifolia* was introduced into Europe principally through agricultural products from several North American sources. Based on molecular studies, repeated introductions occurred during the invasion in different parts of the new range (Genton *et al.*, 2005; Kiss and Béres, 2006; Gaudeul *et al.*, 2011; Hodgins and Rieseberg, 2011; Smith *et al.*, 2013; Ciappetta *et al.*, 2016).

The seeds of *A. artemisiifolia* were not the only ragweed species to follow such routes. Frick *et al.* (2011) showed that *Ambrosia* sp. seeds, including *A. artemisiifolia* as well as other ragweed species, occur in 21 to 75% of the bird feed products available on the German, Hungarian and Danish markets. For instance, *A. trifida* was introduced by imports of commercial grain and oil-seed, e.g. between North America and European countries, which repeatedly ensured the reinforcement of populations into new areas (Follak *et al.*, 2013). Military movements during World War II were also vectors of introduction for *A. trifida* in several sites in Northern Italy (Ardenghi and Polani, 2016).

The mechanism of introduction into the invasive range of *A. psilostachya* and *A. tenuifolia* was likely the same as those mentioned previously (Makra *et al.*, 2015). Data from Moskalenko (2001) and CABI (2017) revealed that Russia cereals coming from Canada were contaminated by seeds of *A. psilostachya*. Verloove (2016b) ascribed the arrival of *A. psilostachya* in Belgium to the American forces during the First World War and Parsons and Cuthbertson (2001) underlined the contribution of United States military movements during World War II to the spread of *A. psilostachya* in Australia and other parts of the world. These latter assumptions were mainly based on the fact that the species was unknown before the arrival of US troops. On the other hand, *A. tenuifolia,* was mentioned (Nelson, 1917) as a "ballast-plant", a species involuntary transported in solid sailing ballasts (currently replaced by water ballasts) and then released in new countries during the de-ballasting phase. This pathway was inferred by the author after the finding of *A. tenuifolia* and other non-native species in dumping areas near harbours in Oregon; nevertheless, this route is also plausible if past transoceanic travels to Europe are considered (Thellung, 1912). In any case, at present, the pathways of introduction of *A. psilostachya* and *A. tenuifolia* are of less certain than those of *A. artemisiifolia*, given the few studies available. Moreover, considering that the species have different dispersal strategies, additional vectors should be taken into consideration. Specifically, the reproduction strategy of *A. psilostachya* is mainly vegetative and the amount of seeds produced is quite small. Thus, the role of alternative propagules (i.e. rhizomes) and different vectors in the global spread of the *taxon* should be considered in defining reliable pathways of introduction.

C. Global distribution: current status and invasion history

Vectors for the spread of ragweed work in very effective ways. The percentage of countries where the species are native or alien and their status (casual, naturalized or invasive) are shown in Fig. 2. Fig. 2 was developed according to the database reported in Table 2.

At the moment three species out of four (*A. artemisiifolia, A. psilostachya, A. tenuifolia*) are present in every continent and the fourth (*A. trifida*) has colonized all continents except for Africa and Oceania. In its non-native range, *A. artemisiifolia* occurs in eighty countries (including those where its native status is uncertain) and it is classified as invasive in 32% of them. *Ambrosia psilostachya* is alien in almost fourty countries, but, although it is naturalized in at least fourteen countries representing the 36% of its non-native range, only in seven (19%) does it show invasive behaviour. Also *A. trifida* has colonized almost fourty countries, but it is included among invasive plants only in three of these (one doubtful), representing 7% of the total. To date, *A. tenuifolia* appears not to be an invasive *taxon* in its non-native range, consisting of fewer than fifteen countries, but it is naturalized in over half of the range of introduction (64%).

Without considering its cultivation in botanical gardens, which dates back to the 18th century, the first record of *A. artemisiifolia* outside its native range comes from the United Kingdom, where the species was recorded as casual in 1836 (Essl *et al.*, 2015). Then, in 1854, it was found in the Hawaiian Islands (Wagner *et al.*, 1990) and in the same decade it was recorded again in Europe, in Switzerland (Bullock *et al.*, 2012). Later, in 1860 and 1863, it was found respectively in Germany (Brandes and Nitzsche, 2006) and France (Chauvel *et al.*, 2006) (Western Europe). In all these countries the species is still present. The native or alien status of *A. artemisiifolia* is uncertain in many countries in the Americas. Essl *et al.* (2015) asserted that

A. artemisiifolia is surely alien to Argentina, Chile, Brazil, Bahamas and the island of Hispaniola. Villaseñor and Espinosa-Garcia (2004) listed *A. artemisiifolia* among the alien species in Mexico, while for Cuban populations there are clearly uncertainties (Acevedo-Rodrıguez and Strong, 2012). Going back to Europe, from the second half of the 19th century onwards, the species has rapidly spread over all the continent. Records of *A. artemisiifolia* in Northern countries are later than Germany and France: Denmark in 1865 (Bullock *et al.*, 2012) and Sweden in 1866 (Anderberg, 2000a). In Eastern Europe, it appeared in 1873 in Poland (Tokarska-Guzik *et al.*, 2011) and ten years later in the Czech Republic (Bullock *et al.*, 2012). In Southern Europe the first signs of introduction probably occurred 1879 in Croatia (Galzina *et al.*, 2010) and then in Italy (1902; Gentili *et al.*, 2016). Newly colonized countries have continued to be recorded also in recent times (e.g. Greece) (Greuter and Raus, 2008).

Concerning Asia, the first record dates back to 1877 and is from Japan, where *A. artemisiifolia* was found as a casual (naturalization stage was recorded around 1925; https://www.nies.go.jp/biodiversity/invasive/DB/detail/80400e.html), while in China the species was found later (1930s) (Qin *et al.*, 2014). The invasive behaviour of *A. artemisiifolia* was reported by Washitani (2004) as beginning in the 1960s. In Taiwan, South Korea and Turkey, *A. artemisiifolia* was found later in the 1990s, whereas in other Asian countries (e.g. Armenia, Kazakhstan, Iran and India) information about the introduction time is not available.

In other parts of the world, Quézel and Santa (1963) reported the presence of *A. artemisiifolia* in Africa in Algerian flora and Lawlree (1947) asserted that the species was found there later than 1890. The species was recorded in other African countries more recently and, at the moment, it is also naturalized in Egypt (Boulos, 2002). Moreover it appears that the species is expanding toward Southern Africa (Botswana, South Africa, and Swaziland) (Setshogo, 2005; Henderson, 2007; Randall, 2012; Swaziland's Alien Plants Database at: http://www.sntc.org.sz/alienplants/index.asp). Skalova *et al.* (2015) also reported the presence of *A. artemisiifolia* in Madagascar, while Kull *et al.* (2012) mention only *A. maritima* as an introduced and naturalized *taxon* on the island. Finally, in Oceania the species officially appeared in 1908 in Australia, spreading rapidly only after 1940s (Parsons and Cuthbertson, 2001), and in 1911 in New Zealand (Webb *et al.*, 1988).

Europe was the first continent that *A. trifida*, was introduction. It is recorded in the 17th century in botanical gardens (e.g. 1699 in the United Kingdom - see Online Atlas British and Irish Flora http://www.brc.ac.uk/plantatlas/index.php?q=plant/ambrosia-trifida). However, the oldest collection in the wild was reported from Western Europe where *A. trifida* was recorded in Belgium in 1829 and has been found with more continuity from 1896 onwards (Verloove, 2016a). It was later collected in Germany in 1877 (Follack *et al.*, 2013). In Northern Europe, the species was found first in Ireland (1894) and, in 1897, in the United Kingdom (Rich, 1994; Sell and Murrell, 2006), Finland (Lampinen and Lahti, 2016), Switzerland (Follak *et al.*, 2013) and Latvia (Gudzinskas *et al.*, 1993). In Southern Europe, the species was first recorded in South Tyrol in 1899 (Chauvel *et al.*, 2015) and recorded in 1909 in Northwest Italy (Vignolo Lutati, 1935); in other countries it has been found in more recent times (1982 in Serbia and 1983 in Spain) (Amor Morales *et al.*, 2012; Follak *et al.*, 2013). In Eastern Europe *A. trifida* was mentioned much later than in other parts of the continent, starting from 1960 (e.g. Czech Republic) (Pyšek *et al.*, 2012) up to the 1980s and beyond.

In comparison to *A. artemisiifolia*, *A. trifida* appeared later in Asia. In 1935 it was observed in China (Qin *et al.*, 2014), and it was noted in Japan almost twenty years later (1952; Invasive species of Japan: https://www.nies.go.jp/biodiversity/invasive/DB/detail/80410e.html). In other countries in Asia, records have been mostly since 1970 (South Korea) and the following decades (Israel, India). In Central America, *A. trifida* has been introduced into Mexico (Villaseñor and Espinosa-Garcia, 2004). Unlike common ragweed, giant ragweed rarely shows invasive behaviour (e.g. China and Japan) and it is often casual (e.g. Austria and British Isles) (Essl and Rabitsch, 2002; Reynolds, 2002; EPPO, 2016), which suggests that its persistence in some areas is only possible due to repeated introductions (Follak *et al.*, 2013).

Ambrosia psilostachya has a wider invasive range than *A. trifida*, but it is not listed alongside giant and common ragweed as invasive species by EPPO (EPPO, 2016). The species occurs in all continents and is naturalized in a large number of countries, although it is not as aggressive as *A. artemisiifolia* (Table 2). In any case, it should be remembered that *A. psilostachya* has not been as deeply studied and is often confused with *A. artemisiifolia* or other *taxa*. For these reasons, its distribution may be affected by misidentification, and dates of introduction are often uncertain. On the American continent, outside its recognized native range, the position of *A. psilostachya* as an independent *taxon* is discussed (Pruski, 2017). On the Hawaiian Islands it is listed as a quarantine weed (Randall, 2012), while it is reported as both wild and cultivated in Guadeloupe (Hibon, 1942). In Europe, it has been found in the United Kingdom since the 1880s (Rich, 1994), where today it is naturalized. However, it is not as widespread in the UK as it is in Germany, where it appeared a few years later in 1897 (NetPhyD: Deutschlandflora WebGIS). At the beginning of the 20th century, *A. psilostachya* was found in Hungary (Puc, 2004) and then in the Netherlands (1905; Odé and Beringen, 2017b), where according to Van Denderen *et al.* (2010) it is the only well established *taxon*. In Southern Europe, it first appeared in Italy at the end of the 1920s (Vignolo Lutati, 1935). In France, colonization probably dates back to the same time, although this may be influenced by misidentification of the specimens (Hibon, 1942; Queney, 1942). New European records of the species have also been collected recently, since the 1980s for instance in Spain, Finland, Czech Republic and Greece (Anderberg, 2005; Amor Morales *et al.*, 2012; Pyšek *et al.*, 2012; Von Raab Straube and Raus, 2016). Concerning Africa, information about the arrival of the *taxon* is quite fragmented. The oldest date of collection (1916) relates to Algeria (Maire, 1928), although an earlier record by Battandier (1888) discusses the presence of a perennial plant growing on maritime sands "with *Ambrosia* leaves" different from *A. maritima* (the only ragweed identified in other Algerian localities, probably native to the Old World (Montagnani *et al.*, 2017). *Ambrosia psilostachya* has also been alien to Moroccan flora since the 1990s (Tanji, 2005). In

Southern Africa, it is a weed of sugar cane fields in Mauritius (Macdonald *et al.*, 2003) and it is naturalized in different areas (Germishuizen and Meyer, 2003; SANBI, 2015a). In Australia, the plant was found in 1922 (Parsons and Cuthbertson, 2001). Records from Asia are quite recent, from the 1990s in India (Ramachandra Prasad *et al.*, 2013) to 2000 in Taiwan (Tseng and Peng, 2004), and the plant is often naturalized and shows an invasive behaviour in several countries (e.g. Japan and India).

Ambrosia tenuifolia is widespread at global level, but is usually much more localized than the other species outside its native range. Fairly close to its native area, *A. tenuifolia* has been introduced into Louisiana (North America), Puerto Rico and Chile, where it was identified for the first time in 1923 (Ugarte *et al.*, 2011; USDA - NRCS, 2017; Acevedo-Rodrıguez and Strong, 2012). In Europe, according to available data, the oldest record (1839) of *A. tenuifolia* is from France (Thellung, 1912). Successive records date one century later - 1935 in Italy (Vignolo Lutati, 1935) and 1954 in Spain (Amor Morales *et al.*, 2012). According to Randall (2012), *A. tenuifolia* also occurs in the United Kingdom, but there is no bibliographic evidence of this. In Asia, the collections of *A. tenuifolia* are few and quite recent: in Israel in1991 (Waisel *et al.*, 2008) and Turkey in 2000 (Behçet, 2004; Özhatay and Kültür, 2006). In Australia and New Zealand, the presence of the species has been confirmed since 1932 and 1950 (Parsons and Cuthbertson, 2001; Howell and Sawyer, 2006) while in Africa, the species is only present in South Africa (Germishuizen and Meyer, 2003; SANBI, 2015b).

V. Environmental barriers

In this section, the main environmental requirements and plant traits, predictor of the likelihood of persistence of the species in new ranges, are reported and discussed. Slatyer *et al.* (2013) found a positive relationship between niche breadth and range size, suggesting that a wide tolerance to abiotic conditions facilitates occupancy of a larger area, and that habitat breadth is a good predictor of a wide distribution. Environmental matching is important along the naturalization-invasion continuum (Richardson and Pysek, 2012). Such generalist, common-habitat colonizer, species are highly competitive and tolerant to disturbance and have great potential to become invasive (Volta *et al*., 2013). Looking at the global distribution of ragweed species (Fig.1), they have generally found suitable conditions to persist and spread, often becoming naturalised (Fig.2). Thus, overcoming environmental barriers appears to be a solvable issue for ragweed species.

A. Habitat types and environmental matching

Before describing and discussing the habitats elected by the ragweed species in both their native and invasive ranges (Table 3), it is necessary to point out that it is currently quite difficult to define the native habitat of *A. artemisiifolia* with any certainty, because, as already mentioned, its distribution has been human-mediated for such a long time (McAndrews, 1988).

It has been suggested that *A. artemisiifolia* should be native to the Great Plains (Hodgins and Rieseberg 2011; Hodgins *et al.*, 2013). However, both in the United States and in its invasive range *A. artemisiifolia* has rarely been found in natural habitats, such as prairies, while it is abundant and often invasive in ruderal ones (roadside verges, wastelands, railway embankments, construction sites, quarries etc.), at the edge of croplands or in arable fields and also on riverbanks (Bassett and Crompton, 1975; Fumanal *et al.*, 2008a; Milakovic *et al.*, 2014; Essl *et al.*, 2015; Gentili *et al.*, 2016). Consistent with this, floras and specialized sources indicate synantropic environments as the main habitats for common ragweed (Basset and Crompton, 1975; Smith *et al.* 2013).

It is likely that common ragweed has shifted gradually from its primary habitat to ruderal areas and croplands, following the advance of human settlements into unexploited American lands, when synantropic environments became more frequent (Basset and Crompton, 1975; Smith *et al.* 2013). In support of this hypothesis, the analysis of herbarium records by Lavoie *et al.* (2007) showed that in Quebec common ragweed spread along rivers at first, and only later entered agricultural fields.

In the last thirty years in the USA (native range), *A. trifida* has also shown the tendency to colonize cultivated fields (e.g. corn, soybean and cotton), probably as local adaptation of the species that originally lived in riparian (riverbanks, floodplains) or non-riparian edge habitats near cultivated areas or railroads and wastelands (Basset and Crompton, 1982; Regnier *et al.*, 2016). On floodplains, where floods occasionally occur, it does not grow at the lowest elevation but dominates in communities located 60 cm above the water level (Menges and Waller, 1983). Outside of North America, *A. trifida* lives along rivers and generally shares the ruderal behaviour of *A. artemisiifolia*, occurring especially in cultivated fields, along railways (Gudzìnskas, 1993; Chauvel *et al.*, 2015), on maritime docks (e.g. Britain) (Rich, 1994) and fluvial ports (e.g. along Rhine and Elbe rivers in Europe) (Chauvel *et al.*, 2015). Nevertheless, in France, Follak *et al.* (2013) and Chauvel *et al.* (2015) found that *A. trifida* is more often recorded in ruderal places and along railways than in native elective riverine habitats.

Regarding *A. psilostachya* and *A. tenuifolia*, elective habitats are more recognizable than the ragweed species previously described. According to Albertson (1937) *A. psilostachya* "*invades the short grasses from the disturbed places along the slopes*". In its native range in North America, *A. psilostachya* shares ruderal habits with *A. artemisiifolia*, as it is common in open disturbed habitats such as abandoned fields, vacant lots and along transportation corridors (Basset and Crompton, 1975). In contrast to *A. artemisiifolia*, however, it is also common in semi-natural/natural environments: it is a typical forb of tallgrass prairies (temperate grasslands) of the American Great Plains (Reece *et al.*, 2004) and a weed in pastures and rangelands where it is favoured by overgrazing and fire (Baker and Guthery, 1990; Abrams, 1988; Vermeire and Gillen, 2000; Funderburg *et al.*, 2014). It is a sand-loving species and colonizes dry sand prairies on sand hills (Hart and Gleason, 1907; Hulett *et al.*, 1988; Ebinger *et al.*, 2006; Uresk, 2012). It also colonizes coastal dunes, mainly secondary dunes and vegetated flats behind them (Carls *et al.*, 1991) mostly where there is a certain grade of human impact (e.g. vehicle passage) (Stephenson, 1999). It is also listed among halophytic plants living in harsh environments such as inland saline plains (Flores-Olvera *et al.*, 2016) and is referred to as a colonizer of riparian habitats, where it is considered a "mesoriparian plant", i.e. not typical of the wettest areas of riverbeds (Stromberg, 2013). Contrary to the other ragweed species, *A. psilostachya* also lives in the understory of non-dense woodland (e.g. *Pinus ponderosa* forests) (Bojorquez Tapia *et al.*, 1990). There is little information in the literature concerning the habitats of *A. psilostachya* outside of its native range. However, it suggests that this species, as in its native range, frequently colonizes coastal areas, dunes, sandy soils usually exposed to human impacts (Rich, 1994; Mandrioli, 1998; Weeda, 2010; Del Vecchio *et al.*, 2015; Fried *et al.*, 2015), rivers and ruderal habitats (Amor Morales *et al.*, 2012; Ardenghi and Polani, 2016). In a recently colonized area of India, *A. psilostachya* has also been observed in croplands and pastures (Ramachandra Prasad *et al.*, 2013).

As with the congeners examined previously, in South America, *A. tenuifolia* is a plant typical of open habitats and, like *A. psilostachya,* it is native to grasslands traditionally subjected to disturbing factors that in this case are ascribable to grazing and periodic flooding (as the result of heavy rainfall, flat topography and poor drainage). In Argentina, it represents a characterizing element of the flooding Pampa grasslands, as one of the co-dominant taxa of one of the most widespread plant communities of the area (e.g. communities characterized by *Piptochaetium montevidense*, *Ambrosia tenuifolia*, *Eclipta bellidioides* and *Mentha pulegium*) (Burkart *et al.*, 1990; Insausti *et al.*, 1995; Insausti and Grimoldi, 2006). The typical community of *A. tenuifolia* usually lives in raised flat lowlands, less subjected to inundation. However, *A. tenuifolia* can also dominate communities typical of more humid conditions, localized along river valleys, drainage basins, and coastal salty lagoons (Burkart *et al.*, 1990). It is also a characteristic element of coastal dune vegetation (Fontana, 2005; Marcomini and López, 2013). In Argentina, Marcomini *et al.* (2016) found it in stable dune systems, occurring between dunes where the vegetation cover is more relevant and dominated by *Cortadera selloana* (*cortaderal* community). As in the Pampean Plains, these environments are subjected to periodic floods, although they are also subjected to drought (Marcomini *et al.*, 2016). Furthermore, *A. tenuifolia* has been listed in Paraguay as an agricultural weed (De Egea *et al.*, 2016). Outside its native range, specifically Spain, *A. tenuifolia* lives in habitats very similar to those colonized by *A. psilostachya* (Amor Morales *et al.* (2012) and in other European countries the two species can be found in the same sites, for instance sharing an halophytic behaviour (e.g. in some areas of Italy) (Mandrioli *et al.*, 1998). Additional findings in Turkey revealed that *A. tenuifolia* can be also found in orchards and cultivated fields (tomatoes, cucumbers, wheat) and that it could prefer humid ruderal places (Behçet, 2004; Özhatay and Kültür, 2006).

Overall, analysis of the spectrum of colonized environments shows that a limited shift of habitat types between native and invasive ranges can be observed. All species are in fact typical of naturally or artificially disturbed open areas, both in America and in the rest of their acquired range. However, all species are more frequently present in natural environments in their native ranges, likely representing their original habitats. It is difficult to have an idea of the primary environments of *A. artemisiifolia*, whereas *A. trifida* spreads from riparian habitats, and the perennial *A. tenuifolia* and *A. psilostachya* originated from temperate grasslands and colonize inland and coastal sand dunes. On the whole, it is clear that all these species spread gradually from their primary habitat to synanthropic environments. It follows that although the spreading of each of these species requires specific conditions, they are capable of quickly shifting their habitat in changing circumstances and taking advantage of environmental disturbance. Being tolerant to disturbance, these common-habitat colonizer species have a great potentiality as invader. They can be considered pioneer species naturally colonizing harsh environments and ready to spread in ruderal habitats, where conditions are maintained suitable mainly by human action.

B. Climate matching and temperature tolerance

Climate matching is a basic requirement for persistence in a new area. According to their global distribution, all these species come from temperate areas (Fig.1). Although with several exceptions, they mainly "move" from/to warm temperate climate regions, generally avoiding equatorial, arid and snow climates (Fig.1). Petitpierre *et al.* (2012) observed a limited shift of climatic niche between the native and adventive range of *A. artemisiifolia*. Analogously, a limited shift also appears valid for the other ragweed species on the basis of our preliminary and basic comparison (Fig.1). In keeping with these observations, many studies demonstrate the influence of climate on ragweed germination, growth and reproduction. Regarding this, *A. artemisiifolia* has been the most widely studied species. About germination, it has been reported that *A. artemisiifolia* seeds can germinate in a wide range of temperatures; the minimum temperature of germination ranges from 3.4 to 3.6° C (Essl *et al.*, 2015) while germination decreases up to 40°C (Bullock *et al.*, 2012). Nevertheless, Leiblein-Wild *et al.* (2014) observed differences between native and introduced populations: in the invasive range, seeds generally have a larger mass and can germinate faster under a wider range of conditions. The authors attributed this better performance to favourable biotic and abiotic factors occurring in the invasive range and speculated about a possible case of Evolution in Increased Competitive Ability (EICA). In any case, *A. artemisiifolia* seeds follow a quite complicated cycle of primary/secondary dormancy and they need an exposure to winter temperature or stratification in lighting conditions to break primary dormancy (Baskin and Baskin, 1980). In sites where the growing season is too short for seed maturation (e.g. Northern Europe) or seasonal temperatures are too high for vernalization (e.g. some areas of the Mediterranean basin), the species cannot become naturalized and occurs just in few small ephemeral populations (Dahl *et al.*, 1999; Kazinczi *et al.*, 2008; Van Denderen *et al.*, 2010; Makra *et al.*, 2014; Smith *et al.*, 2013).

Seasonal temperature variations also play an important role for *A. trifida* (Davis, 1930; Bazzaz, 1979) and *A. tenuifolia* (Insausti *et al.*, 1995), whose seeds need low temperatures to germinate (primary/secondary dormancy cycle). The range of germination temperatures for *A. trifida* is wide (from 4 to 41°C, with an optimum between 10 to 24°C), but only if soil moisture conditions are suitable (17% to 55% soil moisture, with an optimum at 20 to 30%) (Abul-Fatih and Bazzaz, 1979a; Ballard *et al.*, 1996). For *A. tenuifolia*, the lack of alternating temperatures prevents seed germination (Insausti *et al.*, 1995).

The climatic requirements for *A. psilostachya* are not clear (Basset and Crompton, 1975). Martison *et al.* (2011) identified, among climatic and soil variables, mean annual temperature as the factor that mostly contributes to explaining the distribution of *A. psilostachya* in the United States, whereas in Europe Rasmussen *et al.* (2017) found that minimum temperature to be highly influential. The life cycle of the species in relation to seasonality in its native habitat (e.g. snowing, freezing winter and summer drought), indicates that the seeds of *A. psilostachya* should also be characterized by dormancy and they may need a vernalization phase to germinate (Baskin and Baskin, 2014). Nevertheless, the propagation of *A. psilostachya* is mainly vegetative, so if the root system can survive, environmental limits on germination are less important. According to Rich (1994) and Bassett and Crompton (1975), roots are generally cold-resistant, able to survive in the extremely cold of Canadian winters, and can continue growing the following spring for over 30 years. It has been supposed that independence from germination requirements may allow *A. psilostachya* to colonize those countries where *A. artemisiifolia* cannot successfully conclude its life cycle (e.g. The Netherlands; Van Denderen *et al.*, 2010).

Concerning plant development, data are available mainly for *A. artemisiifolia*. Cunze *et al.* (2013) estimated that it requires an accumulated temperature sum of 1400°C to produce mature seeds. In their report, Bullock *et al.* (2012) found that the maximum photosynthetic rate is at 20°C (halved at 30°C). Nevertheless, they also highlighted that *A. artemisiifolia* persists where the climate is hotter, deducing that high temperatures are likely to have a lesser impact on its performance than low temperatures. Bazzaz (1974) attributed its tolerance to high temperatures to high transpiration rates, which allow a transfer of latent heat in leaves at temperatures below ambient temperature. Frost in late spring or early autumn can be fatal for seedlings and adult plants (Essl *et al.*, 2015), although Leiblein Wild *et al.* (2014) observed that seedlings are more frost tolerant in Europe than in native countries, thus supporting the assumption of local adaptation. In general, Rasmussen *et al.* (2017) recently found that common and giant ragweed perform better in relatively wet conditions, while perennial ragweed in drier ones. Growing degree days are generally cited as the most influential climatic factor explaining the distribution of short - day plants *A. artemisiifolia*, *A. trifida* and *A. psilostachya* in Europe. The main climate requirements of the four ragweed species considered are summarized in Table 3.

C. Moisture and soil types tolerance

Soil is another factor determining the colonization and successful survival of plants. Concerning soil pH, few studies were undertaken and the results are not totally consistent. Fumanal *et al.* (2008a) demonstrated that *A. artemisiifolia* can grow both on acid and alkaline soils (extreme values of pH KCl: 4.1–8.6), even if preferentially occupys sites with a pH range between 7 and 8. Coherntly, Essl *et al.* (2015) reported that *A. artemisiifolia* grows best under moderately basic condition (pH = 8). On the other hand, Pinke *et al.* (2011) found the highest common ragweed cover at the edge of Hungarian sunflower fields when the soil pH was acid (< 5); this in agreement with the information reported in Hungarian literature, namely that this weed thrives best on acidic sandy soils (Ujvárosi, 1973; Szigetvári and Benkő, 2008). Regarding germination, Sang and collaborators (2011) demonstrated that *A. artemisiifolia* germination success exceeded 48% in solutions with pH values between 4 and 12, with maximum rates occurring in distilled water at pH 5.57. However, under laboratory conditions, germination occurs in a wider range of pH (Bullock *et al.*, 2012). Silt loam and silt clay loam soils are elected as the optimum by Basset and Crompton (1975) and, in France, Fumanal *et al.* (2008a) found the plant on sand to clay or silty loam, but mostly on sandy soils. Regarding soil water content, *A. artemisiifolia* can be very resilient to short-term drought (Bullock *et al.*, 2012). Nevertheless, Hodgins and Rieseberg (2011) demonstrated the poor survivorship under drought conditions of the European populations in comparison to the American ones, probably due to the evolution of a life-history that has favoured a more rapid growth and reproduction than drought tolerance in the invasive range. Leiblein and Lösch (2011) observed a major growth of *A. artemisiifolia* in moist soil conditions, but also the capacity to survive in dry, moist and waterlogged soils (5%, 22% and 39% of water). In the latter situation, the plants are far smaller, but able to reach maturity and produce seeds, although in small quantities. In keeping with Essl *et al.* (2015), *A. artemisiifolia* is not typical of wet areas, but its seeds can potentially tolerate and remain viable in soils with high water content. Concerning salinity (Table 3), Di Tommaso (2004) showed that the seeds of *A. artemisiifolia* can also germinate at high levels of sodium chloride (5 to 12% of germinated seed at 400 mmol L^{-1}). However, he highlighted that the percentage of germination in his experiment was negatively correlated to the increase in salt, but the recovery in distilled water of viable non-germinated seeds was rapid. This study also suggested an adaptation of *A. artemisiifolia* to local conditions, as the seeds collected from plants living along roadsides showed a higher percentage of germination than those collected in cultivated fields. Another soil parameter that *A. artemisiifolia* appears to manage quite well is the presence of metals. Bae *et al.* (2016) proved that under metal stresses (Zn, Pb, Ni, Cd, Cu), *A. artemisiifolia* performs better in germination and seedling growth in comparison with native flora. This experiment simulated roadside conditions and delineated a potential empty niche where the species would have almost no competitors.

Information about soil requirements for the other ragweed species is not as exhaustive as for *A. artemisiifolia,* although it is possible to understand several differences by reviewing available data. *Ambrosia trifida* is typical of more mesophytic conditions than *A. artemisiifolia* (Abul-Fatih and Bazzaz, 1979a; Basset and Crompton, 1982), consistent with its native habitat (e.g.

floodplains temporarily including presence of standing water; Menges and Waller, 1983). Wortman *et al.* (2012) and Follak *et al.* (2013) showed how the distribution of *A. trifida* is more closely related to the seasonality of precipitation and summer precipitation than other variables such as land use and landscape structure. Low rainfall is a limiting factor in its native range (Basset and Crompton, 1982); germination occurs in a wide range of soil moisture with an optimum of 20-33% (Abul-Fatih and Bazzaz, 1979a). Nonetheless, Schutte *et al.* (2008a) found that giant ragweed seedling emergence is insensitive to dry conditions of the top layers of soil (1 cm of soil) and that emergence usually occurs during relatively dry periods. Soil texture is not specified, but based on habitat (floodplains, drainage ditches, open stream banks), it can be deduced that *A. trifida* colonizes incoherent soils; in cultivated fields, it is usually found in low silty substratum (Basset and Crompton, 1982). There are no data regarding preferences of soil pH and salinity tolerance, while Cui *et al.* (2007) showed that *A. trifida* can live where the concentration of metals (Pb, Zn, Cu, Cd) is quite high and can be considered a good accumulator at root level.

Concerning *A. psilostachya*, as previously stated, it is a sand-loving species and prefers well drained, alkaline soils (Basset and Crompton, 1975). It lives in soils characterized by high salinity both in the native and invasive ranges, although salt can strongly limit the growth of plants (Salzman, 1985). Salzman and Parker (1985) experimentally demonstrated that the wide root system can balance stress through the connection between ramets; taking advantage of local salinity variations, ramets living in lower salinity conditions contribute to the survival of those living in high salinity conditions. This physiological integration (exchange of resources among connected ramets) helps *A. psilostachya* persist in stressful conditions. It boosts its efficiency of colonization and habitat exploration, thus promoting a greater dispersal ability (through rhizomes) in adverse conditions, to increase the probability of finding favourable microsites (Salzman, 1985). Furthermore, *A. psilostachya* persists even when high concentrations of metals in soil are lethal for other plants (e.g. Zn, Cu, Mn, etc.) (Basset and

Crompton, 1975). The successful survival of *A. psilostachya* in metal-rich soils appears to be positively mediated by mycorrhizal symbiosis (Rivera-Becerril *et al.*, 2013). Habitats colonized by Western ragweed are typically subjected to seasonal drought. It is a xeric adapted species (Corbett and Anderson, 2006), with a very long root able to draw water from deep sources and persist without desiccating at more humid deep soil levels (1.83 m in depth according to Stromberg, 2013). In the grasslands of the Nebraska Sandhills, *A. psilostachya* is relatively stable through drought (and grazing), while other resistant perennial grasses are damaged (Reece *et al.*, 2004; Stubbendieck and Tunnell, 2008). Although severe events leading to a serious desiccation of rhizome (- 60% of weight), can have negative effects on shoot emergence (Karnkowsky, 2001). Regarding tolerance to waterlogged conditions, *A. psilostachya* prefers drained soils, but it lives in the riparian habitat and according to Stromberg (2013) it is a mesoriparian species. Finally, from data by Towne (2000), who monitored the impact of large ungulate carcasses (e.g. bison, cattle and deer) on grassland dynamics, it can be argued that *A. psilostachya* dominates in nutrient-rich soils and easily tolerates high levels of organic compounds.

Information about soil preferences of *A. tenuifoilia* is quite dispersed. It prefers fertile, well aerated (Insausti and Soriano, 1987), not very deep hydro halomorphic soils (Burkart *et al.*, 1990; Anton *et al.*, 2012). Soil water content can be determinant in the life cycle of the plant. *Ambrosia tenuifolia* co-/dominates plant communities frequently exposed to floods of varying intensity and duration, usually brief (1-2 months), of reduced magnitude (water cover does not exceed the depth of 7 cm in spring), with only occasionally prolonged events with heavy impact occurring (water cover 10–30 cm deep for 3–5 months) (Insausti and Grimoldi, 2006). Insausti and Soriano (1987) observed that *A. tenuifolia* frequently grows on anthills, and argued that those sites are suitable as they are not affected by prolonged waterlogged soil conditions and the subsequent anoxia is not tolerated by roots for more than 1-2 months (Insausti and Grimoldi, 2006). On the other hand, seeds can tolerate immersion in water and low temperature even for long periods, without negative effects on dormancy release (Insausti *et al.*, 1995). Resilience to drought has not been specifically investigated but a certain degree of tolerance can be inferred as environments where *A. tenuifolia* lives are involved in periods of drought, both on the Pampean Plains (summer drought) and coastal areas (Marcomini *et al.*, 2016). A summary of the aforementioned soil requirements is shown in Table 3.

D. Light requirements and tolerance

The tolerance to light/shade has been briefly discussed in the description of habitats and the main requirements for ragweed species are reported in Table 3. In general, ragweed species are pioneer plants living in open sunny environments. However, based on habitat preferences, tolerance of moderate shade has been shown for *A. psilostachya*, and Essl *et al.* (2015) affirmed that *A. artemisiifolia* is also medium shade-tolerant. Generally, shade suppresses *A. artemisiifolia* (Bullock *et al.*, 2012) and the lack of adequate light intensity strongly contributes to a progressive decrease in plant performance and recruitment (Gentili *et al.*, 2015; 2017). Conversely, *A. artemisiifolia*, both at mature and seedling stage, is extremely tolerant to high light intensities, which are characteristic of open environments (Bazzaz, 1974). *Ambrosia trifida* is not only tolerant to high light intensities but Menges and Waller (1983) indicated it as a high light specialist or light-loving species. The authors distinguished this species from the low light specialists and light generalist herbs in floodplain communities; the early emergence, development of seedlings and the great growth of plants would indicate that *A. trifida* is strongly projected to light exploitation. However, several studies show that the species is tolerant also to shady conditions likely to occur along both the natural vegetation dynamic and cultivated fields. It appears that *A. trifida* can allocate resources differently, based on light situations (Hartnett *et al.*, 1987; Abul-Fatih *et al.*, 1979; Webster *et al.*, 1994; Jurik, 1991).

Although a multi-factorial process, *A. artemisiifolia* germination is also light-induced. For instance, in this species the secondary dormancy (Baskin and Baskin, 1980; 1985) is induced by the lack of light in combination with low temperature fluctuations, high CO_2 concentration in the soil and hot dry summer periods (Bazzaz, 1979; Essl *et al.*, 2015). Nevertheless, in lab experiments, seeds germinated also in the dark in a range of temperature corresponding to late spring and summer (Bullock *et al.*, 2012; Baskin and Baskin, 1980).

Along with alternating temperatures, light and in particular the R:FR ratio also promotes *A. tenuifolia* seed germination and plant growth, which benefits from vegetation gaps (Insausti *et al.*, 1995; Insausti and Grimoldi, 2006). Concerning germination, the same can probably be said for *A. psilostachya* (CABI, 2017). Conversely, light is not one of the main factors promoting the germination of *A. trifida* seeds (Davis, 1930; Schutte *et al.*, 2012), which are bigger in comparison to those of the other species and have different mechanisms of quiescence release mediated by pericarp and/or embryo-covering structures (Harrison *et al.*, 2007; Schutte *et al.*, 2012).

E. Plant traits involved in resistance and resilience

To support and explain environmental requirements, changes in several plant traits have been highlighted as key strategies in enhancing resistance or resilience to abiotic stresses (e.g. dormancy, rhizome features, early emergence of seedlings, etc.). However, stress can also derive from unfavourable biotic interactions with parasites and predators, as well as from competition with the local plant community. Furthermore, on observing colonized environments, there is a series of potential human-mediated disturbances such as fire, grazing, mowing, agricultural practices and human settlement development. All these factors can affect the reproductive and vegetative fitness of individuals or prevent their persistence through direct suppression or a dramatic change in environmental parameters. Ragweed plant traits involved in stress resistance and resilience are analyzed and discussed below.

1. Resistance

Starting from strategies and traits that enhance the resistance of individuals to natural or human perturbation (intending resistance as the capacity of an individual to resist the displacement of its biomass (Grime, 2001), it is found that morphological adaptations can avoid or limit the effect of several perturbations. Spines, pubescent or sclerophyllous leaves, or incorporation of granular minerals into plant tissues are typical defensive structures against grazing (Hanley *et al.*, 2007). In a xeric habitat, waxy leaves or a particular form of plants (e.g. cushion plants) can prevent desiccation and damage from wind, drought or frost, while other morphological structures can promote the persistence of individuals in flooded and waterlogged riparian areas (Catford and Jansson, 2014).

Ragweed plants (Table 4), do not show any evident morphological adaptation to overcome stressing factors that damage aerial parts. Only perennials (*A. psilostachya*, *A. tenuifolia*) have quite densely short-haired leaves that play a relatively protective role in avoiding desiccation; *A. psilostachya* may assume a prostrate habit that enhances resistance to several stresses. The presence of phytoliths (mineral deposits in epidermal cell walls) in aerial parts has been reported for *A. psilostachya* and *A. trifida* (Bozarth, 1992) and this increases resistance to leaf-eating invertebrates (Hanley *et al.*, 2007).

Rather than morphological adaptations, chemical protections, such as leaf-coating resins, are important in ragweeds: *Ambrosia* species characteristically possess glandular trichomes, especially on the lower leaf surfaces but also on stems, thus producing resinous excreta rich in secondary metabolites such as sesquiterpenes and flavonoids (Mitchell *et al.*, 1971; Wollenweber *et al.* 1987; 1995). In general, like many other Asteraceae (Heinrich *et al.*, 1998), *Ambrosia* species can biosynthesize many types of secondary metabolites (Hodgins *et al.*, 2013; Wan *et al.*, 2002; Wang *et al.*, 2005; Kong, 2010; Sülsen *et al.*, 2008, 2013) that contribute to protecting plants from abiotic and biotic perturbations (Table 4) Parts of plants and seeds can be included in the diet of several wild mammals, birds and insects, and due to secondary metabolites ragweed species are unpalatable for cattle that only resort to eating the plants when there is no alternative forage (Marten and Andersen, 1975; Reece *et al.,* 2004; Bullock *et al.*, 2012). It is worth noting that many authors (Gerber *et al.* 2011; Essl *et al.*, 2015; Goeden and Ricker, 1976) have pointed out that *Ambrosia* species are attacked by specialized parasites that affect their life cycles in their native range, rather than in their invasive range where the parasites are less specialized and the damage inflicted is often not relevant.

The allelopathic effects of ragweeds on other plants are also well documented (Table 4). Root exudates, leaf leachate and decaying leaves produce allochemical compounds that inhibit germination and growth of other species, both in natural and agricultural environments. Most studies relate to *A. artemisiifolia* (Rice, 1965; Bullock *et al.*, 2012; Vidotto *et al.*, 2013) and *A. trifida* (Wang *et al.*, 2005; Kong *et al.*, 2007), which have been taken into account as a potential bioherbicide (Kong, 2010; Molinaro *et al.*, 2016). However, allelopathy is known also for *A. psilostachya* (Neill and Rice, 1971; Dalrymple and Rogers, 1983) and *A. tenuifolia* (Mongelli *et al.*, 1997).

Another important factor involved in resistance of ragweed species to stress and disturbance is the presence of mycorrhizal fungi (Table 4). Mycorrhiza improve plant growth and health by enhancing mineral nutrition and increasing tolerance to abiotic and biotic stresses (Lenoir *et al.,* 2016). *Ambrosia artemisiifolia* is considered in obligatory symbiosis with mychorrizal fungi (arbuscular mychorrizal fungi, AMF) and studies have demonstrated that fungal colonization is positively correlated to environment disturbance (Essl *et al.,* 2015). Similarly, *A. psilostachya* has also been found associated with mycorrhizal fungi in disturbed and polluted environments (Busby *et al.*, 2011; Pendleton and Smith, 1983; Rivera-Becerril *et al.,* 2013). For *A. trifida*, evidence of root colonization by mycorrhizal fungi are few (MacDougall and Glasgow, 1929; Bassett and Crompton, 1982) and no data are available for *A. tenuifolia*. Both the species live naturally in environments subjected to seasonal flooding and wet areas are not suitable to mycorrhizal colonization, probably due to the lack of well-aerated soils (Entry *et al.*, 2002; Escudero and Mendoza, 2005).

The re-allocation of resources is considered a further important mechanism allowing ragweed plants to tolerate and respond to environmental stresses (Table 4). For instance, *A. trifida* allocates resources differently as a reaction to light variations (see above). Following defoliation due to herbivory attacks, *A. artemisiifolia* can efficiently re-allocate resources from root to shoot biomass and avoid evident costs for fitness (Gard *et al.*, 2013); it can also enhance ramification when the stem apex has been removed (Brandes and Nitzsche, 2006).

Interestingly, when environmental stress is lower or absent, as can occur in introduced ranges, alien plants can reallocate resources and thereby improve their growth and competitive ability. This is at the foundation of the Evolution of Increased Competitive Ability hypothesis (EICA) which has been associated with *A. artemisiifolia* in relation to changes in climate (Leiblein‑Wild *et al.*, 2014), environmental conditions (Hodgins and Rieseberg, 2011) and parasites (Fukano and Yahara, 2012). Nevertheless, further studies have demonstrated that the hypothesis is not always valid for *A. artemisiifolia* (Genton *et al.*, 2005; MacKay and Kotanen, 2008).

2. Resilience

Traits and strategies related to resilience ensure rapid recovery from disturbance and stress and a return to control levels (Grime, 2001). In the case of highly disruptive natural and human-related perturbations, species need to rely on a series of regenerative strategies to have a speedy and complete return to the earlier status. Attributing traits and strategies of plants to resistance or resilience can often be tricky, and this paragraph focuses on the main strategies involved in recovery from severe events that definitely lead to suppression of individuals or their aerial part in the case of geophytes.

Resprouting capacity (a resistance/resilience trait) can be considered one of the main functional traits related to successfully overcoming fire, mowing, intensive grazing and some severe atmospheric events leading to suppression of the aerial parts of plants (Table 4; Keeley *et al.*, 2011). *Ambrosia psilostachya* and *A. tenuifolia* live on plains traditionally subjected to these types of severe perturbations and are not highly affected by them (Wolfe, 1973; Menghi *et al.*, 1993; Hartnett *et al.*, 1996; Madanes *et al.*, 2007); on the contrary, they are often favoured and thus show their weediness (Abrams, 1988; Hartnett *et al.*, 1996; Vermeire and Gillen, 2000; Vermeire *et al.*, 2005; Insausti and Grimoldi, 2006). This is related to their rhizome, a "resistance" structure that confers resilience on these species. As already underlined, the life strategy of *A. psilostachya* is mainly based on its belowground system which allows it to overcome adverse moments and unpredictability deriving from human action or climate: through the rhizome, *A. psilostachya* can form clones of plants occupying areas larger than 100 m^2 (Karnkowski, 2001). In suitable situations, the presence of the weed can be very massive: 1132 kg ha^{-1} dry weight according to Bovey *et al.* (1966). It has been estimated that the establishment of a "competitive" root system takes one year; after the emergence of a seedling from one of the few mature seeds, a shoot emerges from the root during the second year and in only one season it can colonize an area of 2 m^2 (Basset and Crompton, 1975; Mitich, 1996). Reece *et al.* (2004) demonstrated that *A. psilostachya* can maintain primordia for several years even with limited plant growth, and Wan *et al.* (2002) showed that clipping stimulates the growth of new stems. Limits to rhizome viability/resprouting derive from several climatic conditions and burial depth (Miziniak and Praczyk, 2002). Several authors affirm that sprouting from buds is possible when soil thickness is up to 5 cm (Miziniak and Praczyk, 2002; Vermeire *et al.*, 2005). In comparison to *A. psilostachya*, the life strategy of *A. tenuifolia* is based not only on rhizome sprouting, but also on seeds as explained below. Although fewer investigations have been carried out on the *A. tenuifolia* rhizome, it is clear that resprouting from belowground buds permits the recolonization of vegetation gaps after disturbance (Insausti and Grimoldi, 2006), thus ensuring the persistence of the species (Semmartin *et al.*, 2010). *Ambrosia tenuifolia* is a highly productive species, 1,330 g m^{-2} of total biomass according to Semmartin *et al.*, (2010) and it can advance quite rapidly thanks to rhizomes, with an estimated rate of 1.72- 0.2 m^2/month (Insausti and Grimoldi, 2006). As already mentioned, rhizome persistence in this species is limited by anaerobiotic condition. Resprouting is also important for *A. artemisiifolia* resilience: removal of stem, as can occur in the mowing or grazing regime, induces the resprouting of plants from buds at the base (Brandes and Nitzsche, 2006; Patracchini *et al.*, 2011; Milakovic and Karrer, 2016). By contrast, resprouting capacity has never been reported for *A. trifida* species.

In addition to their reproductive capacity, seeds also play a crucial role as "survival structures" deputized to respond to environmental unpredictability and adversity and so confer resilience to species. Through dispersal, seeds can allow the species to strategically escape from unsuitable conditions. Moreover, seed dormancy leads to a "delayed germination" that prevents the germination of fresh seeds when the environmental parameters are unsuitable and promotes the establishment of a soil seed bank (Finch-Savage and Leubner-Metzger, 2006; Gioria *et al.*, 2016), which buffer plant populations against environmental variability and increase the time of (local) extinction (Thompson, 2000).

Apart from *A. psilostachya*, ragweed species produce large amounts of seeds, which establishes conspicuous soil seed banks (Table 3). For instance, the density of seeds of *A. artemisiifolia* ranged from 4.5 to 536 units per m^2 in the upper 20 cm of soil depending on the habitat type (Fumanal *et al.*, 2008b). As seeds can remain viable in the soil for decades, even more than 40 years (Toole and Browne, 1946), they can be considered as forming long-lasting soil seed banks. However, it must be taken into account that burial depth is crucial for the viability of seeds, decreasing to 4 years on the soil surface (Essl *et al.*, 2015). Experiments and observations have been conducted at a depth between 0 and 25 cm, which is considered the living seed bank limit (Fumanal *et al.*, 2008b; Essl *et al.*, 2015; Karrer *et al.*, 2016). Fumanal *et al.* (2008b) recorded a lower viability of seeds between 0-5 cm than at 5-15 cm. Karrer *et al.* (2016) confirmed that the deep soil condition (down to 25 cm) is more suitable for lengthening seed viability, but differences between seeds buried at 5 and 25 cm are not so pronounced as in the study by Fumanal *et al.* (2008b). The authors also speculated that viability is more influenced by seed origin and habitat than burial depth. In any case, beyond viability, germination of seeds is strongly influenced by burial depth: if seed germination is quite high on the soil surface, it decreases with increasing depth (below 8 cm), where parameters dramatically change and dormancy cannot be interrupted (Essl *et al.*, 2015). Guillemin and Chauvel (2011) observed a decrease in germination for seeds buried from 2 to 8 cm and null germination between 10 and 12 cm of depth. It is likely that with the decrease of soil depth most seeds tend to germinate and leave a greater amount of non-viable seeds in the upper soil. Moreover, seed mass also appears to influence the percentage of germination, and the lightest seeds are more sensitive to burial (Guillemin and Chauvel 2011). On the other hand, the time of germination is also important as demonstrated by Ortmans *et al.* (2016) who showed that *A. artemisiifolia* seed traits have a minimal effect, while foliage cover and aboveground biomass are more relevant.

Burial depth also has a determinant effect on seed germination and seedling emergency for *A. trifida*; germination decreases with depth after the first winter burial period (vernalization) (Harrison *et al.*, 2007). According to Harrison *et al.* (2007), the lowest depth from which giant ragweed can emerge is probably between 16 and 20 cm and no seedling emerges beyond 20 cm of depth. Soil seed bank viability in *A. trifida* is lower than that observed for *A. artemisiifolia*, as the total percentage of germination strongly decreases after 4 years (Harrison *et al.*, 2007), and the combination of low viability and high post-dispersal predation of seeds leads to a limited effectiveness of soil seed banks in this species (Harrison *et al.*, 2001, 2003). In any case, in suitable conditions, *A. trifida* enriches its soil seed bank by repeated dispersal of seeds year after year. Moreover, this species produces polymorphic seeds and, in contrast to *A. artemisiifolia*, their size is relevant for their persistence in soil. Even with some exceptions, small seeds appear to be viable for a longer than larger ones (Schutte; 2008b). Nevertheless, the likelihood of the emergence of seedlings from large seeds is higher at 5 and 10 cm of soil depth (Harrison *et al.*, 2007).

A viable soil seed bank also allows *A. tenuifolia* to be more resilient to critical phases such as floods. As reported above, the root system of this perennial species does not survive in anaerobic conditions due to prolonged water coverage, while seeds remain viable. According to Insausti and Grimoldi (2006), seeds are released in large quantities and they can remain viable for several years in soil seed banks. Unfortunately, information such as germination percentage and critical depth are not available for this species.

Seed production of *A. psilostachya* is very low and, in some studies, the species was even classified as a non-seeded forb (Table 4; Grygiel *et al.*, 2012). Moreover, studies performed in tallgrass prairies and coastal areas showed no seed of this species in the soil seed bank (McNicoll and Augspurger, 2010; Barton *et al.*, 2016). Nevertheless, from samples of soils collected in North American mixed prairies and then stored in artificial conditions, Lippert and Hopkins (1950) observed emergence of seedlings of *A. psilostachya* but in very low numbers. Information about seed viability is very scarce but is likely to be around 3-5 years, independent of persistence in the soil (Barton *et al.*, 2016). Thus, resilience strategies in *A. psilostachya* do not include soil seed banks, but the rhizome is likely to be the target organ in overcoming stressful conditions and disturbances.

F. Competition with local plant communities

From previous sections, it is clear that ragweed species colonize habitats quite far from *equilibrium*, characterized by the influence of several stresses and disturbances. They also occur in "stable" situations, but usually when the *equilibrium* is determined and "arrested" by particular conditions, such as a high concentration of salt or metal in soil. Essl *et al.* (2015)

underlined that germination and early seedling establishment are mostly related to disturbance and lack of competition from local communities. This would explain the rarity of plants in natural habitats. As pioneer species, their life strategies are shaped to harsh situations mostly in early successional stages of vegetation. Accordingly, almost all biological and functional traits of ragweeds can be related to these low evolved environments. For instance, the need of light intensity to break seed dormancy and the need for rather shallow and compact soils, suitable to the growth of seedlings from soil seed banks and resprouting from rhizomes, are all requirements related to poorly evolved or disturbed vegetation. The main characteristics of the four-ragweed species, related to their ability in competing with local plants, are compared in Table 4.

Considering *A. artemisiifolia*, environmental conditions are only suitable for its growth when human action or natural events influence the natural evolution of vegetation by removing competitors or operating on soil components (agricultural practices, excavations, floods, etc.). Gentili *et al.* (2015) demonstrated that the plant is a weak competitor in evolved stages of vegetation. These authors showed that germination and recruitment, as well as plant growth, are mainly inhibited by the presence of perennial and/or winter annual grassland species characteristic of more advanced stages (Gentili *et al.* 2015). In keeping with this, Fenesi *et al.* (2014) reported that in a competitive regime, *A. artemisiifolia* seed germination is delayed and seedling development is restrained by the presence of heterospecific neighbours (e.g. *Erigeron* spp.). They reported that on average the cost in *A. artemisiifolia* biomass associated with only a 3-day emergence delay is very high (-97%).

In contrast to *A. artemisiifolia*, *A. trifida* is usually a good and vigorous competitor. Its life strategies are mostly based on very rapid and relevant growth: early germination, followed by very rapid growth, allows the plant to reach a height and biomass superior to other plants. Accordingly, the growth of later-growing plants is strongly inhibited by the canopy shadow determined by its large leaves (Abul-Fatih and Bazzaz (1979b). Therefore, once giant ragweed finds good conditions in which to persist, it inhibits species diversity, biomass and density of the local community. In its native community, *A. trifida* is in fact a dominant species, one that strongly inhibits the colonization and growth of other annual plants (Abul-Fatih and Bazzaz, 1979b). Early emergence also ensures a timely capitalization of resources that avoid the competition of dominant perennials as well (Hartnett *et al.*, 1987; Schutte *et al.*, 2012). As *A. trifida* is one of the most problematic crop weeds in the United States, its impact on other plants is extremely evident as shown also by the analysis of crop yield losses (Regnier *et al.*, 2016). Interestingly, in agricultural environments, but not in rarely disturbed natural successional areas, *A. trifida* has been reported as being able to modulate its emergence time to adapt to different, "scheduled" selective pressures (Hartnett *et al.*, 1987; Schutte *et al.*, 2012; Regnier *et al.* 2016). In general, environmental or human-mediated disturbance must surely contribute to *A. trifida* persistence but, contrary to *A. artemisiifolia*, it does not disappear when the natural vegetation dynamic evolves and perennials become dominant. Hartnett *et al.* (1987) reported that *A. trifida* can persist for years, even penetrating dense vegetation.

Similarly, perennial ragweed species, being pioneer plants, take advantage from vegetation gaps and also persist in more evolved environments when suitable conditions are maintained. Nevertheless, unlike *A. trifida*, *A. psilostachya* is not a superior competitor of grasses under "normal circumstances", and is in fact present in undisturbed, healthy pastures, but in low quantities (Vermeire *et al.*, 2005). Vermeire and Gillen (2000) demonstrated that its abundance does not affect the presence of other grasses in mixed prairies, and there is a positive correlation between them. However, they speculate that Western ragweed is less abundant where there are grasses with roots forming a dense mat in the upper soil level; in this way the vegetative propagation of the plant is inhibited, as upper soil roots compete with the quite superficial creeping rhizome of *A. psilostachya*. Thus, the species only endures competition with some plants. This is inferred by observing its allopathic effect, which only negatively affects some species.

Again, *A. tenuifolia* takes advantage of gaps in vegetation covers (caused by floods, grazing, etc.) which make light, nutrients and water more available for seed germination and recruitment (Insausti *et al.*, 1995; Insausti and Grimoldi, 2006). As a result, this species is a good competitor in poorly evolved environments, although it usually persists in the following stage of vegetation succession where it can become co-dominant (see above). After disturbance, gaps constitute focal points where recolonization of the grassland by *A. tenuifolia* originates from seedlings, which initially have a slow growth phase. It then grows rapidly and continues outside the original gaps by lateral clonal expansion, thus allowing the species to occupy new areas. In any case, independent of the starting population's abundance, the species multiplies many times the surface of colonization in the quite short time of about 4 months (Insausti and Grimoldi, 2006).

VI. Reproductive and dispersal barriers

Survival without reproduction reduces an exotic species to a casual alien *taxon* as it cannot reach the naturalization phase (Blackburn *et al.*, 2011). In this section, reproductive and dispersal strategies (also human-mediated) of ragweed species are analysed. Dependence on specialized pollinators or particular requirements within reproduction phases (e.g. obligatory outcrossing) are often indicated as traits that prevent the establishment of plants in new ranges (Van Kleunen *et al.*, 2015). In general, when a species does not encounter unfavourable factors that strongly limit reproduction, the road to establishment is much less difficult. As already seen, the life cycle of ragweed species includes a series of adaptations useful in avoiding adversity. However, the chance of easily shifting its range through reproductive structure dispersal can be a positive trait determinant in facing unpredictability and escaping unfavourable conditions (Estrada *et al.*, 2016).

A. Pollination

In ragweed species, flowers are organized in heads containing either male or female flowers. The pollen-producing male raceme grows at the tips of the principal stem and lateral branches; seed producing female heads containing one or a few pistillate flowers are sessile and situated in the axils of the leaves immediately below the staminate spikes (Smith *et al.*, 2013). According to Smith *et al.* (2013), within the Asteraceae family, ragweeds possess a strongly modified inflorescence, highly adapted to wind pollination (Table 5). As highlighted by Franz Essl and coauthors (2015), *A. artemisiifolia* is strongly self-incompatible and has high outcrossing rates, both in its invasive and native ranges. This may limit its reproductive efficiency, but due to the large production of airborne pollen, genetic flux is also maintained between distant or isolated populations. Unfortunately, there is no information about the other ragweed species concerning this.

B. Seed and propagule pressure

In the literature, the term "seed" usually indicates the whole diaspore unit of ragweed, which is a one-seeded cypsela for the species considered. The characteristics of ragweed seeds are shown in Table 5. It can be observed that *A. trifida* produces the largest seeds (more than 6 mm long) with a consistent outer coat (Bassett and Crompton, 1982). The other ragweed species produce smaller seeds: seeds of *A. tenuifolia* are slightly larger, 3-5 mm long (Parsons and Cuthbertson, 2001; Behçet, 2004), than those of *A. artemisiifolia* (~3.5 mm long) (Bassett and Crompton, 1975) and *A. psilostachya* (3-4.5 mm long) (Table 5) (Barton *et al.*, 2016).

Propagule pressure of common ragweed can be very high because the species produces between 3,000 and 100,000 seeds per plant, depending on the size of individuals and thus on growth conditions (Dickerson and Sweet, 1971; Bassett and Crompton, 1975; https://gd.eppo.int/reporting/article-3032; Fumanal *et al.*, 2007). Seed production is also quite noteworthy for giant ragweed and varies between a few hundred and 5000 ca. units per plant, depending on plant density and environmental conditions (Abul-Fatih and Bazzaz, 1979a; Baysinger and Sims, 1991; Harrison *et al.*, 2001; MacDonald and Kotanen, 2010). Nevertheless, unlike *A. artemisiifolia*, the potential dissemination of this species in its native range can be strongly reduced by a relevant post-dispersal predation by rodents and invertebrates (Harrison *et al.*, 2003; Regnier *et al.*, 2008). Moreover, the viability of its seeds is not very high, 50 - 66% (Goplen *et al.*, 2016; Harrison *et al.*, 2001).

In contrast to common and giant ragweed which, being annual species, have seeds as their main dispersal units, Western and slender ragweed are perennial and show additional dispersal structures. Wagner and Beals (1958) observed that only 66 out of 118 flowering heads developed to maturity in one plant and speculated that the reproductive potential by seeds of *A. psilostachya* is six times less than that of *A. artemisiifolia*. Similarly, Basset and Crompton (1975) showed that *A. psilostachya* produces just one seed per flowering head, thus indicating that vegetative reproduction is predominant for the species. In agreement with this, the main dispersal structure of the species is its highly vigorous creeping root system, capable of sprouting from pieces of rhizome, which make this ragweed species an even harder weed to fight than common ragweed (Table 5). Vegetative reproduction through rhizomes is also relevant for *A. tenuifolia*, even though it produces a large number of seeds (Table 5; Insausti and Grimoldi, 2006). Indeed, in this species both these strategies are important for its success in different stages of its life, as they react to dramatic environmental events, such as floods that are frequent on the Pampean Plains or human pressures such as agriculture and grazing (Insausti and Soriano, 1987; Insausti *et al.*, 1995; Insausti and Grimoldi, 2006; Soriano, 1982). As already discussed in previous sections, the rhizome of *A. tenuifolia* is less resistant to extreme conditions (i.e. anoxia due to floods) than seeds that showed a longer viability (Insausti and Grimoldi, 2006). Furthermore, there is no evidence of enemies in the native range that affect the persistence and productivity of this plant, given its toxicity or unpalatability to cattle and the low dietary interest for other vertebrates such as rodents (Freire *et al.*, 2005; Semmartin, 2010; Ellis *et al.*, 1998).

C. Dispersal

Regarding ways of dispersal relevant to local movements (medium-short-range dispersal in native and invasion range), ragweed seeds show no morphological structure strictly representing a specific dispersal vector. According to Basset and Crompton (1975), the primary way of dispersal of *Ambrosia artemisiifolia* seeds is barochory. Anemochory is often cited as a potential dispersal vector, but owing to the absence of suitable structures and the weight of seeds, wind may represent only a "facilitator" of spread rather than a driver of diffusion (Table 5; Bullock *et al.*, 2012). Zoochory and hydrochory (Table 5) were considered by Essl *et al.* (2015), who reviewed all vectors contributing to *A. artemisiifolia* diffusion. Regarding the first, epizoochory by bison was proven in the native range of common ragweed, and endozoochory was also reported as an additional plausible mechanism of dispersion (Rosas *et al.*, 2008; Bullock *et al.*, 2012). Viable seeds of common ragweed resulting from feed intake have been found in cattle manure both in the United States and Europe (Pleasant and Schlather, 1994; Vitalos and Karrer, 2008). In addition, Wright, (1941) and Vitalos and Karrer (2008) proved that seeds are part of the diet of some birds (e.g. sparrows, pheasants, and quails), and Essl *et al.* (2015) reported that these vectors, along with rodents, play a role in dispersal. Hydrochory (intended both as streams, flowing water, and as runoff), has been indicated as a way of dispersal in the native range of the species (Table 5; Payne, 1970). Recently, Fumanal *et al.* (2007) underlined how the polymorphism of seeds of *A. artemisiifolia* contributes to dispersal by flowing water and indicated this mechanism as fundamental in the spread of the *taxon* within France, and also as a long-distance means of diffusion.

Compared to *A. artemisiifolia* and the other ragweed species considered, *A. trifida* produces the largest seeds, reaching almost 1 cm in length (Bassett and Crompton, 1982). Seed size and weight point to barochory as the main way of dispersal also for this species (Table 5).

However, Osawa *et al.* (2013) indicated hydrochory and zoochory as additional important mechanisms for *A. trifida* diffusion, mainly supporting the former in accordance with the shape and size of the seeds. Yoshikawa *et al.* (2013) demonstrated that owing to its weight, a giant ragweed seed transported by a stream settles quite rapidly when the current velocity decreases, thus suggesting that these seeds are transported by water flow rather than floating. Concerning zoochory, although giant ragweed seeds have a quite developed crown of large spines, their size and weight represent a limiting factor for epizoochory. Hejný and Jelík (1972) mentioned the presence of *A. trifida* seeds in wool scraps, but as an exceptional circumstance in the former Czechoslovakia. In addition, Verloove (2016a) reported that it is rarely seen as a wool alien in Belgium and Pyšek (2005) excludes the possibility that *A. trifida* dispersal could be associated to wool processing in Czech Republic. As already mentioned, owing to their palatability, rodents and invertebrates eat seeds (Harrison *et al.*, 2003; 2007), but if they cached instead of being immediately eaten then post-dispersal predation allows an estrangement of viable seeds from the mother plant. An association between *A. trifida* and earthworms has only very recently been observed: in the native range of *A. trifida*, non-native earthworms (*Lumbricus terrestris*) cache its seeds in burrows. Beyond the benefits for the plants (reduction of fast seed predation), giant ragweed appears to increase dispersal opportunities through this acquired form of diplochory (Regnier *et al.*, 2008, 2016; Schutte *et al.*, 2010). However, it allows a very short-range translocation, probably less than one meter from the mother plant, considering the homing capability and movements of earthworms (Nuutinen and Butt, 2005).

Little information is available regarding *A. psilostachya*. However, considering that its seeds are slightly larger than those of *A. artemisiifolia* (Basset and Crompton, 1975), it is likely that this species also mainly disperses through barochory (Table 5). Moreover, the crown of rudimental spines is less developed or even absent in Western ragweed seeds compared to those of common ragweed, which suggests that epizoochory is probably not as important a dispersal mechanism in this species (Wagner and Beals, 1958). However, Amor Morales *et al.* (2012)

and Parsons and Cuthbertson (2001) cited epizoochory for *A. psilostachya* seed dispersal in Spain and Australia, respectively. Finally, although the species is not highly palatable to cattle or bison, endozoochory was also inferred by Rosas *et al.* (2008), who found a percentage of *Ambrosia* spp. seeds in dung of bison grazing in prairies where *A. psilostachya* was a common forb. In any case, although studies about the role of Western ragweed seed intake in bird diets have been published (Campbell-Kissock *et al.*, 1985), clear evidence of seed dispersal by animals is yet to be collected, as well as other means of diffusion. For instance, CABI (2017) reported that in springtime *A. psilostachya* seed can be "transferred by water in ditches, canals and rivers" (hydrochory). Moreover, as discussed above, seeds are probably not the main dispersal unit of Western ragweed, owing to their paucity, but the role of rhizome fragmentation is yet to be investigated.

Like *A. psilostachya*, *A. tenuifolia* is a perennial, but its life strategy is not mainly based on vegetative propagation and seed production is not low, although data on the precise quantity are not available. No real evidence for epizoochory is present in literature, but several sources stress the evidence that seeds are caught on sheep wool (http://www.environment.gov.au/cgi-bin/biodiversity/invasive/weeds/weeddetails.pl?taxon_id=17510#). Available studies suggest that seeds can be dispersed by water flow without losing their viability (Insausti and Soriano, 1982; Insausti *et al.*, 2006).

D. Human-mediated dispersal pathways (medium- and long-distance vectors)

Trade routes and all connected elements, previously discussed as important pathways of introduction and global diffusion, are relevant for short- and medium-range movements (Table 5; Ferus *et al.*, 2015). Nevertheless, on a regional scale, further important vectors of spread linked to human activity stand out: movement of soils, spread of seeds through mowing or agricultural machinery and car and train passage (Table 5). All these vectors are associated with the spread of *A. artemisiifolia* particularly within the European area as extensively reviewed by

Bullock *et al.* (2012) and Essl *et al.* (2015). The presence of common ragweed in a new area, after the setup of a construction site, can easily be attributed to the transport and dumping of contaminated soils from different sites. Moreover, the abundance of common ragweed along railways and road networks indicates transportation corridors as one of the main drivers of introduction. The importance of which is even more stressed by the explanatory power of this variable in spatial distribution models and other studies (e.g. Dullinger *et al.*, 2009 and Joly *et al.*, 2011). However, few experimental data about the dispersion mechanism of propagules are available. Two studies (Vitalos and Karrer, 2009; Von der Lippe *et al.*, 2013) tested the effect of vehicles on dispersion of seeds and both demonstrated that the sole car slipstream or seed attachment cannot completely explain a long-distance dispersal. Even the action of mowing machines along roads, which strongly boosts the process, does not fully explain the distance of dispersal (Vitalos and Karrer, 2009). As a result, the spread of *A. artemisiifolia* along corridors of transportation appears to be a multifactorial phenomenon not yet completely understood. Regarding the impact of agricultural machinery, it is effective at the local and more extended level. Karrer (2014) demonstrated that harvesters and other machines can transport several thousands of viable seeds, colonizing new fields or reinforcing already present metapopulations of common ragweed. Contaminated machines from already colonized French regions are even thought to be responsible for the introduction of *A. artemisiifolia* into some virgin Swiss areas (Buttenschøn *et al.*, 2010).

All these vectors may also be relevant for the other species of ragweeds, and especially for *A. tenuifolia* and *A. psilostachya* as light-seed producers (Table 5). Conversely, *A. trifida* produces large seeds and may exploit these vectors less (Table 5). The transport of viable rhizomes through soil movements may also be an effective vector for the diffusion of *A. psilostachya*, but unfortunately, no evidence for this is available.

VII. Allergenic impact and environment

The *Ambrosia* genus represents a global risk to public health owing to the allergic reactions induced by pollen allergens in atopic subjects. In Europe, ragweed pollen affects more than 36 million people each year and the prevalence of sensitization is growing mainly due to the plant's spread (Mihajlovic, 2015; Bordas-Le Floch *et al.*, 2015). Among all ragweed species, pollen of *A. artemisiifolia*, *A. psilostachya* and *A. trifida* have long been acknowledged as a significant cause of allergic disease (Ziska *et al.*, 2011). Similarly, *A. tenuifolia* is reported to be severely allergenic in its native range and produces a huge amount of pollen (Giscafre and Ragonese, 1942; Vaz Ferreira, 1946; Tejera and Beri, 2005; Del Vitto *et al.*, 2015; pollenlibrary.com). However, more specific and up-to-date medical evidence needs to be collected to better define the allergenic impact of this species (Tejera and Beri, 2005; Marco and Pirovani, 2009).

A. Pollen characteristics related to allergy

The major source of allergenic proteins in ragweed plants is pollen. Ragweed pollen grains are small particles containing air chambers between the layers of the outer wall. These characteristics allow them to become easily airborne under favourable conditions and transported by wind for very long distances at a continental scale, even reaching areas not colonized by *Ambrosia* spp. plants (Smith et al, 2013; Mahmoudi, 2016; Šikoparija *et al.*, 2013). It is striking that these pollen grains maintain their allergenic power over such a long distances, even after spending days in the atmosphere (Makra *et al.*, 2016; Grewling *et al.*, 2016). This means that exposed individuals may become sensitized to ragweed pollen allergens and develop symptoms even in areas where the plant is not widely distributed (Grewling *et al.*, 2016). Furthermore, sub-pollen particles (SPPs) of respirable size (0.5 to 4.5 μm) contain allergens that can be released by *A. artemisiifolia* pollen after hydration (i.e. after thunderstorms). These particles, along with pollen fragments, can also be transported for long distances, thus contributing to allergen exposure even when no airborne pollen grains are identifiable. This generates out-of season pollinosis in highly ragweed-sensitive subjects (Table 6) (Busse *et al.*, 1972; Bacsi *et al.*, 2006; Pazmandi *et al.*, 2012).

The species' morphological characteristics are similar (Table 6) and identifying pollen grains to a single species by optical microscopy is not usually feasible. A few authors have investigated the pollen structure of ragweed species other than *A. artemisiifolia*. They show that *A. psilostachya* pollen grains are likely to be larger than the other species (Table 6) (Jacobson and Morris, 1976; Robbins *et al.*, 1979; Wan *et al.*, 2002) and that *A. artemisiifolia* pollen is distinguishable from that of *A. trifida* through the analysis of exine characters. Specifically, Bassett and Crompton (1982) reported that *A. trifida* has 60-65 spines on one-half of the grain surface, whereas *A. artemisiifolia* has 70-75 spines. No distinctive traits are reported for *A. tenuifolia* pollen.

B. Pollen Allergens

The allergens of the four ragweed species officially recorded by the International Union of Immunological Societies (IUIS) are shown in Table 7. The pectate lyase Amb a 1 is currently considered the most important allergenic group for the *Ambrosia* genus (Gadermaier *et al.*, 2014), although it has been identified only in *A. artemisiifolia* and not in the other species. Concerning *A. artemisiifolia*, ten different allergen groups are reported in the IUIS database and they were extensively reviewed by Gadermaier *et al.* (2014) and Bordas-Le Floch *et al.* (2015). Briefly, the list includes: Amb a 1 (comprising the formerly called Amb a 2, recently designated as Amb a 1 isoallergen 5), to which more than 95% of ragweed pollen allergic patients are sensitized; Amb a 3, classified as a minor allergen (sensitization prevalence of 30–50%); Amb a 4 (defensin), to which sensitization frequencies are variable; Amb a 5 (unknown function) a minor allergen, affecting only 10% to 15% of ragweed pollen-allergic individuals; the panallergen Amb a 6 (non-specific lipid transfer protein) which is considered a minor allergen (sensitization prevalence of 21% among ragweed sensitized patients); Amb a 7 (plastocyanins), another minor allergen (reaction in 15% to 20% of ragweed pollen-allergic patients); Amb a 8 (profilin), highly cross-reactive with mugwort (*Artemisia*) profilin (Art v 4); Amb a 9/Amb a 10 (polcalcins), minor panallergens (reaction in 10% to 15% of ragweed pollen-allergic patients). Finally, the list includes the very recently discovered allergen Amb a 11 (cysteine protease), which has been classified as one of the major allergens along with Amb a 1 for this ragweed species (Bouley *et al.*, 2015). Additional IgE reactive pollen proteins, identified by trascriptomic and proteomic approaches, have been indicated as "*bona fide* allergens", probably extending the list of *A. artemisiifolia* allergens (Bordas-Le Floch *et al.*, 2015).

In contrast to *A. artemisiifolia*, *A. trifida* and *A. psilostachya* allergens are less characterized. Only two (Amb t 5, Amb t 8) and one allergenic proteins (Amb p 5) have been identified respectively in *A. trifida* and *A. psilostachya*, and reported in IUIS and/or allergome databases. Amb t 5 and Amb p 5 belong to the 5 group of allergens of the *Ambrosia* genus and cross-react with Amb a 5. In *A. psilostachya*, two isoforms of Amb p 5, Amb p 5.0101 and Amb p 5.0201 have been characterized. Ghosh *et al.* (1994) investigated the variants of Amb p 5 from *A. psilostachya* pollen and suggested that these forms are part of the natural variation within the *A. psilostachya* species, which exhibits polyploidy and can form hybrids with related ragweed species. Amb t 8 is a profilin, an actin binding proteins (Girodet, 2013). However, these data are not present in the IUIS database and only scanty information about it is available.

A. artemisiifolia, *A. trifida*, and *A. psilostachya* pollen allergens have long been considered largely cross-reactive (Weber *et al.* 2007), and it is generally believed that one species is sufficient for skin testing and immunotherapy. However, in the Northern area of Milan (widely invaded only by *A. artemisiifolia*), about 50% of patients submitted to injection of specific immunotherapy with *A. trifida* showed little or no clinical response, although an excellent outcome was obtained if they were shifted to *A. artemisiifolia* specific immunotherapy (Asero *et al.*, 2005). By comparing the proteome of *A. artemisiifolia* with those of *A. trifida* and *A. psilostachya*, Barton and Schomacker (2017) recently found that only *A. psilostachya* pollen contains all five Amb a 1 isoallergens identified in *A. artemisiifolia* and reported in the IUIS database. In contrast, they found only three Amb a 1 isoallergens (Amb a 1.2, Amb a 1.4, and Amb a 1.5) in *A. trifida*, the lesser IgE reactive isoforms. Although more specific analyses are needed to characterize the allergenic profile of these species, this information suggests that *A. artemisiifolia* is more similar to *A. psilostachya* than to *A. trifida*, thus explaining the results reported by Asero and collaborators (2005). The allergenicity of *A. tenuifolia* is still poorly known (no allergens are reported in allergen databases), but it shows little cross-reactivity with the other *Ambrosia* species (Girodet, 2013).

C. Allergenic impact and environment

Regarding quantities of pollen, ragweed has the potential to release billions of pollen grains: for *A. artemisiifolia* it is well known that 1.19 ± 0.14 billion pollen grains can be released per plant (Fumanal *et al.*, 2007; Smith *et al.*, 2013). However, pollen production is closely related to size, growth, phenology and fitness of plants. For *A. artemisiifolia*, there is a positive correlation between dry plant biomass and reproductive success, as bigger individuals produce more pollen grains (Fumanal *et al.*, 2007), although decreasing plant size is generally associated with increasing maleness and decreasing femaleness (Paquin and Aarssen, 2004). Biomass and flowering phenology can follow a latitudinal gradient (Allard, 1945; Dickerson, 1968; Leiblein Wild, 2014): both in Europe and North America, plants from southern populations grow larger and flower later than northern populations (e.g., Gudzinskas, 1993; Li *et al.*, 2015). The time of flowering greatly depends on germination time and the average springtime temperature (April, May and June) (Kazinczi *et al.*, 2008); for instance, it has been shown that earlier germination during spring leads to higher biomass allocation and higher pollen and seed production. Consequently, environmental conditions can alter plant fitness and result in pollen production change (Smith *et al.*, 2013). It is worth noting that adaptations to newly invaded environments (e.g. Europe) often have a positive effect on the fitness of plants, reproduction, and biomass allocation as well as influencing the length of flowering time (Hodgins and Rieseberg, 2011; Leiblein Wild, 2014).

Furthermore, pollen production is influenced directly or indirectly by human practices. Sensitization of the population to *A. artemisiifolia* is constantly increasing and is probably correlated with the increased civilization, urbanization and pollution of the last decades (D’Amato, 2007; Ghiani, 2012). Several studies warn that global changes are going to worsen the situation in the next few decades. Effects will include changes in ragweed distribution, plant growth and life cycle as well as pollen allergenicity itself (e.g. Ziska and Caulfield, 2000; Rogers *et al.*, 2006). Species Distribution Models (SDMs) for *A. artemisiifolia* predict that its potential distribution will increase globally (Essl *et al.*, 2015; Chapman *et al.*, 2016). In Europe, warmer summers and later autumn frosts will allow a spread of *A. artemisiifolia* northward and uphill, leading by the mid-21st century to the inclusion of northern areas (e.g. southern Scandinavia and the British Isles) in its climatically suitable regions, and southward a regression of the species’ range. Regarding the *Ambrosia* genus in North America, Ziska *et al.* (2011) showed an increase in recent decades (since 1995) of the duration of the ragweed (*Ambrosia* spp.) pollen season as a function of latitude (latitudinal effects are primarily associated with a delay in first frost of the fall season and lengthening of the frost free period). *Ambrosia trifida* in China is predicted to slightly increase its range (<1%) although it had the potential to spread northward (Qin *et al.*, 2014). Recently Rasmussen *et al.* (2017) found that, by the year 2100, the distribution range of *A. artemisiifolia*, *A. trifida* and *A. psilostachya* will increase towards Northern and Eastern Europe under all climate scenarios and consequently the high allergy risk areas will expand in Europe. Effects of the increase in temperature influence the flowering season length, but also the growth of plants and pollen production. Wan *et al.* (2002) tested the effects of warming and mowing on *A. psilostachya*, and showed that both can increase above ground biomass of plants (AGB), and the ratio of ragweed AGB to total AGB. With warming, total pollen production increased by 84% because ragweed stems were more abundant.

Moreover, experimental warming significantly increased pollen diameter (13% increase). El Kelish *et al.* (2014) demonstrated that both an elevated level of CO_2 and drought stress have an effect on *A. artemisiifolia* pollen allergenicity because expressed sequence tags (ESTs) encoding allergenic ragweed proteins increased under those conditions. Zhao *et al.* (2016) showed the direct influence of elevated NO_2 on the increased allergenicity of ragweed pollen and Ghiani *et al.* (2012) demonstrated that traffic-related pollution enhanced ragweed pollen allergenicity, showing that pollen collected along high-traffic roads had a higher whole allergenicity than pollen from low-traffic roads and vegetated areas. Conversely, several studies have shown no effect on the content of the major ragweed allergen Amb a 1 due to high concentrations of ozone or extended exposure of the plant to this pollutant (Sénéchal *et al.*, 2015; Kanter *et al.*, 2013).

VIII. Conclusion

The successful invasion of the ragweed species considered can be ascribed to a synergy of anthropogenic and bio-ecological factors. The globalization of commerce and changes in land use have dramatically favoured their spread into new areas. Firstly, the species were used as medicinal plants in the Americas and were transported to Europe and cultivated in botanical gardens. They then spread as a contaminant of crop and forage seeds, and in a wide variety of goods, by means of transportation, to become noxious pests. Climatic changes are predicted to worsen the impact of these species by increasing both their colonisation range and allergenic potential. Thus, the setting up of effective measures to prevent and stop their spread is essential. Until now, researchers have mainly focused on common ragweed, the most widespread species, and the results have often been automatically associated with the other three species, although their ecology, biology and allergenic and ecological impact can differ significantly. Although other ragweeds are less widespread globally than *A. artemisiifolia*, their impact could differ in terms of type and magnitude. For instance, *A. psilostachya*, *A. tenuifolia*, and *A. trifida* are able to colonize environments different from *A. artemisiifolia*, thus potentially expanding their range of impacts as one of the most "black-listed" genera in the world. For this reason, further research efforts and data collection about factors that have allowed ragweed species to overcome geographical and environmental barriers are needed. Specifically, more in-depth research is necessary about:

- The impact, biology and ecology of ragweeds other than *A. artemisiifolia*, which may represent a severe threat to local plant communities, given their ability to colonize semi-natural habitats;
- dispersal vectors and introduction pathways and their role in the spreading of *taxa*, with a particular focus for the rhizomatous "low-seed producer" *A. psilostachya;*
- allergenic impact of ragweed species other than *A. artemisiifolia*;
- taxonomy of ragweeds to clarify their distribution and relations among them;
- competition mechanisms and strategies with local plant communities (all ragweed species).

In conclusion, "for a fistful of ragweeds" a great deal of work has been done, but it is mandatory to remain alert and not underestimate the role of basic research in elaborating consistent strategies and models (e.g. SDMs) for better understanding and controlling of the ragweed invasion.

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Tables

Table 1 – *Ambrosia* species characteristics: morphological data allowing the identification of the four ragweeds.

Species	***Ambrosia artemisiifolia* L.**	***Ambrosia trifida* L.**	***Ambrosia psilostachya* DC.**	***Ambrosia tenuifolia* Spreng.**
Life form	Annual	Annual	Perennial	Perennial
Plant size (cm)	10 to 250	40 to 400	10 to 90	20-100
Belowground	Taproot	Taproot	Root sprouter	Root sprouter
Stem	+/- intensively branched, branches with wide angles	+/- intensively branched	Few branches, with narrow angles	Few branches, with narrow angles
Leaves	Pinnatifid to bipinnate, rarely entire; leaf segments broadened and separated, rarely narrow; lower leaves with distinct narrow petiole; upper leaves alternate; long and short hairs mixed	Palmate, 1 to 5 lobes; glabrous or few short hairs; all leaves opposite	Pinnatifid, rarely entire; leaf segments lineal and connected, often sharped towards the tip; +/- sessile; upper leaves alternate; dense short hairs	Bipinnate to pinnatifid; leaf segments as narrow as the rachis, lineal, connected; lower leaves with distinct narrow petiole; upper leaves alternate; dense short hairs
Diaspore coat	Few hairs and glands; 2-5 short lateral spines with sharpened tips; dark brown	Glabrous or few hairs; 2-4 indistinct lateral spines; dark brown to black	Few glands and short hairs; blunt, short lateral spines few or none; dark brown	Short hairs and glands, 2-5 lateral short blunt spines; olive to dark brown

Table 2 - Geography of *Ambrosia* (ragweed) species: distribution, time of arrival (first record in the wild), current status of ragweeds and references supporting reported data.

Continent	Country	Species	First record	Status	References
Europe	Albany	*Ambrosia artemisiifolia* L.	/	Doubtful occurrence	Barina *et al.*, 2013; Barina *et al.*, 2014
Africa	Algeria	*A. artemisiifolia*	> 1890	Alien Casual	Lawalree, 1947; Quézel and Santa, 1963; Greuter, 2006
Africa	Algeria	*A. psilostachya* DC.	1916	Alien Naturalized	Maire, 1928; Quézel and Santa, 1963; Greuter, 2006
America (S)	Argentina	*A. artemisiifolia*	/	Species occurring	Freire *et al.*, 2008; Gerber *et al.*, 2011; Essl *et al.*, 2015
America (S)	Argentina	*A. tenuifolia* Spreng.	/	Native	Freire *et al.*, 2008; Novara and Gutiérrez, 2010
Asia	Armenia	*A. artemisiifolia*	/	Alien Naturalized	Tamanyan and Fayvush, 2010; Randall, 2012
Oceania	Australia	*A. artemisiifolia*	1908	Alien Invasive	Parsons and Cuthbertson , 2001; Essl, *et al.*, 2015
Oceania	Australia	*A. psilostachya*	1922	Alien Invasive	Parsons and Cuthbertson , 2001
Oceania	Australia	*A. tenuifolia*	1932	Alien Naturalized	Parsons and Cuthbertson , 2001
Europe	Austria	*A. artemisiifolia*	1883	Alien Invasive	Essl *et al.*, 2009; Smith *et al.*, 2013
Europe	Austria	*A. trifida* L.	1948	Alien Casual	Essl and Rabitsch, 2002; Follak *et al.*, 2013
Europe	Austria	*A. psilostachya*	/	Alien Casual	Essl and Rabitsch, 2002
Asia	Azerbaijan	*A. artemisiifolia*	/	Alien Invasive	Greuter, 2006; Gerber *et al.*, 2011
America (C)	Bahamas	*A. artemisiifolia*	/	Species occurring	Acevedo-Rodrıguez and Strong, 2012; Essl *et al.*, 2015
Europe	Belarus	*A. artemisiifolia*	/	Alien Naturalized	Greuter, 2006
Europe	Belarus	*A. psilostachya*	/	Alien status unknown	EPPO, 2016
Europe	Belarus	*A. trifida*	/	Alien Casual	EPPO, 2016
Europe	Belgium	*A. trifida*	1829	Alien Casual	Verloove, 2016a
Europe	Belgium	*A. psilostachya*	1917	Alien Naturalized	Verloove, 2016b
Europe	Belgium	*A. artemisiifolia*	1883	Alien Naturalized?	Bullock *et al.*, 2012; Verloove, 2016c
America (S)	Bolivia	*A. artemisiifolia*	/	Alien status unknown	Jørgensen *et al.*, 2014
America (S)	Bolivia	*A. tenuifolia*	/	Native	Jørgensen *et al.*, 2014
Europe	Bosnia Herzegovina	*A. artemisiifolia*	/	Alien status unknown	Kazinczi *et al.*, 2008; Smith *et al.*, 2008
Africa	Botswana	*A. artemisiifolia*	/	Alien Naturalized	Setshogo, 2005; Randall, 2012; Skarpe *et al.*, 2014

America (S)	Brazil	*A. artemisiifolia*	/	Species occurring	Mondin and Nakajima, 2015; Essl *et al.*, 2015; Alves and Rocha, 2016
America (S)	Brazil	*A. tenuifolia*	/	Native	Sáenz and Gutiérrez, 2008
Europe	Bulgaria	*A. artemisiifolia*	1975	Alien Naturalized	Kazinczi *et al.*, 2008; Bullock *et al.*, 2012
Europe	Bulgaria	*A. trifida*	2014	Alien status unknown	Stoyanov *et al.*, 2014
America (S)	Canada	*A. artemisiifolia*	/	Native	Bassett and Crompton, 1975; Kazinczi *et al.*, 2008
America (N)	Canada	*A. psilostachya*	/	Native	Bassett and Crompton, 1975
America (N)	Canada	*A. trifida*	/	Native	Bassett and Crompton, 1982
America (S)	Chile	*A. artemisiifolia*	1959	Alien Naturalized	Essl *et al.*, 2015; Ugarte *et al.*, 2011; Fuentes *et al.*, 2013
America (S)	Chile	*A. tenuifolia*	1923	Alien Naturalized?	Ugarte *et al.*, 2011
Asia	China	*A. artemisiifolia*	1930s	Alien Invasive	Qin et a., 2014
Asia	China	*A. trifida*	1935	Alien Invasive	Qin et a., 2014
Asia	China	*A. psilostachya*	/	Alien status unknown	Chen and Hind 2011
America (S)	Colombia	*A. artemisiifolia*	/	Species occurring	Gerber *et al.*, 2011; CABI, 2017
Europe	Croatia	*A. artemisiifolia*	1879	Alien Invasive	Galzina *et al.*, 2010; Csontos *et al.*, 2010; Kazinczi *et al.*, 2008
America (C)	Cuba	*A. artemisiifolia*	< 1873	Species occurring	Sauvalle Chanceaulme, 1873; Acevedo-Rodriguez and Strong, 2012
Europe	Czech Republic	*A. artemisiifolia*	1883	Alien Invasive	Kazinczi *et al.*, 2008; Smith *et al.*, 2008; Bullock *et al.*, 2012
Europe	Czech Republic	*A. trifida*	1960	Alien Casual	Pyšek *et al.*, 2012
Europe	Czech Republic	*A. psilostachya*	1999	Alien Casual	Pyšek *et al.*, 2012
Europe	Denmark	*A. psilostachya*	/	Alien Casual	Greuter, 2006
Europe	Denmark	*A. trifida*	/	Alien Casual	EPPO, 2016
Europe	Denmark	*A. artemisiifolia*	1865	Alien Casual	Bullock *et al.*, 2012
America (S)	Ecuador	*A. artemisiifolia*	/	Species occurring	Jørgensen and León-Yánez, 1999
America (S)	Ecuador (Galapagos)	*A. artemisiifolia*	/	Alien Casual	Tye, 2001; Jaramillo Díaz and Guézou, 2013.
Africa	Egypt	*A. artemisiifolia*	2002?	Alien Naturalized	Greuter, 2006; Shaltout, 2004.
Europe	Estonia	*A. artemisiifolia*	1954	Alien Casual	Gudzinskas, 1993
Europe	Estonia	*A. psilostachya*	/	Alien Casual	Greuter, 2006
Europe	Estonia	*A. trifida*	/	Alien Casual	EPPO, 2016

Europe	Finland	*A. artemisiifolia*	1900<1950	Alien Naturalized	Finnish Ministry of Agriculture and Forestry, 2012; Lampinen and Lahti, 2016
Europe	Finland	*A. trifida*	1900<1950	Alien status unknown	Lampinen and Lahti, 2016
Europe	Finland	*A. psilostachya*	1990s	Alien status unknown	Lampinen and Lahti, 2016
Europe	France	*A. tenuifolia*	1839	Alien Naturalized	Thellung 1912; Chauvel *et al.*, 2015
Europe	France	*A. artemisiifolia*	1863	Alien Invasive [Corse- Alien Casual]	Chauvel *et al.*, 2006; Csontos *et al.*, 2010
Europe	France	*A. trifida*	1901	Alien Naturalized	Chauvel *et al.*, 2015
Europe	France	*A. psilostachya*	1931	Alien Naturalized (Invasive?)	Hibon, 1942; Fried *et al.*, 2015
Asia	Georgia	*A. artemisiifolia*	/	Alien Invasive	Kikodze *et al.*, 2010; EPPO, 2016
Asia	Georgia	*A. trifida*	/	Alien status unknown	Kikodze *et al.*, 2010
Europe	Germany	*A. artemisiifolia*	1860	Alien Naturalized	Buttler and Harms, 1999**;** Brandes and Nitzsche, 2006; Otto, 2006; Kazinczi *et al.*, 2008; Bullock *et al.*, 2012; Buttler, 2016.
Europe	Germany	*A. trifida*	1877	Alien Naturalized	Buttler and Harms, 1999**;** Follak *et al.*, 2013; Buttler, 2016; DAISIE, Species Factsheet: *A. trifida*. available at http://www.europe-aliens.org/speciesFactsheet.do?speciesId=21722# (Accessed in January 2017); Deutschlandflora WebGIS. Floristische Verbreitungskarten in Deutschland: https://deutschlandflora.de (Accessed in January 2017)
Europe	Germany	*A. psilostachya*	1897	Alien Naturalized	Buttler and Harms, 1999; Buttler, 2016; Bundesamt für Naturschutz - Floraweb, 2017: http://www.floraweb.de/pflanzenarten/artenhome.xsql?suchnr=20068& (Accessed in January 2017); Deutschlandflora WebGIS. Floristische Verbreitungskarten in Deutschland: https://deutschlandflora.de (Accessed in January 2017)
Europe	Germany	*A. tenuifolia*	/	Alien Casual	Buttler and Harms, 1999; Buttler, 2016
Europe	Greece	*A. psilostachya*	2016	Alien Naturalized?	Von Raab-Straube and Raus, 2016
Europe	Greece	*A. artemisiifolia*	2008?	Alien status unknown	Arianoutsou *et al.*, 2010; Greuter and Raus, 2008
America (C)	Guadeloupe	*A. artemisiifolia*	/	Alien status unknown	Gerber *et al.*, 2011
America (S)	Guatemala	*A. artemisiifolia*	/	Alien status unknown	Gerber *et al.*, 2011

America (C)	Hawaiian Islands	*A. artemisiifolia*	1854	Alien Invasive	Wagner *et al.*, 1990; Pacific Island Ecosystems at Risk (PIER), 2013a
America (N)	Hawaiian Islands	*A. psilostachya*	/	Alien status unknown	Randall, 2012; Pacific Island Ecosystems at Risk (PIER), 2013b
America (C)	Hispaniola (Dominican Republic)	*A. artemisiifolia*	/	Species occurring	Acevedo-Rodrıguez and Strong, 2012; Essl *et al.*, 2015
Europe	Hungary	*A. psilostachya*	1900 ca.	Alien Invasive	Puc, 2004; CABI, 2017
Europe	Hungary	*A. trifida*	/	Alien Invasive?	Plank *et al.*, 2016
Europe	Hungary	*A. artemisiifolia*	1922	Alien Invasive	Csontos *et al.*, 2010
Europe	Iceland	*A. artemisiifolia*	1948	Alien Casual	Wasowicz *et al.*, 2013
Asia	India	*A. artemisiifolia*	/	Alien Invasive	Khuroo *et al.*, 2012; Kohli *et al.*, 2012
Asia	India	*A. psilostachya*	1990s	Alien Invasive	Ramachandra Prasad *et al.*, 2013
Asia	India	*A. trifida*	2004-2009	Alien status unknown	Kumar *et al.*, 2009; Randall, 2012
Asia	Iran	*A. artemisiifolia*	/	Alien status unknown	Gerber *et al.*, 2011; Randall, 2012; Bararpour, 2014.
Asia	Iran	*A. psilostachya*	/	Alien status unknown	Cheraghian, 2016a
Asia	Iran	*A. trifida*	/	Alien status unknown	Randall, 2012; Bararpour, 2014; Cheraghian, 2016b
Europe	Ireland	*A. trifida*	1894	Alien Casual	Reynolds, 2002
Europe	Ireland	*A. artemisiifolia*	1900	Alien Casual	Rich, 1994; Reynolds, 2002; Bullock *et al.*, 2012; Essl *et al.*, 2015
Asia	Israel	*A. artemisiifolia*	1925	Alien Casual	Waisel *et al.*, 2008; Yair *et al.*, 2017
Asia	Israel	*A. tenuifolia*	1984	Alien Naturalized	Greuter and Raus, 1995; Danin, 2000; Waisel *et al.*, 2008; Yair *et al.*, 2017
Asia	Israel	*A. trifida*	1987	Alien Casual (still present?)	Danin, 2000; Waisel *et al.*, 2008; Danin, 2016; Yair *et al.*, 2017
Asia	Israel	*A. psilostachya*	2006 ca.	Alien Naturalized	Yair *et al.*, 2017
Europe	Italy	*A. trifida*	1899	Alien Naturalized	Vignolo-Lutati, 1935; Mandrioli *et al.*, 1998; Celesti-Grapow *et al.*, 2009; Chauvel *et al.*, 2015
Europe	Italy	*A. psilostachya*	1927	Alien Invasive	Vignolo-Lutati, 1935; Mandrioli *et al.*, 1998; Conti *et al.*, 2005
Europe	Italy	*A. tenuifolia*	1935	Alien Naturalized	Vignolo-Lutati, 1935; Mandrioli *et al.*, 1998; Conti *et al.*, 2005
Europe	Italy	*A. artemisiifolia*	1902	Alien Invasive	Gentili *et al.*, 2016

America (S)	Jamaica	*A. artemisiifolia*	/	Alien status unknown	Gerber *et al.*, 2011
Asia	Japan	*A. artemisiifolia*	1877	Alien Invasive	Auld *et al.*, 2003; Kazinczi *et al.*, 2008; Fukano and Yahara, 2012; Essl *et al.*, 2015; Invasive Species of Japan (NIES). *A. artemisiifolia*. Available at: https://www.nies.go.jp/biodiversity/invasive/DB/detail/80400e.html (Accessed January 2017)
Asia	Japan	*A. trifida*	1952	Alien Invasive	Auld *et al.*, 2003
Asia	Japan	*A. psilostachya*	/	Alien Invasive	Auld *et al.*, 2003; Mito and Uesugi, 2004; Ramachandra Prasad *et al.*, 2013.
Asia	Kazakhstan	*A. artemisiifolia*	/	Alien status unknown	Gerber *et al.*, 2011
Asia	Kazakhstan	*A. psilostachya*	/	Alien Naturalized	Von Raab-Straube and Raus, 2016.
Asia	Korean Peninsula	*A. trifida*	1964	Alien Invasive	Lee *et al.*, 2010; Kim and Kil, 2016
Asia	Korean Peninsula	*A. artemisiifolia*	1955	Alien Invasive	Song *et al.*, 2012; Kim and Kil, 2016.
Europe	Latvia	*A. trifida*	1900	Alien Casual?	Gudzinskas, 1993
Europe	Latvia	*A. artemisiifolia*	1936	Alien Casual	Gudzinskas, 1993
Europe	Latvia	*A. psilostachya*	/	Alien Casual	DAISIE, Species Factsheet: *A. coronopifolia* available at http://www.europe-aliens.org/speciesFactsheet.do?speciesId=21701# (Accessed in January 2017)
Europe	Liechtenstein	*A. artemisiifolia*	1995	Alien Casual	Greuter, 2006; Waldburger and Staub 2006
Europe	Lithuania	*A. trifida*	1987	Alien Casual	Gudzinskas, 1993
Europe	Lithuania	*A. artemisiifolia*	1884	Alien Casual	Gudzinskas, 1993
Europe	Luxembourg	*A. artemisiifolia*	/	Alien Naturalized	Ries, 2017
Africa	Lybia	*A. artemisiifolia*	/	Doubtful occurrence	Greuter, 2006
Africa	Madagascar	*A. artemisiifolia*	/	Doubtful occurrence	Kull *et al.*, 2012; Skálová *et al.*, 2015
America (C)	Martinique	*A. artemisiifolia*	/	Alien status unknown	Gerber *et al.*, 2011
Africa	Mauritius	*A. psilostachya*	/	Alien Invasive	Macdonald *et al.*, 2003
America (C)	Mexico	*A. artemisiifolia*	/	Species occurring	Villaseñor and Espinosa-Garcia, 2004; Gerber *et al.*, 2011.
America (C)	Mexico	*A. psilostachya*	/	Native	Vibrans, 1998; Roldán & Vibrans, 2009
America (C)	Mexico	*A. trifida*	/	Species occurring	Villaseñor and Espinosa-Garcia, 2004; EPPO, 2016; CABI, 2017.

Europe	Moldova	*A. artemisiifolia*	1975?	Alien Naturalized	Greuter, 2006;Bullock *et al.*, 2012
Europe	Moldova	*A. trifida*	/	Alien Casual	EPPO, 2016
Asia	Mongolia	A. trifida	/	Alien status unknown	EPPO, 2016
Europe	Montenegro	*A. artemisiifolia*	?	Alien status unknown	Stešević and Petrović 2010; Karrer, 2016
Europe	Montenegro	*A. psilostachya*	/	Alien status unknown	Greuter, 2006
Africa	Morocco	*A. psilostachya*	1994	Alien status unknown	Tanji, 2005
Europe	Netherlands	*A. artemisiifolia*	1875	Alien Naturalized	Van Denderen *et al.*, 2010; Odé and Beringen, 2017a
Europe	Netherlands	*A. psilostachya*	1905	Alien Naturalized	Van Denderen *et al.*, 2010; Odé and Beringen, 2017b
Europe	Netherlands	*A. trifida*	more frequent from 1960s	Alien Casual	Van Denderen *et al.*, 2010; Odé and Beringen 2017c
Oceania	New Zealand	*A. tenuifolia*	1950	Alien Casual	Howell and Sawyer, 2006
Oceania	New Zeland	*A. artemisiifolia*	1911	Alien Casual	Webb *et al.*, 1988; Essl *et al.*, 2015
Europe	Norway	*A. artemisiifolia*	1930	Alien Casual	Fremstad and Elven 1997; Kazinczi *et al.*, 2008
Europe	Norway	*A. psilostachya*	/	Alien Casual	Greuter, 2006
Europe	Norway	*A. trifida*	/	Alien Casual	Randall, 2012; EPPO, 2016; CABI, 2017; DAISIE, Species Factsheet: *A. trifida*. available at http://www.europe-aliens.org/speciesFactsheet.do?speciesId=21722# (Accessed in January 2017)
America (S)	Paraguay	*A. artemisiifolia*	/	Species occurring	Zuloaga *et al.*, 2008; Essl *et al.*, 2015; CABI, 2017; Tropicos.org. Missouri Botanical Garden. 01 Feb 2017 <http://www.tropicos.org/Name/2701648
America (S)	Paraguay	*A. tenuifolia*	/	Native	Sáenz and Gutiérrez, 2008
America (S)	Perù	*A. artemisiifolia*	/	Species occurring	Gutte, 1978; Gerber *et al.*, 2011; Zárate *et al.*, 2015; Tropicos.org. Missouri Botanical Garden. 20 Jan 2017 <http://www.tropicos.org/Name/2701648>
America (S)	Perù	*A. tenuifolia*	/	Native	Randall, 2012
Europe	Poland	*A. artemisiifolia*	1873	Alien Naturalized	Gudzinskas, 1993; Kazinczi *et al.*, 2008; Tokarska-Guzik *et al.*, 2011
Europe	Poland	*A. psilostachya*	/	Alien Naturalized	Kazinczi *et al.*, 2008; Tokarska-Guzik *et al.*, 2011
Europe	Poland	*A. trifida*	/	Alien Casual	Kazinczi *et al.*, 2008; Tokarska-Guzik *et al.*, 2011

Europe	Portugal	*A. artemisiifolia*	1972	Alien Invasive (Isle of Madeira Alien Casual)	Borges *et al.*, 2008; Amor Morales *et al.*, 2012
America (C)	Puerto Rico	*A. tenuifolia*	/	Alien Naturalized	Liogier, 1997; Acevedo-Rodriguez and Strong, 2012; Gann *et al.*, 2015-2017
Europe	Romania	*A. artemisiifolia*	1907	Alien Invasive	Kazinczi *et al.*, 2008; Csontos *et al.*, 2010; Bullock *et al.*, 2012; Sîrbu, 2012
Europe	Romania	*A. trifida*	1970-1980	Alien Naturalized	Sîrbu, 2012; Stoyanov *et al.*, 2014
Europe	Romania	*A. psilostachya*	/	Alien Naturalized	Sîrbu, 2012
Europe	Russia	*A. psilostachya*	/	Alien Naturalized	EPPO, 2016
Europe	Russia (European)	*A. artemisiifolia*	1918	Alien Invasive	Gudzinskas, 1993; Csontos *et al.*, 2010; Vinogradova *et al.*, 2010; Randall, 2012
Europe	Russia (European)	*A. trifida*	/	Alien Naturalized	Randall, 2012; EPPO, 2016
Europe	Russia (European)	*A. psilostachya*	/	Alien Naturalized	EPPO, 2016
Europe	Serbia	*A. artemisiifolia*	1935	Alien Invasive	Vrbničanin *et al.*, 2004; Kazinczi *et al.*, 2008; Bullock *et al.*, 2012
Europe	Serbia	*A. trifida*	1982	Alien Naturalized	Vrbničanin *et al.*, 2004; Follak *et al.*, 2013; EPPO, 2016
Europe	Serbia	*A. tenuifolia*	/	Alien Naturalized	Vrbničanin *et al.*, 2004
Europe	Slovakia	*A. artemisiifolia*	1949	Alien Invasive	Medvecka *et al.* 2012
Europe	Slovakia	*A. trifida*	1980	Alien Casual	Medvecka *et al.* 2012
Europe	Slovenia	*A. artemisiifolia*	1993 (after WW II?)	Alien Invasive	Kazinczi *et al.*, 2008.; Galzina *et al.*, 2010; Zelnik, 2012
Europe	Slovenia	*A. trifida*	late 1980s	Alien Casual	Follak *et al.*, 2013; EPPO, 2016
Africa	South Africa	*A. artemisiifolia*	/	Alien Naturalized	Germishuizen and Meyer, 2003; Henderson, 2007; Essl *et al.*, 2015
Africa	South Africa	*A. psilostachya*	/	Alien Naturalized	Wells *et al.*, 1986; Germishuizen and Meyer, 2003; Randall, 2012; SANBI, 2015a
Africa	South Africa	*A. tenuifolia*	/	Alien Naturalized	Germishuizen and Meyer, 2003; SANBI. 2015b
Europe	Spain	*A. tenuifolia*	1954	Alien Naturalized	Amor Morales *et al.*, 2012
Europe	Spain	*A. psilostachya*	1981	Alien Invasive	Amor Morales *et al.*, 2012
Europe	Spain	*A. artemisiifolia*	1983	Alien Invasive	Amor Morales *et al.*, 2012
Europe	Spain	*A. trifida*	1983	Alien Naturalized	Amor Morales *et al.*, 2012
Europe	Spain-Baleares	*A. tenuifolia*	2004	Alien Naturalized	Fraga and García, 2004

Africa	Swaziland	*A. artemisiifolia*	/	Alien Naturalized	Randall, 2012; Swaziland's Alien Plants Database. http://www.sntc.org.sz/alienplants/index.asp
Europe	Sweden	*A. trifida*	1909	Alien Casual	Anderberg, 2000; Gerber *et al.*, 2011; Randall, 2012; DAISIE, Species Factsheet: *A. trifida*. available at http://www.europe-aliens.org/speciesFactsheet.do?speciesId=21722# (Accessed in January 2017)
Europe	Sweden	*A. psilostachya*	1928	Alien Naturalized	Dahl *et al.*, 1999; Anderberg, 2005
Europe	Sweden	*A. artemisiifolia*	1866	Alien Casual	Dahl *et al.*, 1999; Anderberg, 2000; Smith *et al.*, 2013; Smith *et al.*, 2008; Dahl, 1999; Smith *et al.*, 2013
Europe	Switzerland	*A. trifida*	1900	Alien status unknown	Follak *et al.*, 2013; EPPO, 2016.
Europe	Switzerland	*A. psilostachya*	/	Alien status unknown	Greuter, 2006; Hess *et al.*, 2006
Europe	Switzerland	*A. artemisiifolia*	1850s	Alien Invasive	Taramarcaz *et al.*, 2005; Kazinczi *et al.*, 2008; Bullock *et al.*, 2012
Asia	Taiwan	*A. artemisiifolia*	1971	Alien Naturalized	Wu *et al.*, 2004; Wu *et al.*, 2010; Peng, 2013
Asia	Taiwan	*A. psilostachya*	2000	Alien Naturalized	Tseng *et al.*, 2004; Ramachandra Prasad *et al.*, 2012; Wu, *et al.*, 2010; Chen and Hind, 2011
Asia	Turkey	*A. artemisiifolia*	1995	Alien Invasive	Byfield and Baytop 1998; Zemmer *et al.* 2012; Behçet 2004; Onen *et al.*, 2014; Arslan *et al.*, 2015
Asia	Turkey	*A. tenuifolia*	2000	Alien Naturalized?	Behçet 2004; Özhatay and Kültür, 2006
Europe	Ukraine	*A. artemisiifolia*	1925	Alien Invasive	Smith *et al.*, 2013; Bullock *et al.*, 2012; EPPO, 2016.
Europe	Ukraine	*A. psilostachya*	/	Alien status unknown	Greuter, 2006
Europe	Ukraine	*A. trifida*	/	Alien Casual	Yavorska, 2009
Europe	United Kingdom	*A. artemisiifolia*	1836	Alien Invasive	Rich, 1994; Bullock *et al.*, 2012; Essl *et al.*, 2015
Europe	United Kingdom	*A. trifida*	1897	Alien Casual	Rich, 1994; Sell and Murrell, 2006; EPPO, 2016; Online Atlas British and Irish Flora: http://www.brc.ac.uk/plantatlas/index.php?q=plant/A.-trifida
Europe	United Kingdom	*A. psilostachya*	1880s	Alien Naturalized	Rich, 1994; Sell and Murrell, 2006; On line Atlas of the British and Irish Flora: http://www.brc.ac.uk/plantatlas/index.php?q=plant/A.-psilostachya
Europe	United Kingdom	*A. tenuifolia*	/	Doubtful occurrence	Stace, 2010; Randall, 2012
America (N)	United States of America	*A. psilostachya*	/	Native	Bassett and Crompton, 1975

America (N)	United States of America	*A. tenuifolia*	/	Alien status unknown	Liogier, 1997; USDA - NRCS, 2017
America (N)	United States of America	*A. trifida*	/	Native	Bassett and Crompton, 1982
America (N)	United States of America	*A. artemisiifolia*	/	Native	Bassett and Crompton, 1975
America (S)	Uruguay	*A. artemisiifolia*	/	Species occurring	Tejera and Beri 2005; Zuloaga *et al.*, 2008; Essl *et al.*, 2015
America (S)	Uruguay	*A. tenuifolia*	/	Native	Sáenz and Gutiérrez, 2008

Table 3 - Environmental requirements of *Ambrosia* species (ragweeds): main data related to colonized habitat types (native and invasive range), suitable climatic, soil and light conditions. Requirements of each species are highlighted in grey and doubtful attributions are signaled by "(?)".

Species	***Ambrosia artemisiifolia* L.**	***Ambrosia trifida* L.**	***Ambrosia psilostachya* DC.**	***Ambrosia tenuifolia* Spreng.**
	Disturbed open habitat	Disturbed open habitat	Disturbed open habitat	Disturbed open habitat
	Semi-natural grasslands	Semi-natural grasslands	Semi-natural grasslands	Semi-natural grasslands
	Croplands	Croplands	Croplands	Croplands
	Along transportation corridors	Along transportation corridors	Along transportation corridors	Along transportation corridors
	Wastelands	Wastelands	Wastelands	Wastelands
	Riparian habitat	Riparian habitat	Riparian habitat	Riparian habitat
	Dunes	Dunes	Dunes	Dunes
	Non dense wood	Non dense wood	Non dense wood	Non dense wood
	Disturbed open habitat	Disturbed open habitat	Disturbed open habitat	Disturbed open habitat
	Semi-natural grasslands	Semi-natural grasslands	Semi-natural grasslands	Semi-natural grasslands
	Croplands	Croplands	Croplands	Croplands
	Along transportation corridors	Along transportation corridors	Along transportation corridors	Along transportation corridors (?)
	Wastelands	Wastelands	Wastelands	Wastelands
	Riparian habitat	Riparian habitat	Riparian habitat	Riparian habitat (?)
	Dunes	Dunes	Dunes	Dunes
	Non dense wood	Non dense wood	Non dense wood	Non dense wood
	Warm temperate climate (with exceptions)	Warm temperate climate	Warm temperate climate (with exceptions)	Warm temperate climate
	Drought tolerant	Drought tolerant	Drought tolerant	Drought tolerant
	Freeze tolerant	Freeze tolerant	Freeze tolerant	Freeze tolerant
	Alkaline	Alkaline?	Alkaline	Alkaline?
	Acid	Acid	Acid	Acid
	Silty	Silty	Silty	Silty
	Sandy	Sandy	Sandy	Sandy
	Well drained/ Dry	Well drained/ Dry	Well drained/ Dry	Well drained/ Dry
	Moist/Wet	Moist/Wet	Moist/Wet	Moist/Wet
	Saline	Saline	Saline	Saline
	Metal	Metal	Metal	Metal
	Heliophylous	Heliophylous	Heliophylous	Heliophylous
	Shady-tolerant	Shady-tolerant	Shady-tolerant	Shady-tolerant

Table 4 - Life strategies of *Ambrosia* species (ragweeds): relevant traits contributing to strenghten resistance, resilience and competition of ragweeds in the wild. Traits of each species are highlighted in gray.

Species	***Ambrosia artemisiifolia* L.**	***Ambrosia trifida* L.**	***Ambrosia psilostachya* DC.**	***Ambrosia tenuifolia* Spreng.**
	Morphologic structures	Morphologic structures	▨ Morphologic structures	▨ Morphologic structures
	▨ Chemical defence against stress and predators	▨ Chemical defence against stress and predators	▨ Chemical defence against stress and predators	▨ Chemical defence against stress and predators
	▨ Allelopathy	▨ Allelopathy	▨ Allelopathy	▨ Allelopathy
	▨ Mychorrhiza	▨ Mychorrhiza	▨ Mychorrhiza	Mychorrhiza
	▨ Reallocation biomass	Reallocation biomass	Reallocation biomass	Reallocation biomass
	▨ Resprouting	▨ Resprouting	▨ Resprouting	▨ Resprouting
	Rhizome	Rhizome	▨ Rhizome	▨ Rhizome
	▨ Secondary dormancy	▨ Secondary dormancy	▨ Secondary dormancy	▨ Secondary dormancy
	▨ Soil seed bank	Soil seed bank	Soil seed bank	▨ Soil seed bank
	▨ Long lasting soil seed bank	Long lasting soil seed bank	Long lasting soil seed bank	▨ Long lasting soil seed bank
	▨ Advantages from vegetation gaps	▨ Advantages from vegetation gaps	▨ Advantages from vegetation gaps	▨ Advantages from vegetation gaps
	▨ Weak competitor in more evolved vegetation stages	▨ Weak competitor in more evolved vegetation stages	▨ Weak competitor in more evolved vegetation stages	▨ Weak competitor in more evolved vegetation stages
	Persistence in more evolved vegetation stages	Persistence in more evolved vegetation stages	▨ Persistence in more evolved vegetation stages	▨ Persistence in more evolved vegetation stages

Table 5 - Reproduction and disperasal of *Ambrosia* species (ragweeds): relevant data in understanding the reproductive and dispersal potential of ragweeds. The characteristic of each species is highlighted in grey and doubtful attributions are signaled by "(?)".

Species	***Ambrosia artemisiifolia* L.**	***Ambrosia* trifida L.**	***Ambrosia psilostachya* DC.**	***Ambrosia tenuifolia* Spreng.**
POLLINATION	Anemophylous	Anemophylous	Anemophylous	Anemophylous
	Sexual	Sexual	Sexual	Sexual
	Vegetative	Vegetative	Vegetative	Vegetative
SEED DIMENSION	3.5 mm long	more than 6 mm long	3-4.5 mm long	3-5 mm long
	Very high	Very high	Very high	Very high
	High	High	High	High (?)
	Scarce	Scarce	Scarce	Scarce
	Existing	Existing	Existing	Existing?
	Highly relevant	Highly relevant	Highly relevant	Highly relevant
	No evidences	No evidences	No evidences	No evidences
	Vernalization	Vernalization	Vernalization	Vernalization
	Light	Light	Light	Light
	Soil moisture	Soil moisture	Soil moisture	Soil moisture
PRIMARY SEED DISPERSAL	Barochory	Barochory	Barochory	Barochory
	Anemochory	Anemochory	Anemochory (?)	Anemochory (?)
	Epizoochory	Epizoochory	Epizoochory	Epizoochory
	Endozoochory	Endozoochory	Endozoochory (?)	Endozoochory
	Hydrochory	Hydrochory	Hydrochory	Hydrochory
	Movement of soils	Movement of soils (?)	Movement of soils (?)	Movement of soils (?)
	Mowing or agricultural machinery	Mowing or agricultural machinery (?)	Mowing or agricultural machinery (?)	Mowing or agricultural machinery (?)
	Car and train passage	Car and train passage (?)	Car and train passage (?)	Car and train passage
	Grain, vegetables, fodder, bird food and oil-seeds commercial exchanges	Grain, vegetables, fodder, bird food and oil-seeds commercial exchanges	Grain, vegetables, fodder, bird food and oil-seeds commercial exchanges	Grain, vegetables, fodder, bird food and oil-seeds commercial exchanges

Table 6 - Allergenic potential of *Ambrosia* species (ragweeds): relevant elements of plants contributing to determine and increase allergy reaction. Elements of each species are highlighted in gray.

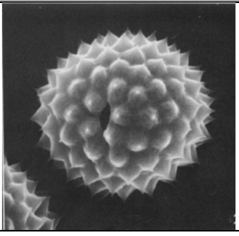
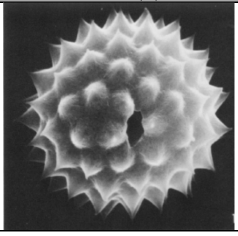
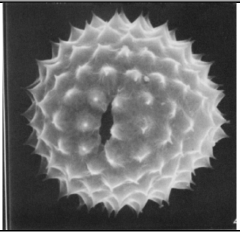
Species	**Ambrosia artemisiifolia L.**	**Ambrosia trifida L.**	**Ambrosia psilostachya DC.**	**Ambrosia tenuifolia Spreng.**
	Pollen	Pollen	Pollen	Pollen
	Plant debris	Plant debris	Plant debris	Plant debris
POLLEN DIMENSION	18–22 μm	19.25 μm	21 - 23 μm up to 26.4 μm	?
CROSS-REACTIVITY	Amb a 5 and Amb t 5	Amb a 5 and Amb t 5	Amb a 5 and Amb p 5	poorly known
	Long-distance transport of pollen	Long-distance transport of pollen (?)	Long-distance transport of pollen (?)	Long-distance transport of pollen (?)
	Atmospheric Pollution	Atmospheric Pollution(?)	Atmospheric Pollution (?)	Atmospheric Pollution (?)
	Warming climate	Warming climate	Warming climate	Warming climate (?)
	Disturbance	Disturbance (?)	Disturbance	Disturbance (?)
POLLEN GRAIN (from Robbins *et al.*, 1979)				-

Table 7 - Allergens in *Ambrosia* species (ragweeds).: characteristics of identified allergens of each analyzed species (Source: * = IUIS, ** = ExPASy).

Allergen*	Isoform*	MW(SDS-PAGE) (kDa)*	Theoretical pI **	Biological function*	Allergenic Potential (%)*
***Ambrosia artemisiifolia* L.**					
	Amb a 1.0101		5.58		
	Amb a 1.0201		6.63		
	Amb a 1.0202		6.63		
	Amb a 1.0301		5.72		
	Amb a 1.0302		5.72		
	Amb a 1.0303		5.79		
	Amb a 1.0304		5.79		
	Amb a 1.0305		5.79		
	Amb a 1.0401		5.61		
	Amb a 1.0402		5.22		
	Amb a 1.0501		6.00		
	Amb a 1.0502		5.79		
Amb a 3	Amb a 3.0101	11	6.11	Plastocyanin	51
Amb a 4	Amb a 4.0101	30	4.88	Defense-like protein	Unknown
Amb a 5	Amb a 5.0101	5	8.19	unknown	10-20
Amb a 6	Amb a 6.0101	10	8.93	Lipid Transfer protein (LTP)	21
Amb a 7	Amb a 7.0101	12	-	Plastocyanin	15-20
	Amb a 8.0101	14	4.79		
	Amb a 8.0102		4.88		
	Amb a 9.0101	10	4.17		
	Amb a 9.0102		4.15		
Amb a 10	Amb a 10.0101	18	4.25	Polcalcin-like protein	10-15
Amb a 11	Amb a 11.0101	37 kDa (natural purified mature protein), 52 kDa (natural purified zymogen)	6.43	Cysteine protease	54
***Ambrosia psilostachya* DC.**					
	Amb p 5.0101				
	Amb p 5.0201				
***Ambrosia trifida* L.**					
Amb t 5	Amb t 5.0101	5		Unknown	5

Figures Legend

Figure 1 - Global distribution of *Ambrosia* species (ragweeds). **Alien**: the species is not native to a country. Status (*invasive, naturalized, and casual*) is attributed when the condition is confirmed at country and/or local level; “?” indicate uncertainty due to lack of confirmations. **Alien status unknown:** the species is alien to a country, but its status is indefinite. **Species occurring**: the species occurs in one country, but there are uncertainties/ inconsistencies about its origin (alien/native). **Native:** the species is not introduced from other countries; it is part of local flora. **Doubtful occurrence**: the occurrence of the species is not confirmed.

Figure 2 - Status of *Ambrosia* species (ragweeds) at world level. Each pie chart describes the percentage of countries where the species is native or alien, their status and the table below the numbers for each category.