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Monographs on invasive plants in Europe N° 5: *Ambrosia trifida* L.

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ABSTRACT

Ambrosia trifida L. (giant ragweed, Asteraceae) is native to the North American continent and was introduced into Europe and Asia at the end of the 19th century. In its native range, this tall annual species is common in riparian and ruderal habitats and is also a major weed in annual cropping systems. For nearly a century, *A. trifida* has also been of great concern in the U.S. for its highly allergenic pollen, necessitating targeted control measures to reduce its impact on human populations. Based on the distribution of *A. trifida* in North America and in its introduced range, riparian systems in the rest of the world may be particularly at risk to invasion, with potential negative consequences for their biodiversity. Currently, *A. trifida* has invaded Asia more widely than Europe, likely due to the more favourable local conditions in Asia. Throughout its introduced range, *A. trifida* is host to a limited number of invertebrates and pathogens and only a few biological agents are available for its control. The main impacts of *A. trifida* at a global level are on crop yield and human health, resulting in significant socio-economic impacts. The success of *A. trifida* invasion in areas in which it has been introduced is still unclear, but climate change may increase climate suitability, increasing the potential for *A. trifida* to spread. While effective management in cultivated fields seems potentially possible, the development and control of *A. trifida* in natural riparian habitats is of great concern due to the difficulty of management in these areas.

ARTICLE HISTORY

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Taxonomy

Names and classification

Taxonomy (APG IV 2016)

Kingdom: *Plantae*, Tracheophytes, Angiosperms, Eudicots (*Eudicotyledoneae*), Asterids (*Asteridae*), *Asterales*, *Asteraceae*, *Ambrosia*,

Species *Ambrosia trifida* L., 1753.

Sub-species: The USDA Database includes two sub-species that are *Ambrosia trifida* var. *texana* and *Ambrosia trifida* var. *trifida*

EPPO code: AMBTR

Synonyms

Ambrosia aptera DC., *Ambrosia integrifolia* Mulh. ex Willd., *Ambrosia trifida* var. *aptera* (DC.) Kuntze, *Ambrosia trifida* var. *heterophylla* Kuntze, *Ambrosia trifida* var. *integrifolia* (Mulh. ex. Willd) Torr. & A.Gray, *Ambrosia trifida*

f. *integrifolia* (Mulh. ex. Willd) Fernald, *Ambrosia trifida* var. *polyploidea* J.Rousseau, *Ambrosia trifida* var. *texana* Scheele, *Ambrosia trifida* subsp. *trifida*, *Ambrosia trifida* var. *trifida*, *Ambrosia trifida* f. *trifida*.



Common names

Chinese: 三裂叶豚草 (sān liè yè tún cǎo); Dutch: Driedelige ambrosia; English: Giant ragweed; French: Ambrosie trifide; Grande herbe à poux (Québec); German: Dreilappiges Traubenkraut; Japanese: オオブタクサ; Russian: Амброзия трехраздельная

Morphological description

Species description

Ambrosia trifida, a member of the Asteraceae, is a tall annual plant with a main taproot and lateral fibrous roots, and thick stem (Bassett and Crompton 1982)

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that can attain heights of up to 6 m in favourable growth conditions. The name “giant” (giant ragweed) reflects its unusually large features for an annual plant, including its cotyledons, seedling size, stem diameter, and mature height. *Ambrosia trifida* germinates in the spring and summer (Bassett and Crompton 1982; Royer and Dickinson 1999). Cotyledons (2–4 cm long and 1–1.5 cm wide) are spoon-shaped with an attenuated petiole (Figure 1a).

Seedlings can be up to 20 cm in width (Bassett and Crompton 1982). The first true leaves are opposite, simple, lance-shaped with toothed margins and petiole. The base of the leaf blade is cuneate. Succeeding

leaves measure from 4 to 15 cm and are usually deeply lobed with 3–5 lobes, however, the number of lobes can vary within and among plants and leaves sometimes lack lobes entirely. Leaves are rough, slightly hairy, with toothed margins and a long petiole of 3 to 12 cm (Royer and Dickinson 1999; Figure 1b). Unlike other *Ambrosia* species, leaves are opposite except, on occasion, those that subtend the inflorescence. The main stem is rough, hairy and varies from unbranched to frequently branched, depending on light availability (Jurik 1991).

Flowering occurs from early August to the first killing frost, or when the plant senesces, depending

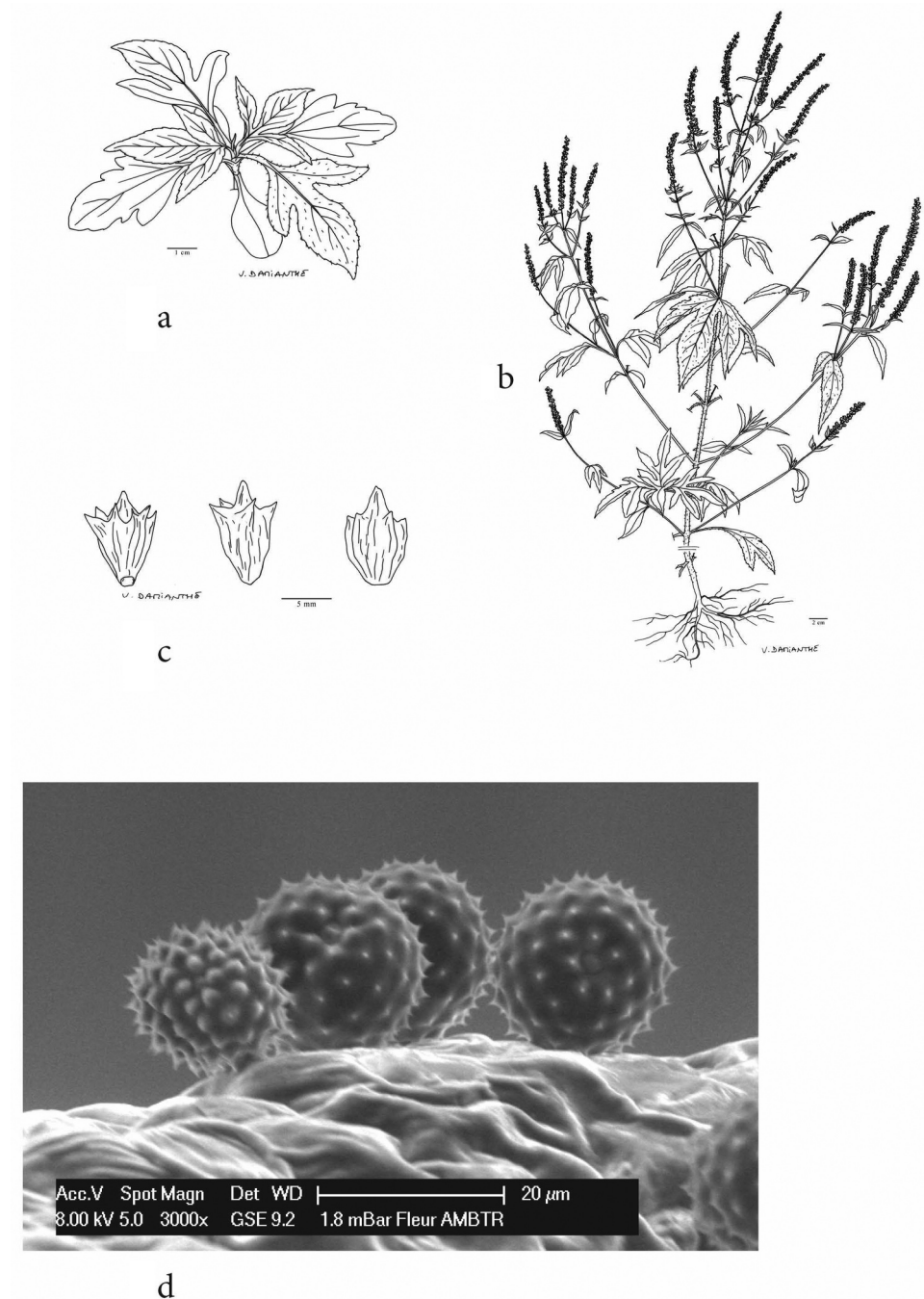


Figure 1. /a seedling with cotyledons and the first six leaves/b: flowering plant, note the opposite leaves and the branched stems/ c: fruit (achene) with high degree of variability/d: pollen grain. (a, b, c, d: V. Damianthe/Observatoire des ambroisies ©; d: INRAE).

on its germination date and habitat (Allard 1945; Abul-Fatih et al. 1979c). Male and female flowers are separated on the same individual (monoecious plant – Payne 1964). Male inflorescences are up to 30 cm long, terminal, and consist of individual clusters of 10–50 yellow flowers. Female inflorescences are grouped at the base of the male inflorescences and sometimes in the axils of the upper leaves. Female flower heads contain a single flower lacking a corolla, composed of a single pistil and ovule, and enclosed by an involucre (Curtis and Lersten 1995). Stigmas extend through the involucre and pollination occurs when the involucre is about 1 mm wide and the stigmas are maximally exposed (Curtis and Lersten 1995). *Ambrosia trifida* is a wind-pollinated and mostly outcrossing species (Bassett and Crompton 1982).

The fruit consists of the hardened involucre enclosing an achene (single-seeded fruit; Gunn 1972). The involucre is cup-shaped, tipped with a central beak (2–3 mm) surrounded by a crown of five or more protrusions, and varies considerably in colour, size, and shape. Involucres range from grey to brown to black, from 3 to 14 mm in length and 2 to 10 mm wide, and weigh on average about 35 mg (up to 50 mg) (Payne 1970; Washitani and Nishiyama 1992; Royer and Dickinson 1999; Sako et al. 2001; Figure 1c). Involucres vary from spherical to flattened and protrusions from short-blunt to long-tapered. The fruit is the unit of dispersal and will be referred to hereafter as “seed”.

The highly allergenic tricolpate, three-celled pollen is characteristic (Figure 1d) of *Ambrosia* species (Curtis and Lersten 1995; Liu et al. 2012). Pollen grains (16–27 µm in diameter) are nearly spherical with numerous spines (4 to 10) and spinules (Wodehouse 1945; Bassett and Terasmae 1962). Pollen grains of *Ambrosia* species are not easily distinguishable using ordinary pollen identification techniques despite some differences in pollen size (Robbins et al. 1979). Although the duration of *A. trifida* pollen viability is unknown, viability of three-celled pollen is generally thought to be brief (Curtis and Lersten 1995).

Intraspecific variation

Ambrosia trifida is characterized by large morphological and genetic variability for many traits, from seed size to herbicide tolerance (Patzoldt and Tranel 2002; Schutte et al. 2008a; Hovick et al. 2018). Like many weeds in cultivated areas, *A. trifida* height (from about 1.50 m to 6.00 m; Bassett and Crompton 1982) and degree of branching vary in response to the proximity and height of neighbouring vegetation. Lobing of leaves, as mentioned earlier, is also variable. Seed shape and size, which are usually stable characteristics, are extremely variable in *A. trifida* both within and

between populations (Payne 1970; Harrison et al. 2007; Hovick et al. 2018; Sako et al. 2001; Schutte et al. 2008a; Figure 1c). Phenotypic variation has also been observed in *A. trifida* seed production: western populations in the U.S. Corn Belt were nearly four times more fecund and had a nearly 50% greater allocation to reproduction than eastern populations (Hovick et al. 2018). Variation in seed morphology and seed production may facilitate germination under different conditions and expansion of *A. trifida* into new areas.

Few data exist on genetic variability in *A. trifida*. High variability of acetolactate synthase (ALS) alleles was identified in a sample from a population of *A. trifida* resistant to ALS-inhibiting herbicides (Patzoldt and Tranel 2002). This suggested a relatively high initial frequency of resistant ALS alleles may have been present in the founding population, facilitating resistance development (Patzoldt and Tranel 2002). Genetic study of the variability of *A. trifida* may be facilitated by the fact that 40% of gSSR and EST-SSR markers identified for *A. artemisiifolia* are transferable to *A. trifida* (Meyer et al. 2017).

Distribution and status

Native range

Ambrosia trifida is native to North America where it has expanded as a plant of disturbed areas over the last 200 years (Bassett and Crompton 1982). The species is observed primarily at latitudes between 30° and 45° North due to its fairly strict photoperiod requirement for flowering (Allard 1943). *Ambrosia trifida* grows primarily in the east-central United States (U.S) (from Virginia to Missouri) and southeast Canada (southwest Quebec) (Clark and Fletcher 1906; U.S. Agricultural Research Service 1970; Bassett and Crompton 1982), but is now present in almost all U.S. states and Canadian provinces with a lesser presence in the western part of the continent. It has been found in the northern states of Mexico (Sonora, Chihuahua) since the end of the nineteenth century (GBIF.org 2020).

Introduced range

Ambrosia trifida has been successful in all northern temperate continents. GBIF.org (2020) indicate occurrences at latitudes between 33° (Japan) and 66° North (Finland).

Ambrosia trifida has been reported in at least 24 European countries (Figure 2; Table 1), although most of these records correspond to casual populations. The invasive success of *A. trifida* has been limited despite numerous introductions. Of 324 observations of

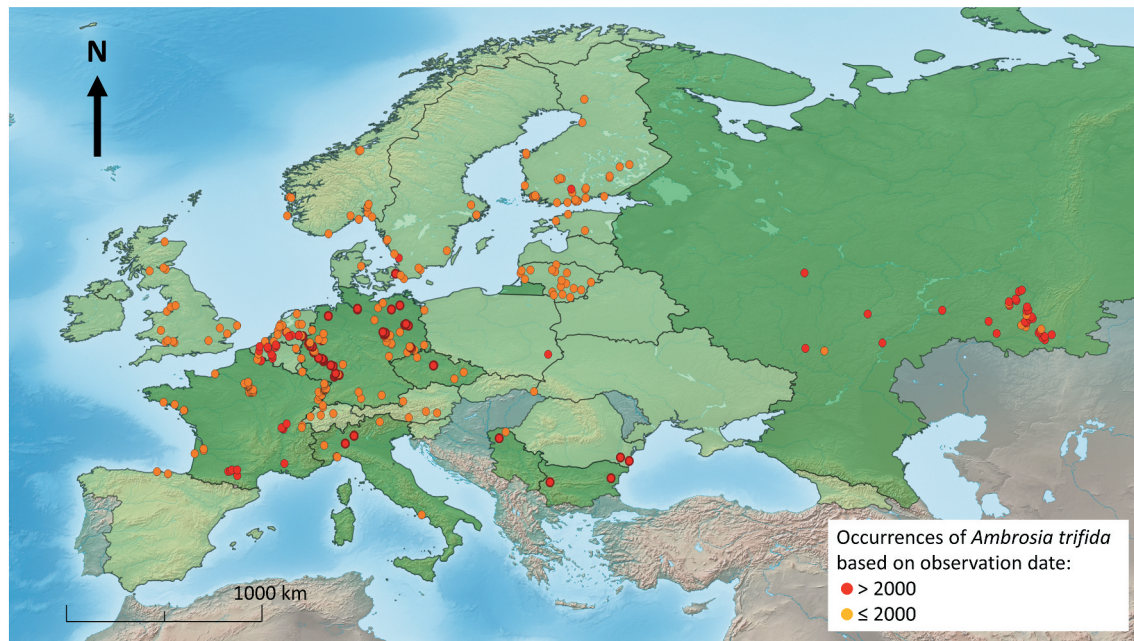


Figure 2. Distribution of *Ambrosia trifida* in Europe (occurrence downloaded from GBIF.org 2020) and from references used in the document. Data from botanical gardens or without indication of date or location or very close to each other geographically were not kept. ●: ≤2000; ●: >2000; ■: very rare and casual. At the scale of the countries ■: rare and casual; ■: rare but naturalized

Table 1. Occurrence, date of introduction and current status of *Ambrosia trifida* in Europe.

Country	Date of introduction	Status	Reference
Austria	1948	Casual	Follak et al. 2013
Belarus	1994	Casual	Tzvelev 1994
Belgium	1894	Casual	Verloove 2006
Bulgaria	1993	Naturalized	Stoyanov et al. 2014
Czech Republic	1930	Naturalized	Rydlo et al. 2011
Denmark	1997	Casual	GBIF.org 2020
Estonia	1989	Casual	From EPPO Global data base 2020
France	1901	Naturalized	Chauvel et al. 2015
Finland	1920	Casual	GBIF.org 2020
Georgia	1935	Eradicated	Kott 1953
Germany	1877	Naturalized	From Follak et al. 2013
Ireland	2014	Casual	Reynolds 2002
Italy	1899	Naturalized	Celesti-Grappo et al. 2009
Israel	2001	Eradicated	Yair et al. 2019
Latvia	1900	Casual	From Gudzinškas 1993
Lithuania	1947	Casual	Gudzinškas 1993
Luxembourg	1950	Casual	GBIF.org 2020
Netherlands (The)	1900	Casual	Vuyck 1902
Norway	1917	Casual	GBIF.org 2020
Poland	1903	Casual	Lacowitz 1903
Romania	1970	Casual	Anastasiu and Negrean 2006
Russia	1950	Naturalized	Kott 1953; Flora URSS 1959
Serbia	1982	Naturalized	Koljadžinski and Šajinović 1982
Slovakia	1980	Casual	Follak et al. 2013
Slovenia	Late 1980s	Casual	Vasić 1990; Follak et al. 2013
Spain	1982	Casual	GBIF.org 2020
Sweden	1897	Casual	GBIF.org 2020
Switzerland	1900	Casual	Thellung 1907
Ukraine	1993	Casual	Tokhtar 1993
United Kingdom	1897	Casual	Rich 1994

A. trifida populations in Central Europe, only 27% were considered to be naturalized (Follak et al. 2013). *Ambrosia trifida* is classified as naturalized in Bulgaria, the Czech Republic, France, Germany, Italy, Russia and Serbia. Problematic populations have been limited to southwestern France and northern Italy, where *A. trifida* has recently undergone a rapid

expansion. Ruderal habitats occupied by *A. trifida* differ according to region. In Italy and Russia, occurrences are mostly along riverbanks and flood plains (Abramova 2011, 2017; Follak et al. 2013), whereas in France, well-naturalized populations are observed in agroecosystems that include summer-irrigated crops (Chauvel et al. 2015). In the Czech Republic and

Slovakia, *A. trifida* has been found along railway tracks (Jehlik 1995).

Outside of Europe, *A. trifida* has been introduced in Asia in China, Japan, Mongolia, and South Korea. The spread of *A. trifida* in Asia could result in the species becoming a major agricultural and public health problem. In Japan, *A. trifida* was first recorded in 1952 (from Miyatake and Ohno 2010) and subsequently invaded natural areas during the 1990s (Washitani 2001). It now occurs in natural areas throughout the entire country (Washitani 2004) – predominantly in the floodplains of large rivers (Miyawaki and Washitani 2004) – and is considered one of Japan's 16 most invasive species (Muranaka et al. 2005). In South Korea, *A. trifida* was first recorded in the Seoul metropolitan area during the 1970s and is now widely naturalized in roadsides and riverbanks throughout the country (Choi et al. 2007; Lee et al. 2010). In China, *A. trifida* was introduced from North America in 1935 (Xie et al. 2001; Qin et al. 2014) and has been observed in Inner Mongolia since the 1960s (Wan et al. 2017). Since the 1950s, it has been considered a major invasive weed of Northeast China (Table 2).

In other parts of the world, *A. trifida* has been reported several times in Israel in the past but seems to have since disappeared (Yair et al. 2019). The species does not seem to have been reported in Armenia (Fayvush and Tamanyan 2014). It seems to be absent from the African continent, Australia (CISS (Centre for Invasive Species Solutions) 2020) and South America (Peru) despite detection of its seeds in imported crop seed (Peru) (COSAVE 2018).

Despite the strong adaptability of *A. trifida* to different habitats observed in N. America, introduction of *A. trifida* outside its native range has not necessarily resulted in naturalization or spread. Unfavourable local conditions may account for this: lack of sufficient moisture (e.g. Israel) and early frost events that disrupt seed maturation (e.g. northern and central Europe) may explain poor naturalization and spread of *A. trifida* in these areas. The distinctive size and shape of the plant, which enable early detection and weed control efforts, may also restrain its invasiveness.

History of introduction and spread in Europe

Ambrosia trifida was introduced into Europe at the end of the nineteenth century and has expanded its range since the Second World War (Follak et al. 2013; Chauvel et al. 2015). It is the latest species in the genus *Ambrosia* to have been introduced, following

A. tenuifolia (about 1830), *A. artemisiifolia* (about 1860) and *A. psilostachya* (about 1875). The first introductions of *A. trifida* (1877) were reported in the current territory of Germany (appendix 1D) and Switzerland in river ports along the Rhine and Elbe Rivers (Aellen (Von) 1916). In the Netherlands (Vuyck 1902; appendix 1C) and in Belgium (appendix 1A), *A. trifida* was first observed in 1900. Follak et al. (2013) collated numerous records in eastern and central Europe, providing precise times of introduction: the Czech Republic (1930), Austria (1948), Slovakia (1980), and Serbia (1981). In the United Kingdom, the first definitive records of *A. trifida* are from 1897 (Murray 1808) and it is at present recorded as very scattered (Stace 2019) and casual (Rich 1994). In Sweden (appendix 1F), *A. trifida* was observed for the first time in 1893 near Danvik and later in 1916 on waste disposal areas over a period of four years (Laurent 1919). Its origin was never elucidated. In Switzerland, the plant was found following the movement of the American circus Barnum and Bailey (in 1903 Herbarium G – see picture appendix 1B). In Georgia, *Ambrosia trifida* was registered initially in 1935 as a weed of essential oil-geranium plantations and later in wheat fields (Kott 1953). According to local quarantine service reports, the weed was finally eradicated in fields in 1986 (Kott 1953), demonstrating that *A. trifida* can be controlled in cultivated fields. For some countries in Europe, for example, Bosnia and Herzegovina (Maslo 2016), Croatia, Hungary and Ukraine, no introductions have yet been observed (EPPO Global data base 2020).

One of the main pathways of introduction of *A. trifida* into Europe has been through grain imports for the agri-food industry (Verloove 2006) and as a contaminant of crop seeds for planting, including spring wheat (*Triticum aestivum*) (Ministère Fédéral de l'Agriculture Canada 1930; Stebler 1906), soybean (*Glycine max*) (Chauvel et al. 2015), maize (*Zea mays*) (Stoyanov et al. 2014; Chauvel et al. 2015), forages (Bandricourt 1918), sunflower (*Helianthus annuus*) and sorghum (*Sorghum bicolor*; Anses 2017). In the United Kingdom, records of incidence are correlated with North-American trade and areas around shipping docks (Rich 1994). In France, forage for horses brought from North America during the First World War was clearly an initial pathway for *A. trifida* (Bandricourt 1918): it was identified in combat areas in France and Russia in both British and American military camps and fodder was designated the vector of introduction (Coste 1916; Bandricourt 1918; Maury

Table 2. Occurrence, date of introduction and current status of *Ambrosia trifida* in Asia.

Country	Year of introduction	Status	Reference
China	1935	Naturalized	Xie et al. 2001
Japan	1952	Naturalized	from Miyatake and Ohno 2010
South Korea	1964	Naturalized	from Do Sung 2005

1922; Kott 1953; appendix 1E). Similar observations were made in France for *A. artemisiifolia*: thus, these two plants can be categorized as polemochorous species (Aymonin and Flament 2011).

Records maintained by botanical societies and herbarium specimens with their informative labels have facilitated the study of *A. trifida* introduction and spread in Europe. In many European cities, *A. trifida* was cultivated in botanical gardens for botanical studies, for example, in Paris (1765), Strasbourg (1807; Chauvel et al. 2015), Madrid (1766; GBIF.org 2020) and Liège (1829; Verloove 2006). There is no evidence that escapes occurred from these botanical gardens.

Ecology

Response to abiotic factors

Climate and potential distribution (see maps – Figure 3a, Figure 3b)

Various models have been developed to predict climatic zones favourable to *A. trifida*. An early model for Central and Eastern Europe developed by Follak et al. (2013) predicted that only 16% of the territory considered in their study would be favourable for *A. trifida* due to limitations imposed by the distribution of precipitation across the year as well as during the summer months. Currently, the species occupies less than 1.5% of the areas predicted to be climatically favourable by their model.

Anses (2017) modelled the potential distribution of *A. trifida* using Maxent (Phillips and Dudik 2008) and suggested favourable climatic conditions may be present in France, Spain (northeast), northern Italy (mainly the Po Valley) and much of Central Europe from Germany to Romania (Figure 3a). They found that mean temperature and precipitation during the warmest quarter were the most important factors in the distribution of *A. trifida*, accounting for 56.4% and 36.3%, respectively, of the overall variation in its

distribution, suggesting that drought stress and cold temperature may be critical limiting factors. Finally, an ensemble distribution model (EPPO 2019) using methods for modelling invasive non-native species distributions (Chapman et al. 2019) suggested that suitability for *A. trifida* was most strongly determined by winter temperature, solar energy (potential evapotranspiration) and moisture availability. Across Europe and the Mediterranean region, the ensemble model predicted a large, climatically suitable range spanning most of Europe below $\sim 55^{\circ}\text{N}$, excluding the Mediterranean coastline, and generally increasing in suitability towards the more continental east. The model suggested that naturalization in northern Europe will be limited by low energy availability, while warm winters mainly limit establishment around the Mediterranean and Black Sea coastlines most likely due to the need for stratification to break seed dormancy. Drought stress was suggested to be the most important limiting factor in the driest parts of southern Russia and in Turkey. *Ambrosia trifida* is currently absent, recorded sporadically or unrecorded from the central part of this predicted distribution (Figure 3b), suggesting a potential for much wider establishment.

Differences in these model projections reflect choice of modelling methodology, distribution data and climatic predictors. For example, in EPPO (2019), presence records in Germany were used as naturalized populations, while they were treated as casual (and so excluded from the model) by Anses (2017). As a result, greater suitability in northwest Europe was estimated by EPPO (2019). Populations in Germany appear to be a mixture of casual and naturalized, with greater naturalization reported in the east (Bundesamt für Naturschutz 2020). As such the suitability in northwest Europe may be intermediate to that depicted by both models. Additionally, summer precipitation in southern Europe may be a stronger limiting factor than reflected in the model by EPPO (2019), which did not include this variable

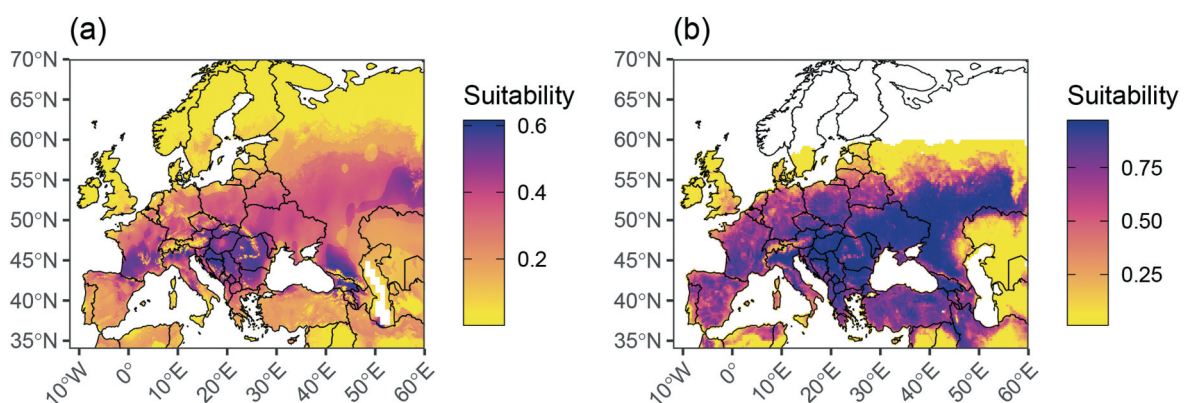


Figure 3. (a): habitat suitability for Europe for *A. trifida*. The stronger the suitability index, the more similar the environmental conditions are to those in the areas where the species is present. (b): projection of climatic suitability for *A. trifida* establishment Europe. A greater suitability in northwestern Europe can be observed with the model used by EPPO (EPPO 2019); Both models indicated a strong potential for ragweed invasion in Europe.

although it was found to have a strong effect by both Anses (2017) and Follak et al. (2013). Despite these inherent uncertainties, these three modelling studies all support the likely influence of low summer temperature and drought stress in limiting invasion by the species in parts of Europe. This is supported by experimental studies showing strong effects of temperature and moisture on demographic performance of *A. trifida* (Wortman et al. 2012). The three modelling studies also all suggest a potential for much wider establishment in Europe. Similar conclusions were reached for China in another distribution modelling study (Qin et al. 2014).

Light – substratum – water

Ambrosia trifida is a heliophilous species that grows mostly on moist, rich soil, preferentially in disturbed and open habitats (Bassett and Crompton 1982; Korres et al. 2015). Water-flooded soils or poorly drained areas are not favourable for its survival but *A. trifida* can establish on levees of marshes and wetlands (Sickels and Simpson 1985; Park et al. 2020). *Ambrosia trifida* is not well adapted to drought and has not been observed in areas with a long summer drought unless there is irrigation (Allard 1945), as in southwestern France. *Ambrosia trifida* may modify soils through release of nutrients from its rapidly decomposing litter, improving soil fertility for growth of its progeny (Mun and Lee 2020).

Response to biotic factors

In annual plant communities, *A. trifida* can become dominant, producing most of the total plant biomass (over 90%) and suppressing associated species. Plant species richness was reduced at ruderal sites subjected to intense invasion by *A. trifida* (Abul-Fatih and Bazzaz 1979b).

Natural succession is generally not favourable to maintaining annual plant populations; Although undisturbed, closed natural environments dominated by established biennial and perennial vegetation may limit *A. trifida* seedling establishment (Hartnett et al. 1987), nevertheless, it can survive in perennial communities. As often occurs in annual plants, early emergence and rapid development of the first true leaves is required to avoid competitive stress from other plants (Hartnett et al. 1987). In comparison with other annual species, *A. trifida* has large seeds and seedlings, and a high photosynthetic rate (Bazzaz 1979), which assist its establishment in perennial vegetation. Further, development of secondary dormancy in *A. trifida* seeds (Davis 1930) protects them from germinating under conditions unfavourable for seedling growth. In the event of disturbance, new seedlings can emerge and establish themselves quickly due to their high photosynthetic rates.

During subsequent growth and development, *A. trifida* populations are regulated through competition at both the level of individual leaves (Hartnett et al. 1987: death of the first order of leaves; see also Abul-Fatih and Bazzaz 1980) as well as the whole plant (Hartnett et al. 1987). In open habitats, *A. trifida* can establish dense monospecific stands and adapt to intraspecific competition for light through high leaf turnover that favours the production of new leaves higher along the stem in a more favourable light-environment (Abul-Fatih et al. 1979c). Rapid growth in height allows *A. trifida* to dominate such crops as soybean (Page and Nurse 2015) and irrigated maize (Figure 4a, Figure 4c). Under optimal conditions, the size of the plant can exceed 5 m (Figure 5).

The Figure 5 is composed of two figures with an identical legend]

Perhaps not surprisingly, studies have shown that increasing the diversity of recipient plant communities does not prevent establishment of *A. trifida*, necessitating further management efforts to suppress its dominance (Byun and Lee 2018). Thus, its invasion cannot be regulated easily by competition from the plant community, and, in addition, the release from above- and belowground natural enemies outside natural range of *A. trifida* favours its growth and development (Zhao et al. 2020).

Habitats and syntaxonomy

Ambrosia trifida moved northward in the North American continent following the retreat of the

last glacial ice (Basset and Terasmae 1962) and is by origin a riparian species of riverbanks and floodplains (Bassett and Crompton 1982; Leck and Simpson 1994). With the break-up of land by European settlers, *A. trifida* colonized crop fields and expanded its ecological niche to a variety of non-riparian edge habitats such as fencerows, upland forest borders, roadsides, railroad embankments, and urban and industrial waste sites (Groh and Minshall 1940; Bassett and Crompton 1982; Sosnoskie et al. 2007; Venkatesh et al. 2013; Korres et al. 2015). Over the last 150 years, *A. trifida* has continued to adapt to agricultural conditions – including, recently, cropping systems with genetically modified crops – and is regarded today as a major weed (Regnier et al. 2016; Ganie et al. 2017). The development of giant ragweed as a weed in crop fields is variable across the U.S. Corn Belt but seems to follow initial colonization of edge habitats in the local area (Regnier et al. 2016).

A geographic pattern of distribution primarily in non-crop edge habitats with variable invasion of agricultural fields has also been observed in Europe (Chauvel et al. 2015). The species seems to occur particularly in fields liable to be flooded, probably due to the plant's preference for moist soils and



Figure 4. A: *Ambrosia trifida* outgrowing irrigated maize in southwestern France (INRAE ©)/b: Dense stand of *A. trifida* along the margin of a cereal field in the Czech Republic (S. Follak ©)/c: Maize field in Serbia/d: in winter wheat (L. Mario ©)/e: abandoned livestock farms in Republic of Bashkiria, Russia (LM. Abramova ©).

movement of the buoyant seeds in runoff water and through watercourses (Weed 1910; Chauvel et al. 2015). It is observed mainly in disturbed environments such as cultivated fields (Rydlo et al. 2011; Amor Morales et al. 2012; Chauvel et al. 2015); banks of major water courses such as the Rhine (Germany), Po (Italy) and Elbe (Czech Republic; Jehlik and Hejny 1974); road networks; disturbed environments (e.g. abandoned industrial sites, wastelands; Krippel and Colling 2006) and green urban areas (gardens) (Follak et al. 2013). In Spain, the plant occurs in fields, roadsides and fallows (Láinz and Loriente 1983; Amor Morales et al. 2012). In contrast, in southwestern France since the 2000s, the species has been observed only in cultivated fields mores especially in summer annual crops (Belhacène 2010; Chauvel et al. 2015). In Russia, *A. trifida* is partially present on arable lands adjacent to the Volga river basin (Volga upland; Silaeva 2011; Vasyukov 2011; Senator and Vasyukov 2019). In

Asia, the plant occupies various habitats such as river banks, crop fields and roadsides (Kim and Choi 2008; Xu et al. 2012). The reason why giant ragweed invades crop fields in some regions but not in others is unknown but would be of vital importance in containing the spread of this species. In summary, from a phytosociological point of view (Mucina et al. 2016), *A. trifida* is mainly found in plant communities of summer-sown crops belonging to the order *Chenopodietalia albi*, in pioneer vegetations at the edge of wetlands belonging to the order *Bidentetalia tripartitae*, and to a lesser extent in ruderal vegetations belonging to the class *Sisymbrietea officinalis*.

Ecological interactions

Granivory and herbivory

Invertebrates. In its native area, *A. trifida* is a food or host plant for a number of invertebrates including species from the orders Diptera (e.g. *Euaresta festiva*;

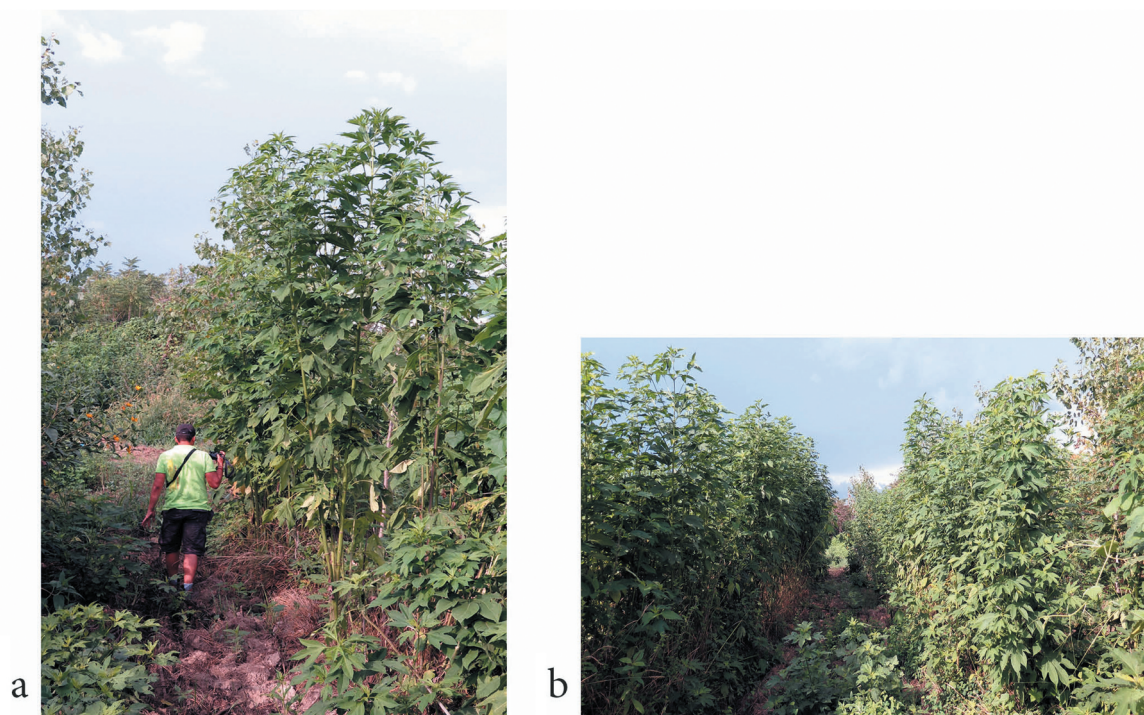


Figure 5. *Ambrosia trifida* in Italia (Pavia) in a site along the Po River (August 2015). To give an idea of the size of the plants, the man on the picture is 1.75 m tall (P. Tóth ©).

Blatchley 1920), Lepidoptera (e.g. *Chlosyne lacinia*; Beal 2007) and Coleoptera (e.g. *Dectes spinosus* Say; Blatchley 1920). The larvae of *E. festiva* can destroy between 2% and 25% of the seeds (Vitolo and Stiles 1987). Seeds of *A. trifida* are also eaten by the larvae of two weevils (Coleoptera: Curculionidae, *Chionodes mediofuscella* and *Smicronyx flavicans*) and a moth (Lepidoptera: Gelechiidae, *Conotrachelus geminatus*) (Harrison et al. 2001). Together, insect larvae caused 13–19% *A. trifida* seed loss (Harrison et al. 2001). In addition to seed-boring insects, the aphid, *Uroleucon ambrosiae* specializes on *A. trifida* in eastern North America (Bernays and Funk 1999).

Vertebrates. Seeds of *A. trifida* are rich in fat and protein (Willson and Harmeson 1973; Harrison et al. 2003) and are highly predated by vertebrates (Harrison et al. 2003). About 90% of *A. trifida* seeds are predated during the year after their dispersal in crop fields in the U.S. Corn Belt, with rodents being the primary predator (Harrison et al. 2003). *Ambrosia trifida* seeds can also be predated by native birds (Willson and Harmeson 1973). The intensity of predation of *A. trifida* seeds by vertebrates varies according to abiotic and biotic factors, including trophic interactions that regulate seed predator populations and activity (Davis and Raghu 2010). A unique interaction of the European earthworm (*Lumbricus terrestris*) and *A. trifida* observed in the U.S. Corn Belt has the potential to impact predation of *A. trifida* seeds by vertebrates. In cultivated fields, *L. terrestris* collects and buries large numbers of the

seeds. Regnier et al. (2008) hypothesized that seed burial could benefit *A. trifida* by protecting the seeds from detection and consumption by seed predators and benefit earthworms indirectly through increasing plant establishment and litter return near their burrows. The potential for *L. terrestris* to bury seeds and facilitate seedling recruitment is increased by mild, moist conditions in the fall (Schutte et al. 2010). Management strategies to increase seed losses to predation by leaving soils untilled and seeds vulnerable to detection on the soil surface by seed predators may be counteracted by the burial activities of this earthworm species. An improved understanding of species interactions among seed predators and the influence of the environment on seed predator activity will be key to managing *A. trifida* seed losses in agricultural and natural environments.

Despite a high level of regulation of *A. trifida* in its native area by different organisms at different life stages – rarely observed for an arable weed species – biological regulation is not expected by itself to maintain *A. trifida* densities below economic threshold levels in cultivated fields (Harrison et al. 2003). Due to the extremely low thresholds for this highly competitive species (Harrison et al. 2003), only a few seeds are sufficient to establish the next generation that will pose problems for the farmer.

Other biotic relations

Ambrosia trifida is listed in the U.S. as a host of the *Xylella fastidiosa* bacteria (Black et al. 2004), which

could cause serious damage to olive trees cultivated in Europe. *Ambrosia trifida* is also described as an alternate host for aster yellows, chrysanthemum stunt, tobacco mosaic, tobacco ring spot and tobacco streak viruses (Royer and Dickinson 1999). Mycorrhizal structures have been observed on *A. trifida* roots but their role in the growth of the plant is unknown (McDougall and Glasgow 1929). A parasitic plant, *Orobanche ludoviciana* Nutt., has been recorded by parasitizing *A. trifida* (Schneck 1898). In abandoned cropland in China (Liang et al. 2007), higher number of nematodes taxa (plant parasites and bacterivores) was found under *A. trifida* plants that could affect soil processes.

Biology

Phenology

Ambrosia trifida seeds can emerge from up to 16 cm deep in the soil (Figure 6), but optimal depth for emergence is 2 cm and occurs earlier for shallow compared to deeply buried seeds (Abul-Fatih and Bazzaz 1979b). Seeds germinate under a wide range of temperatures with optimum germination occurring between 10°C and 24°C (Abul-Fatih and Bazzaz 1979a; Royer and Dickinson 1999). Base temperature estimates for emergence varied from 2 to 13°C (Goplen et al. 2018). Colder overwinter temperatures increased emergence rate (Davis et al. 2013; Goplen et al. 2018), likely by alleviating dormancy more quickly (Washitani and Nishiyama 1992; Ballard et al. 1996; Schutte et al. 2012). Warmer and more fluctuating soil

temperatures during seedling recruitment accelerated emergence by reducing the lag phase, whereas cooler, less fluctuating temperatures increased the lag phase and prolonged emergence (Goplen et al. 2018). Goplen et al. (2018) suggested cooler temperatures under established canopies may explain why *A. trifida* emergence was delayed and prolonged in alfalfa (*Medicago sativa*) compared to annual row crops (Goplen et al. 2017, 2018).

In its native range, *A. trifida* emerges earlier than most other summer annual species – typically, in March – but the length of its emergence period varies with geographic area and habitat and there is an interaction between these two factors. Populations of *A. trifida* that occur in successional habitats exhibit early and brief emergence (Sprague et al. 2004; Johnson et al. 2007a; Schutte et al. 2012). This phenology is observed across different types of successional habitats (e.g. railroad embankments, forest borders, old fields) and across different geographic regions. Early, synchronous emergence provides a competitive edge in successional environments by ensuring seedling establishment before perennial vegetation resumes growth following winter (Hartnett et al. 1987). In contrast, populations of *A. trifida* that occur in agricultural fields (Figure 4b, Figure 4c) have a prolonged emergence period that extends from March through August (>100 days), allowing re-infestation of a crop field following weed control measures (Davis et al. 2013; Schutte et al. 2008b, 2012). However, this prolonged emergence is



Figure 6. Elongation capacity of hypocotyl within *Ambrosia trifida* (D. Marisavljevic ©).

observed only in the east-central region and not in the western and northern regions of the U.S. Corn Belt, where emergence phenology of *A. trifida* populations in crop fields is early and brief, just as it is in successional habitats (Sprague et al. 2004; Johnson et al. 2007a; Werle et al. 2014; Kaur et al. 2016; Goplen et al. 2018). Delayed emergence in east-central populations is associated with greater embryo dormancy that prevents emergence at the low temperatures typical of early spring (Schutte et al. 2012). Different emergence phenologies in the different regions may reflect different selection histories in agricultural fields and/or differences in the adaptability of local populations. The prolonged emergence phenology is also observed in *A. trifida* populations in agricultural fields in France, especially in irrigated fields (Mamarot and Rodriguez 2014).

As mentioned earlier, flowering of this annual plant is induced by reduction of the photoperiod (Allard 1932, 1943). Flowering begins first for male inflorescences and proceeds later for female inflorescences (Allard 1945). As photoperiod shortens the proportion of male to female inflorescences decreases: under long photoperiods plants produced only male inflorescences whereas under extreme conditions of reduced day length, plants generally produced only female inflorescences and were also greatly dwarfed (Allard 1945). As mentioned earlier, in its native range, *A. trifida* flowers from early August until the first killing frost (Allard 1945), and seeds begin to ripen in September (Harrison et al. 2001; Johnson et al. 2007a). The structure of the male inflorescences allows a continuous slow release of pollen (Curtis and Lersten 1995) that is probably favourable to reproduction but undoubtedly also harmful to those individuals allergic to the pollen. Pollen emission follows a characteristic diurnal pattern beginning an hour or two after sunrise with a peak a few hours later and decreasing throughout the afternoon (Ogden et al. 1969).

Physiological data

Ambrosia trifida has high photosynthetic (C3 photosynthesis system) (Bazzaz 1979) and net assimilation rates (Abul-Fatih and Bazzaz 1979b) compared to several other weed species with similar ecology and phenology (e.g. *Amaranthus retroflexus*, L. and *Abutilon theophrasti* Medik; Bazzaz 1979). These traits contribute to its strong competitive ability.

Responses to stress (water – nutrient)

Seeds germinate over a wide range of soil moisture levels, but highest germination rates were observed at 20 to 33 % soil moisture (Abul-Fatih and Bazzaz 1979b). Base water potential estimates for seedling emergence vary widely from -0.15 to -30 MPa and *A. trifida* seeds are able to germinate under very dry conditions (Davis et al. 2013). As mentioned earlier,

unlike some other species of the genus *Ambrosia*, *A. trifida* is not described as a plant adapted to dry conditions (Allard 1945), and in natural areas, its establishment is favoured by moist environments (Korres et al. 2015). *Ambrosia trifida* seems to be able to tolerate a wide variety of soil types but no salt tolerance has still been reported in the literature. In maize, nitrogen fertilization timing did not affect early *A. trifida* growth but did affect dry weight of mature plants, with delayed N application increasing dry weight compared to early N application (Johnson et al. 2007b). The plants can accumulate nitrogen in large quantities (up to 104 kg N ha^{-1} at densities of $0.5 \text{ plants m}^{-2}$), thus limiting crop growth (Johnson et al. 2007b).

Seed biology

Seed production in *A. trifida* is low compared to many other annual weeds due to the relatively large size of the seeds. Considerable variability in fecundity has been observed in response to several factors, including environmental conditions, habitat, geographic region, and competition from neighbouring plants. Values for seed production range from 275 to 1,818 seeds per plant (Abul-Fatih and Bazzaz 1979b; Bazzaz and Carlson 1979; Harrison et al. 2001; Goplen et al. 2016). Relatively low seed production is compounded by low seed viability at dispersal due to destruction by pre-dispersal seed predators and pollination failure. Seed viability at dispersal ranges from less than 50% to 66% (Goplen et al. 2016; Harrison et al. 2001).

Davis (1930) indicated that seeds are dormant at maturity (primary dormancy). In natural habitats and under controlled experimental conditions, primary dormancy is removed by exposure to moist, cool temperatures (optimum temperature is 5°C) for a period of about three months (Davis 1930). Variation in seed dormancy level contributes to a prolonged emergence period in some populations (Schutte et al. 2008b, 2012). Secondary dormancy is induced in embryos that fail to germinate following stratification, and dormancy induction is due to restricted respiration at high temperatures (Davis 1930).

Ambrosia trifida can establish a soil seed bank for 4 to 21 years depending on seed burial depth, with seed longevity increasing with burial depth (Toole and Brown 1946; Stoller and Wax 1974). Harrison et al. (2007) found some seeds remained viable for nine years when buried 20 cm. The majority (90% or more) of *A. trifida* seeds buried 10 cm or less lost viability after four years (Stoller and Wax 1974; Harrison et al. 2007). Similarly, data from China (Dong et al. 2020) showed that in grassland, more than 98% of the seeds disappeared during the first year and germination rates

fell by 40% after three years. Due to the relatively short duration of seed longevity in soil at depths below 10 cm, strict control of *A. trifida* just after its introduction should be successful in managing the weed relatively quickly.

Reproductive biology

Hybrids

Ambrosia trifida is a diploid species ($2n = 24$; Payne 1964) that reproduces through cross-pollination. *Ambrosia trifida* can hybridize with *A. artemisiifolia* ($2n = 36$) (Wagner 1958; Vincent and Cappadocia 1987; Vincent et al. 1988) giving rise to a new taxon, *A. x helenae* Rouleau 1944.

This taxon was observed in 1915 in Canada (from Wagner 1958) in common gardens and waste places and described as sterile (Vincent et al. 1988). This hybrid was also observed in France in 1939 in the Bordeaux Botanical Garden (*Ambrosia ballaisii* – specimen found in Herbarium G et BORD) (Figure 7). Hybrids are difficult to recognize due to the high variability in leaf morphology in the hybrids as well as in *A. artemisiifolia*.

Natural spread

Seeds of *A. trifida* spread naturally mainly by barochory a few meters around the mother plant. For populations growing on sloping land, runoff can carry seeds downslope, and for populations near rivers, dispersal by hydrochory can carry seeds several kilometres. In North America, seeds can be moved short distances (around 25 cm) by

the earthworm *L. terrestris* (Regnier et al. 2008; Schutte et al. 2010) and greater distances by rodent and avian seed predators (Harrison et al. 2003). During cold periods, seeds and leaves frozen together and inflorescence fragments can also be transported over ground or snow short distances by wind each day (Foerste 1882), which can amount to a considerable distance over the entire winter season.

Human-assisted spread

The spread of *A. trifida* during the last several decades is due mainly to human-assisted spread. This mode of spread can be extensive, as seeds of *A. trifida* may contaminate agricultural products (seed, grain, forage material) and thus be spread over long distances from one region to another. Locally, seeds may be dispersed within a field and between fields by agricultural machinery such as combine harvesters and tillage implements. For example, in southwestern France, *A. trifida* was first detected in only a few crop fields in 1992. In 2013, the species was reported in at least 20 crop fields in about 12 municipalities (Chauvel et al. 2015). In 2018, more detailed monitoring revealed the presence of *A. trifida* in at least 105 crop fields and 24 non-crop areas in 27 municipalities (Fried et al. 2019). Although it is difficult to estimate the rate of spread from these different surveys, particularly since multiple independent introductions cannot be ruled out, nonetheless these surveys show clearly that *A. trifida* can spread rapidly from field to field across a large agricultural region.

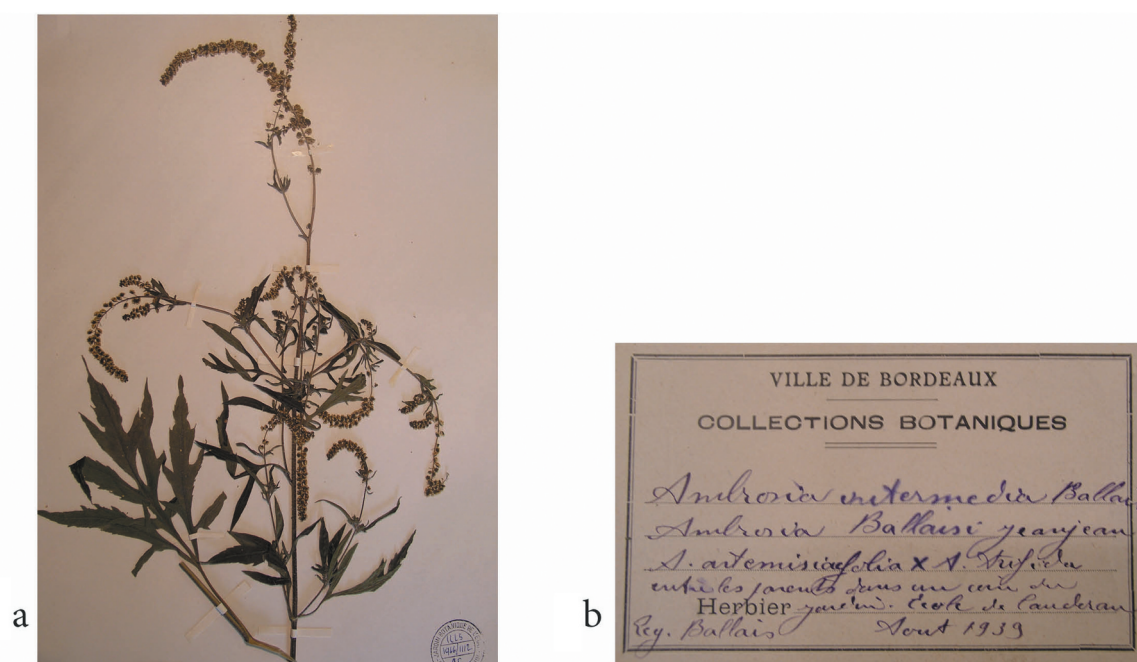


Figure 7. Hybrid *A. x helenae* Rouleau 1944 (named of this herbarium specimen *Ambrosia. balaisii* Jeanjean) – Herbarium BORD.

Economic importance and impacts

Uses and positive impacts

Ambrosia trifida seeds were used as a food resource thousands of years ago by indigenous North Americans (Asch and Hart 2004). *Ambrosia trifida* leaves have been used in traditional medicine as an astringent, emetic, and febrifuge, for insect bites and skin complaints (Beal 2007), and for mercurial salivation (Roberston 1846). The seedheads and sap have been used as a red dye (Beal 2007). Ornithological studies of natural floodplains in Ontario, Canada, showed that *A. trifida* seeds provide an important source of food and cover for winter riparian birds as well as for spring and autumn migrants (Robel and Slade 1965; Dance et al. 2012). *Ambrosia trifida* can be used as a forage of higher nutritive value than many local American common grasses (Dustman and Shriver 1931; Dickinson and Royer 1999). The plant seems to be not toxic and allergenic compounds are not found in livestock products.

Steam-extracted essential oils may have commercially useful antimicrobial and antifungal properties (Beal 2007). Roots of *A. trifida* exude chemical compounds with nematocidal, bactericidal and fungicidal activity (Wang et al. 1998, 2006). *Ambrosia trifida* biochar derived from vegetative tissues has been investigated for removal of cadmium and lead ions from aqueous solutions (Yakkala et al. 2013). The biochar could be a low-cost adsorbent for removal of heavy metal ions from wastewaters (Yakkala et al. 2013).

Negative impacts

Biodiversity impacts

In its native range, *A. trifida* is a highly competitive, dominant species that can establish monospecific stands in ruderal areas, forest edges, riparian habitats, and grasslands (Sickels and Simpson 1985; Regnier et al. 2016). In Europe, no data are available regarding the effects of *A. trifida* on plant community diversity or ecosystem function. Because of the low densities presently observed in most areas, it may not yet be possible to measure its impact on native plant communities. Only the more heavily invaded areas in the Po River valley (river banks, wet grasslands, gravel pits and ditches) may perhaps show a negative impact of *A. trifida* on biodiversity.

Based on *A. trifida*'s preference for open, disturbed habitats, most natural habitats of high conservation value would likely be unsuitable for *A. trifida*, and thus its potential negative effects on biodiversity have not yet aroused great concern. However, *A. trifida* has been observed to dominate natural vegetation in Russia where it has been spreading in floodplain ecosystems in the Southern Urals (Republic of Bashkortostan) since the mid 1990s (Abramova 1997). This spread likely developed from the economic reforms of that time

(the so-called perestroika), which resulted in an abandonment of cultivated fields. The species was first observed in pastures, livestock farms, roadsides, ruderal communities and subsequently in riverbanks and riparian communities. In some plant communities, *A. trifida* has become dominant and caused the formation of so-called derivative communities (secondary community; Abramova 2017). Once naturalized, *A. trifida* can maintain its populations by impeding natural succession. Control measures in semi-natural communities have had only limited impacts.

In contrast to Europe, impacts of *A. trifida* on natural communities have been observed in parts of Asia where climatic conditions could be more favourable for *A. trifida*. In invaded river banks in Japan, plant diversity decreased as *A. trifida* density increased (Washitani 2001). Lee et al. (2010) showed in Central-Western South Korea that when *A. trifida* dominated the vegetation, plant community composition and plant species diversity was reduced in comparison with uninvaded riparian communities. Thus, although *A. trifida* may pose a minor threat to most natural communities, it can reduce plant diversity in alluvial habitats when present at high densities.

Agriculture impacts

In its native range, *A. trifida* causes major economic losses in agriculture. As early as 1889, *A. trifida* was listed as one of the 10 most harmful weeds in the U.S. (Halsted 1889) but was not considered difficult to manage provided interventions were carried out sufficiently early (Georgia 1916). Rapid growth of *A. trifida* allows it to compete with summer annual crops such as soybean, cotton and maize and it is recognized as the most competitive summer annual weed in grain production in the U.S. Corn Belt (Harrison et al. 2001). Yield losses are greatest when the crop and weed emerge simultaneously and decrease when the weed emerges after the crop (Barnett and Steckel 2012; Harrison et al. 2001). Densities as low as one plant per 25 m² reduced maize yield 5%, a phenomenon rarely observed for other weed species (Harrison et al. 2001). A density of less than 2 plants per 9 m of row reduced soybean yield up to 50% and a density of 16 plants per 9 m of row reduced yield up to 92% (Baysinger and Sims 1991). Total losses of yield have been reported due to the presence of *A. trifida* (Ganie et al. 2017). Gibson et al. (2008) observed low-quality soybeans (protein content) were harvested from plots dominated by *A. trifida*. In Europe, infestations in cultivated fields can be found in southwestern France, but yield losses have not yet been quantified (Chauvel, personal com.).

In a recent survey of certified crop advisors in the U.S. Corn Belt, 45% of respondents indicated that *A. trifida* was the most difficult weed to manage in their county, while 57% reported problems with herbicide resistance, either to acetolactate synthase

(ALS) inhibitors, glyphosate (EPSP synthase inhibitor) or to both sites of action (Regnier et al. 2016). The first resistant populations appeared in 1998 in soybean in the U.S. followed by multiple resistant populations in different U.S. states as well as in Canada (Heap 2020).

Ambrosia trifida releases allelopathic chemicals into the environment which can inhibit the germination and growth of wheat and maize (Wang et al. 2005; Kong et al. 2007; Saric-Krsmanovic et al. 2020). Volatile allelochemicals released by *A. trifida* can also stimulate the germination of weeds such as *Echinochloa crus-galli* (L.) P. Beauv. (Saric-Krsmanovic et al. 2020).

Health impacts

Historically, allergenic *Ambrosia* species (including *A. trifida*) have been identified as a public health problem in North America for a long time (Scheppegrel 1920; Wodehouse 1945). The allergens of this genus have been studied since the early 1900s (Brocq-Rousseu 1923) and are now well characterized (Pollenlibrary 2014). As early as the 1930's, *Ambrosia*

species growing in urban areas were destroyed to protect human health (Groh and Winshall 1940): hundreds of thousands of people were affected by allergy problems (Gahn 1933) (Figure 8). Today, *A. trifida* and its congeners *A. artemisiifolia* and *A. psilostachya* are one of the main causes of seasonal allergic rhinitis in the eastern and central U.S. (Arbes et al. 2005). In Canada, the pollen of *A. trifida* is an important cause of hay fever during August and September, especially in Ontario (http://www.omafr.gov.on.ca/english/crops/facts/ontweeds/giant_ragweed.htm). Pollen of *Ambrosia* species contributes to the exacerbation of asthma and allergic conjunctivitis (Oh 2018). Individuals allergic to the pollen of *Ambrosia* sp. may show signs of oral allergy syndrome caused by cross-reactivity between the different *Ambrosia* allergens (Asero et al. 2005). The public health problem is so critical that a vaccine is currently under development as a potential new treatment for allergies to *Ambrosia* pollen (El-Qutob 2015).

Ambrosia species have also had an impact on tourism and outdoor recreation: health effects were of such significance, historically, that visitor numbers at some tourist sites were depressed by the presence of *Ambrosia* species (Groh and Winshall 1940; Durham 1949). Today, individuals allergic to *Ambrosia* pollen are advised to moderate their outdoor activities to avoid contact with the allergen (e.g. <https://www.aaafa.org/ragweed-pollen/>) and the absence of *Ambrosia* species from tourist destinations remains an incentive for attracting tourists (<http://www.ragweed.digitalbishop.com/>). In addition to its allergenic effects, the growth of thick stands of *A. trifida* along riverbanks can restrict access to waterbodies and impede recreational activities.

To date, there has been no documented impact of *A. trifida* on public health or recreational activity in Europe. However, if *A. trifida* populations increase sufficiently, susceptible individuals will experience an allergic reaction and outdoor activities may become limited. Climate change has increased the number of days in the fall of *Ambrosia* pollen season, increasing potential exposure time to *Ambrosia* allergens and subsequent effects on public health (Ziska et al. 2011).

Control costs

In some areas of the U.S., the failure of management measures to control this species has resulted in a total loss of maize yield, even at low weed densities (Ganie et al. 2017). The increasing problem of herbicide resistance development in *A. trifida* (Norsworthy et al. 2011; Regnier et al. 2016) generates additional production costs through increased weed management and/or rotation to less profitable crops or fallow.

In Europe, data are not yet available to quantify the economic impact of this species, but where *A. trifida* is present, there is a significant risk of economic loss due



Figure 8. Leaflet from the U.S. Department of Agriculture explaining how to control ragweed species (Gahn 1933).

to increased production costs stemming from greater weed control and seed cleaning costs. In France, farmers report additional costs for hand weeding *A. trifida*, and there have been reports of destroying crops before harvest where *A. trifida* densities are high. These costs (from a few hundred euros to a few thousand euros per ha) have not yet been studied quantitatively. Despite these reports, a recent survey in southwestern France indicated farmers had no serious concerns regarding *A. trifida*, although its management seemed complex to them, particularly because of its prolonged emergence period (Fried et al. 2019). Although costs at local levels can be significant, these costs are negligible across Europe given the limited distribution of the species and the highly localized nature of existing populations (Follak et al. 2013; Chauvel et al. 2015).

In Asia, the need to preserve natural sites and sustain growing conditions for threatened plants seems to be a major concern (Washitani 2001), but the costs of protecting these sites has not yet been quantified.

Legislation and management

Legislation

Ambrosia trifida is regulated at different levels in the U.S., Canada and in China. In Europe, *A. trifida* is listed as regulated in Azerbaijan, Belarus, Moldova, Russia, Serbia and Ukraine. In the EU, grain intended for animal feed is subject to regulations that severely restrict the presence of seeds of *Ambrosia* species (50 mg/kg of grain, Regulation (EU) 2015/186 of 6 February 2015). In France, imports of seed for spring-grown crops are not subject to any specific regulations with regard to *Ambrosia* species. Nevertheless, from a health point of view, two national texts have been published (decree n° 2017–645, 26 April 2017 and ministerial order), both relating to the fight against *A. artemisiifolia*, *A. trifida* and *A. psilostachya*. Those texts forbid intentional introduction, intentional transport, use, sale or purchase of the three *Ambrosia* species.

Ambrosia trifida is included in the National List of quarantined organisms in Russia (Golovanov et al. 2018) and in the List of the Eurasia Economic Union (EAEU: Belarus, Kazakhstan, Armenia, Kyrgyzstan, Russia). All lots of crop seeds, food grains and legume shipments imported by Russia and the EAEU are checked for the presence of *Ambrosia* seeds. In Bashkortostan (Russia), *A. trifida* is considered one of three priority species for research and control (Golovanov et al. 2018). Based on a Pest Risk Analysis carried out in 2019 (EPPO 2019), *A. trifida* was added to the EPPO A2 List of pests recommended for regulation as quarantine pests. Measures for controlling this species are recommended in all EPPO member countries.

Management

Early detection – seed contamination

Early detection is important to identify new occurrences of the species. *Ambrosia trifida* should be monitored and eradicated, contained or controlled where it occurs in endangered areas, i.e., areas where it could have negative ecological impacts or pose a public health hazard. In addition, public awareness campaigns in countries with a high health risk are necessary to prevent spread from existing populations. If these measures are not implemented by all countries, they will not be effective since the species could spread from one country to another. To ensure that *A. trifida* does not invade new areas, national measures to control the purity of seed lots to avoid contamination with *A. trifida* should be combined with international measures, and there should be international coordination to manage the species. According to current legislation, crop seeds containing seeds of *Ambrosia* species are forbidden to import to sell or to use. Public awareness should be increased: in this regard the distinctive size and shape of *A. trifida* leaves allow for easy identification. Information for the professional public (i.e., farmers and field advisers) should include tips for quick and easy identification and management information on how to control it before it can establish a soil seed bank.

Prevention

The risk of introduction of *A. trifida* seeds in imported crop seeds was studied in Canada (Wilson et al. 2016). This study indicated that the presence of *A. trifida* seeds intercepted in maize, soybean, and small grains from the U.S. highlights that grain cleaning and processing methods have to be maintained to prevent introduction of *A. trifida* seed into new environments. At a larger scale, some countries such as Russia, Israel, and Egypt ban imports of small grains contaminated by *Ambrosia* species (see 7.1.). In some countries in the EU, official organizations have been created to promote the control of *Ambrosia* species. In France and Belgium, “Ragweed Observatories” are responsible for disseminating information about the management of *Ambrosia* species so as to limit their negative impacts on human health (Observatoire des ambrosies 2011; Observatoire wallon des ambrosies 2020).

In ruderal environments contiguous to agricultural areas (Figure 4e), competition from ruderal species with *A. trifida* is unlikely to limit its expansion due to its ability to establish a competitive advantage quickly through early emergence, large initial size, and rapid early growth (Bassett and Crompton 1982). In agricultural environments, it is also unlikely that competition by summer annual cultivated plants alone will prevent the establishment of the species. A high frequency of summer annual crops such as

maize, soybean and sunflower in crop rotation systems strongly promote the establishment of *A. trifida* once a field has become contaminated; in the U.S. Corn Belt, *A. trifida* populations in crop fields were associated with continuous soybean production (Regnier et al. 2016). The introduction of winter annual crops in the crop sequence can be an effective strategy that makes the field at least temporarily unsuitable for *A. trifida* (Fried et al. 2017). Perennial crops such as *Miscanthus* sp. also strongly limit the development of *A. trifida* (Plan de surveillance 2018). These data are confirmed by modelling approaches that confirm that diversified crop rotation systems of at least five different crop species, including both annual and perennial species, are likely to be valuable for managing *A. trifida* (Liebman and Nichols 2020). Such diversified systems provide variation in sowing dates that impede *A. trifida* seedling establishment as well as a better buffer against decreases in herbicide efficiency (Liebman and Nichols 2020).

Cultural practices, including crop density, planting date, row spacing and choice of cultivar also affect the crop's ability to compete with *A. trifida*. For example, soybeans planted in 19-cm rows reduced *A. trifida* biomass more than when planted in 76-cm rows (Hock et al. 2006). Page and Nurse (2015) demonstrated that competitive crop varieties can limit the growth of *A. trifida* and help prevent situations where *A. trifida* management is almost exclusively dependent on the efficacy of herbicide treatment. Increasing the diversity of crop species in the rotation also provides increased opportunities to use a broader variety of chemical and non-chemical weed control practices.

Tillage and irrigation are also factors that influence *A. trifida* populations. In the U.S. Corn Belt, *A. trifida* populations were associated with reduced tillage (but not with conventional tillage or no-tillage) (Regnier et al. 2016). Irrigation may also favour this mesohygrophilic species, particularly beyond its climate envelope in areas where the limiting factor is the level of summer precipitation (areas of southern Europe, North Africa, Israel and Jordan).

Control

Chemical control. *Ambrosia trifida* can be controlled effectively in crop fields through the use of pre-emergence (e.g. imazaquin) and/or post-emergence (e.g. dicamba and 2,4-D) broadleaf herbicides (Soltani et al. 2011; Vink et al. 2012). In soybean, a wide range of active ingredients can be used in the U.S. (Baysinger and Sims 1992), but many of these compounds are no longer authorized in Europe. The efficiency of chemical treatments often depends on soil moisture conditions (Baysinger and Sims 1992). As mentioned earlier, repeated herbicide use has selected populations in North America with varying levels of

resistance to two main herbicide sites of action; acetolactate synthase (ALS) inhibitors and EPSP synthase inhibitors (glyphosate) (Heap 2020). Presently, no resistant populations have been observed outside the U.S.

Field studies in the U.S. indicate that biotypes of *A. trifida* have cross-resistance to three chemical families of ALS-inhibiting herbicides, suggesting that herbicides with other modes of action will be required to achieve effective management (Taylor et al. 2002). *Ambrosia trifida* exhibits different resistance mechanisms to ALS-inhibiting herbicides and to glyphosate (Patzoldt and Tranel 2002; Harre et al. 2017), reflecting a high level of adaptation in this species. Based on fitness traits of glyphosate-resistant plants in the presence and absence of glyphosate and on *A. trifida* outcrossing rates, Brabham et al. (2011) predicted that glyphosate-resistant biotypes of *A. trifida* would persist in the field as the dominant phenotype if glyphosate were used as the only herbicide every other year. Eradication of resistant plants without the use of this active ingredient would require several years.

In genetically modified crops, the development of glyphosate-resistant *A. trifida* plants increases the difficulty of control because farmers cannot rely on glyphosate alone and must use an integrated approach that combines tillage and pre- and post-emergence herbicide treatments at the beginning of the season to reduce *A. trifida* densities (Ganie et al. 2016, 2017; Ditschun et al. 2016). Chemical control options are becoming increasingly restricted in the EU, necessitating the use of other practices to limit the spread of *A. trifida*. To find new, effective chemical controls for *Ambrosia* species, imazamox and tribenuron-tolerant (ALS inhibitor) sunflower varieties have been developed (Pfenning et al. 2008), however, the risk of selecting for resistant biotypes with this type of herbicide is high (Anses 2020) and the use of these varieties is currently being questioned in the EU (EUR-Lex 2018).

In natural habitats and especially in protected areas, weed control programs – regardless of the type of control (e.g. tillage, mowing or chemical) – must be tested to avoid potential negative impacts on the environment and on local diversity.

Physical control. Tillage can help reduce *A. trifida* populations in crop fields within a given year, but is not a suitable tool for eradicating the weed. Nevertheless, tillage strategies using mouldboard ploughing (deep seed burial) should be considered based on weed density. In fields invaded by *A. trifida*, double harrowing before crop emergence followed by an additional harrowing after emergence is recommended (Mordovets et al. 1979). In the case of high soil seed densities, spring tillage can be an effective weed control approach for *A. trifida*, especially when used in conjunction with other effective weed

control strategies such as herbicide treatment (Goplen et al. 2018). In cases of very low plant densities in small areas, removal by hand weeding of the species at an early stage of growth is an effective preventive management practice. Changes in crop rotation are recommended, e.g. inclusion of winter cereals, autumn seeded cover crops, perennial pasture and hay crops; and avoidance of sunflower and soybean (Regnier et al. 2016; Liebman and Nichols 2020).

Biological control. Natural enemies of *A. trifida* have been identified (see paragraph on granivory and herbivory) and research has been conducted in Europe to find candidates for biological control (Gerber et al. 2011; Cabi 2019). For example, *Ophraella communa* LeSage, 1986 (Coleoptera: Chrysomelidae) is a beetle native to North America (Futuyma 1990). This insect has already been observed in Asia (Miyatake and Ohno 2010) and in some European countries such as Italy, Slovenia, and Croatia (Zadravec et al. 2019; Schaffner et al. 2020). Although the beetle does not feed on *A. trifida* in its native area (Fukano and Doi 2013), it was shown to feed on *A. trifida* in Japan (Yamazaki et al. 2000; Miyatake and Ohno 2010; Fukano and Doi 2013) and has been suggested for biological control. However, the benefits and risks of introducing this beetle have to be evaluated, and it seems doubtful that predation by *Ophraella communa* alone would be sufficient to control the expansion of *A. trifida* (Iqbal et al. 2020). Batra (1981) observed that the rust *Puccinia xanthii* Schwein (1822) attacks leaves of *A. trifida*, reducing seed and pollen production, seed weight and seedling vigour. However, no further studies have been conducted to evaluate this pathogen for biological control of *A. trifida* in Europe. A *Xanthomonas* spp. strain evaluated on different Asteraceae species, including *A. trifida*, caused 65% mortality and 70% biomass reduction (Boyette and Hoagland 2013), however, these trials were conducted in controlled conditions and were not being used in field conditions.

Conclusion

Ambrosia trifida has received major scientific attention and this attention has increased over the past 30 years with over 250 publications on topics ranging from allergology to agronomy (Diekmann et al. 2013). Eradication of *A. trifida* where it is well naturalized in numerous different habitats over large areas, e.g. N. America, is certainly no longer possible today due to its near-ubiquitous presence. However, in regions where *A. trifida* has not yet become broadly naturalized, complete control of recently introduced *A. trifida* populations present at low densities should be achievable due to its relatively low reproductive capacity and short-lived soil seed bank. Nonetheless, control efforts must be diligent and

persistent due to the ability for some seeds to remain viable for over two decades should they become deeply buried in the soil (e.g. through tillage) and also due to the dispersal of seeds through many avenues, particularly through human activities. In Europe, for example, rigorous management of the species may keep it at low densities and prevent wider spread, thus avoiding the development of human health and agronomic problems. Currently, there is no regional program for control of *A. trifida* in Europe, even though *A. trifida* is present in various habitats, including river banks, from which eradication is difficult. Fortunately, the large size and distinctive plant architecture and leaf morphology of *A. trifida* facilitate its identification, allowing early detection of new incursions, which is critical to the implementation of local eradication schemes.

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CHAPMAN Daniel: drafted the review as an expert of *A. trifida* distribution modelling. CHAUVEL Bruno: drafted

the whole review (initially as an EPP0 Pest Risk Analysis). FOLLAK Swen: provided additions with regards to distribution and drafted the review. FRIED Guillaume: contributed particularly to the invasion history, the response to climate, preferred habitats and co-drafted the whole review. KULAKOVA Yuliana: provided comments with regards to distribution of *A. trifida* and drafted the review. LE BOURGEOIS Thomas: drafted the risk analysis of *Ambrosia trifida* in France and checked the manuscript. MARISAVLJEVIC Dragana: checked the manuscript. MONTY Arnaud: drafted the risk analysis of *Ambrosia trifida* in France. REGNIER Emilie: provided comments to distribution, biology and phenology of *A. trifida* and co-drafted the whole review. ROSSI Jean-Pierre, STARFINGER Uwe, TANNER Rob, TASSUS Xavier, VAN VALKENBURG Johan: checked the manuscript.

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Appendix 1

A: Wilsele. 21 July 1903. Wasteland. [Belgium] – Herbarium G.

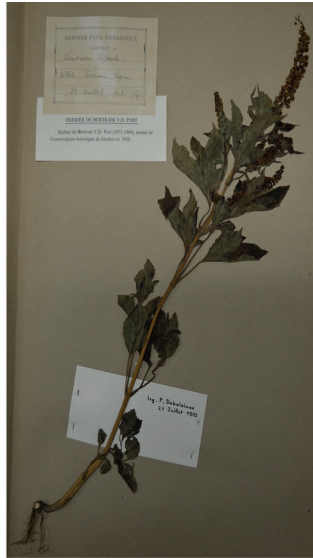
B: Bern. August 1903. Introduced in Kirchenfeld in 1902 by the Barnum and Bailey Circus. Disappeared in 1904. [Switzerland] – Herbarium G.

C: Middelburg. 1900–08-01. At the flour factory. [The Netherlands] – Herbarium L.

D: Ludwigshafen. July, August 1904. On Schützen street. Alluvium. Altitude 95 m. Ruderal plant. [Germany] – Herbarium G.

E: Lempire. War front in Champagne region. July 1918. [France] – Herbarium G.

F: Göteborg. 19–09-27. Agnesberg by the mill. [Sweden] – Herbarium G.



a



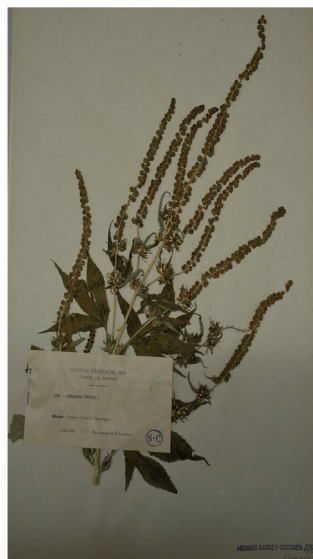
b



c



d



e



f