

Monographs on invasive plants in Europe: *Ageratina adenophora* (Spreng.) R. M. King & H. Rob

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Abstract

Ageratina adenophora (Spreng.) R.M. King & H. Rob. (Crofton weed) is a triploid, apomictic perennial herb or sub-shrub native to Mexico that is highly invasive in many parts of the world. This species thrives in diverse habitats, from wet forest margins to dry slopes and disturbed urban areas. Initially introduced globally as an ornamental plant, it has now naturalized across many continents, including Europe, Asia, Africa, Oceania, and the Americas, often displacing native flora and altering ecosystems. Its introduction to Europe dates back to the 19th century, with naturalization first recorded on the French Riviera. *Ageratina adenophora* is now established in several southern European countries (Portugal, Spain, France, Italy, Croatia, Greece) and across the Macaronesian islands. It spreads via wind- and water-dispersed seeds and can also propagate vegetatively, particularly along riparian systems and disturbed sites. Despite its prolific reproduction and adaptability, its expansion in Europe has so far remained moderate, possibly due to climatic limitations and unsuitable habitats. Ecologically, *A. adenophora* exhibits remarkable phenotypic plasticity and physiological adaptations that enable it to survive a range of abiotic stresses including cold, drought, and variable light levels. The species benefits from mutualisms with soil microbes and displays enhanced nitrogen-use efficiency in introduced ranges. Although initially valued for ornamental and medicinal purposes, *A. adenophora* is now widely recognized as a harmful invader. It invades both natural and semi-natural habitats and has demonstrated a capacity to alter soil chemistry, suppress native vegetation through competition and allelopathy, and host diverse pathogens and endophytes. *Ageratina adenophora* negatively impacts biodiversity, ecosystem functioning, and agriculture by forming dense, mono-specific stands and disrupting native communities. Its presence in biodiversity hotspots and protected areas—such as Himalaya, South Africa, and the Canary Islands—poses significant conservation challenges. Control efforts, including the use of biological agents such as *Procecidochares utilis* Stone 1947, have yielded mixed results. The most effective method for small areas is to physically remove *A. adenophora* before it sets seed. This can be done by hand-pulling or cutting. Given the continued spread and resilience of this species there is an urgent need for coordinated management strategies and increased awareness, especially in the face of climate change which may further facilitate its expansion in Europe and beyond.

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1. Taxonomy

1.1. Names and classification

Kingdom: Plantae, Division: Magnoliophyta, Class: Angiospermae, Order: Asterales, Family: Asteraceae, Tribe: Eupatorieae, Genus: *Ageratina* Spach, Species: *Ageratina adenophora* (Spreng.) R.M.King & H.Rob Phytologia 19: 211 (1970). This information is sourced from POWO (2025), which follows the APG IV classification system.¹

1.1.1. Main synonyms

Homotypic synonym: *Eupatorium adenophorum* Spreng.

Heterotypic synonyms: *Ageratina trapezoidea* (Kunth) R.M.King & H.Rob., *Eupatorium glandulosum* Kunth, *Eupatorium pasadenense* Parish, *Eupatorium pascuarensense* J.Dix, *Eupatorium trapezoideum* Kunth

1.1.2. Common name

English: Crofton weed, Mexican devil, sticky snake-wort, sticky snakeroot, sticky eupatorium. French:

agératine du Mexique, eupatoire blanc, eupatoire glanduleuse. German: Drüsiger Wasserdost. Portuguese: abundância, inça-muito. Italy: Ageratina appiccicosa, Diavolo messicano. Russian: агератина железистая. Spanish: ageratina, espumilla, hediondo. Nepali: Banmara (CABI 2022; EPPO 2025).

1.2. Morphological description

1.2.1. Species description

The following description of the morphology of *A. adenophora* was summarized from the Flora of North America (Nesom 1993+), the Flora of Tropical East Africa (Beentje and Ghazanfar 2005) and the Flora of China (Wu and Raven 1994).

Ageratina adenophora is a perennial herb or a (sub)shrub 30 to 150 (–220) cm high (Figure 1(a)). The stem is erect, purplish when young which changes to blackish at maturity, somewhat woody, with opposite branches, obliquely ascending. The stem is covered with short glandular hairs that become more densely pubescent towards the apex, or conversely more

glabrous towards the base. The leaves are opposite and have a petiole of 10–25 mm and triangular-ovate, or rhombic-ovate blades of (1.5–)2.5–7.5 (–8) cm long and 1.5–3 cm wide (Figure 1(b)); the base of the blade is truncate or slightly cordate, margin coarsely crenate, apex acute to acuminate, mainly 3-veined from the base; both sides of the leaf blades are somewhat puberulent, more densely on the underside (which is pale) and on the veins (the upper side is more green). The synflorescences (structures composed of multiple grouped inflorescences, in this case, capitula) are terminal, somewhat leafy, in corymbs or compound corymbs, up to 12 cm in diameter (Figure 1(c)). The capitula are numerous, 40–50(72) flowered; they are borne on 5–12 mm long peduncles, densely stipendiate-glandular and sometimes also slightly viscid-puberulent. A mature plant may produce approximately 2000 capitula (Datta et al. 2017). The involucre are broadly campanulate, ca. 3 × 4 mm; the phyllaries are 2-seriate, linear or linear-lanceolate, 3.5–5 mm. The corolla are 3.5 mm long, white to cream with filiform tube and campanulate limb, tube



Figure 1. (a) Habit (13 April 2022), (b) leaves (04 February 2022) and (c) synflorescences (14 April 2022) of *Ageratina adenophora*. Photos by Guillaume Fried, Saint-Jean-Cap-Ferrat (France).

prominently 5-veined, lobes triangular, ± 0.2 mm long, thickened, sparsely hairy externally; anthers ± 1 mm long, basally sagittate, apically with ovate appendages; style 3.5–4.5 mm long, bifid for 0.5–1.5 mm, style-arms exerted for ± 1.5 mm, papillate. Cypselae black-brown, narrowly elliptic, 1–1.5 mm, 5-angled, glabrous; pappus setae 10, basally connate, white, fine, equal to corolla. $2n = 3x = 51$ (Nesom 1993+).

The complete chloroplast genome has been sequenced and published (Nie et al. 2012). The Barcode of Life Data Systems (BOLD; <https://www.boldsystems.org/>) contains eight sequences for *A. adenophora*. Within the framework of the EPP0 Pest Risk Analysis (PRA) on *A. adenophora* (EPP0 2023) additional sequence data have been generated for plants from France and Hawai'i (<https://qbank.eppo.int/plants/>).

1.2.2. Distinguishing features

The genus *Ageratina* Spach is native to the Americas (King and Robinson 1987). In Europe, there are two related non-native species (Greuter 2006+):

Ageratina riparia (Regel) R. M. King & H. Rob. is native to South Mexico. It is naturalized on the Canary Islands (Spain) and Madeira (Portugal) where it grows in the same habitats as *A. adenophora* (Greuter 2006+; Silva et al. 2008). *Ageratina riparia* differs from *A. adenophora* in several ways. Firstly, it is typically smaller in stature, with a maximum height of 1 m. Secondly, it often exhibits a prostrate stem, and its leaves are more oval to elliptical in shape than those of *A. adenophora*, with fewer teeth. The flower heads are similar in appearance but are smaller and more loosely arranged in the inflorescence (Figure 2A). *Ageratina riparia* is native to the same subtropical to tropical biome, and is also considered as invasive (Figure 2B), but exhibits a preference for slightly wetter environments and displays reduced drought resistance in comparison to *A. adenophora* (Silva, Ojeda Land, Rodriguez Luengo, et al. 2008).

Ageratina altissima (L.) R. M. King & H. Rob. is native to the temperate zones of North America (Canada and the United States) (POWO 2025). It is considered casual in several central European countries (Austria, Belgium, Czech Republic, Germany, Hungary, Italy and Poland; EPP0 (2023)). This species exhibits a closer resemblance to *A. adenophora* in terms of its upright growth habit (up to 120 cm height) and the overall shape of its leaf blades (Figure 3). A notable difference is observed in the morphology of the peduncles, which are puberulent (in contrast to the glandular character observed in *A. adenophora*). The leaves are larger in size, reaching up to 11 (13) cm in length and 8 (9) cm in width. They are also thinner and exhibit a deltate-ovate to ovate or broadly lanceolate shape, more rarely ovate-lanceolate (Flora of North America Editorial Committee 2006). Finally, while *A. adenophora* can affect grazing livestock, *A. altissima* is much more notorious for its toxicity. This species contains tremetol, a compound that can cause tremetol poisoning in livestock (particularly cows) and humans who consume contaminated milk, leading to “milk sickness” (Burrows and Tyrl 2013).

1.2.3. Variations at the infraspecific level

No subspecies or varieties are currently recognized within *Ageratina adenophora*. However, individuals from introduced ranges, such as China, exhibit greater plant height, stem diameter, leaf length, leaf width, and leaf area compared to those from the central part of its native range, in the regions of Michoacán, Jalisco, Querétaro, and Guanajuato in Mexico (Feng et al. 2009).

2. Distribution and status

2.1. Native range

According to the website efloramex.ib.unam.mx (Project “eFloraMEX: La flora electrónica de México” and the references cited therein), *A. adenophora* is



Figure 2. (a) Leaves and synflorescences of *Ageratina riparia*; (b) small invasive stands of *A. riparia* (15 October 2015). Photos by Guillaume Fried, Saint-Paul, reunion island (France).



Figure 3. Leaves and synflorescences of *Ageratina altissima*. Photos by Guus de Vries, available at <https://waarneming.nl/observation/259704246/>.

native to Mexico where it occurs in the following states: Aguascalientes; Chiapas; Chihuahua; Colima; Distrito Federal; Durango; Guanajuato; Guerrero; Hidalgo; Jalisco; Michoacán de Ocampo; Morelos; México; Nayarit; Oaxaca; Puebla; Querétaro de Arteaga; San Luis Potosí; Sinaloa; Veracruz de Ignacio de la Llave; Zacatecas. It is reported as absent in Tlaxcala (Central), Baja California, Baja California Sur, Sonora, Coahuila, Nuevo Leon, Tamaulipas (northern), Tabasco, Campeche, Yucatan and Quintana Roo (southern) (Pruski et al. 2018). In its native range, the species can be found up to 2400 m above sea level. Distribution records for Mexico can also be retrieved from the website of Sistema Nacional de Información sobre Biodiversidad de México (2023).

2.2. Introduced range

Beyond its native range in Mexico, the species is recorded further north in California (USA) (Nesom 1993+; DiTomaso et al. 2013; POWO 2025), and further south in Costa Rica and Jamaica (POWO 2025). *Ageratina adenophora* has also been introduced to South America, specifically in Peru (Peru, POWO (2025)). In Africa, the species is present in several southern countries: Angola (Rejmánek et al. 2017; Goyder et al. 2019), Kenya (Witt and Luke 2017), in all provinces of South Africa except Free State and

Northern Cape (ARC LNR 2023; POWO 2025), Uganda (USDA 2023), Zambia (Beentje and Ghazanfar 2005); and Zimbabwe (Mapaura and Timberlake 2004; POWO 2025), as well as in the north of the continent in the Maghreb: Algeria (Meddour et al. 2020) and Morocco (Greuter 2006+; POWO 2025). It is present across the Macaronesian archipelago where it is considered invasive (Weber 2003): Azores (Greuter 2006+), Madeira (Greuter 2006+), Canary Islands (Greuter 2006+), and Cape Verde (USDA 2023; POWO 2025). In Europe, aside from Germany where it is only casual (Greuter 2006+), it is mainly present and naturalized in the southern part of the continent: in Portugal (Greuter 2006+), Spain (Greuter 2006+), France (Fried 2023), Italy (Del Guacchio 2013), Croatia (Greuter 2006+), and Greece (Arianoutsou et al. 2010) (Figure 4).

In Asia, *A. adenophora* is widely distributed and invasive in the southeastern part of the continent: Bhutan (APFISN 2012; USDA 2023), Cambodia (Rundel and Middletown 2017), China (Wu and Raven 1994; Feng et al. 2009; Fu et al. 2018; POWO 2025), India (APFISN 2012; Datta et al. 2017), Indonesia including Java (APFISN 2012; Nyuanti et al. 2020; POWO 2025), Laos (USDA 2023; POWO 2025), Myanmar (USDA 2023), Nepal (Thapa et al. 2017; Darji et al. 2021; POWO 2025), Philippines (APFISN 2012, USDA 2023; POWO 2025), Sri Lanka (APFISN 2012), Thailand (USDA 2023; POWO 2025), and Vietnam (USDA 2023). It is also reported in Lebanon (Greuter 2006+). In Oceania, it is naturalized in eastern Australia, including New South Wales, Norfolk Island and Queensland (Auld and Martin 1975; Parsons and Cuthbertson 2001; POWO 2025), and on the North Island of New Zealand (New Zealand Plant Conservation Network 2023). It is present on several Pacific islands: Society Islands (France) and Hawaii (USA) (USDA 2023).

3. History of introduction and spread

Ageratina adenophora was first introduced outside of its native range (Mexico) as an ornamental plant to the United Kingdom (Europe) in 1826 (Auld and Martin 1975) and then to Hawaii (USA) in 1860 (Muniappan et al. 2009) and Australia in 1875 (Auld and Martin 1975). It is believed to have been introduced as a garden plant to India (Asia) in 1924 (Tripathi et al. 2006), but herbarium specimens were collected as early as 1914 from the Nilgiri mountains in southern India (based on herbarium serial number 225,216, deposited at Central National Herbarium, Calcutta). It was generally assumed that the plant spread naturally to China during the 1940s, traveling from Myanmar along the international highway (Wang and Wang 2006; Dong et al. 2008). It was first recorded from New

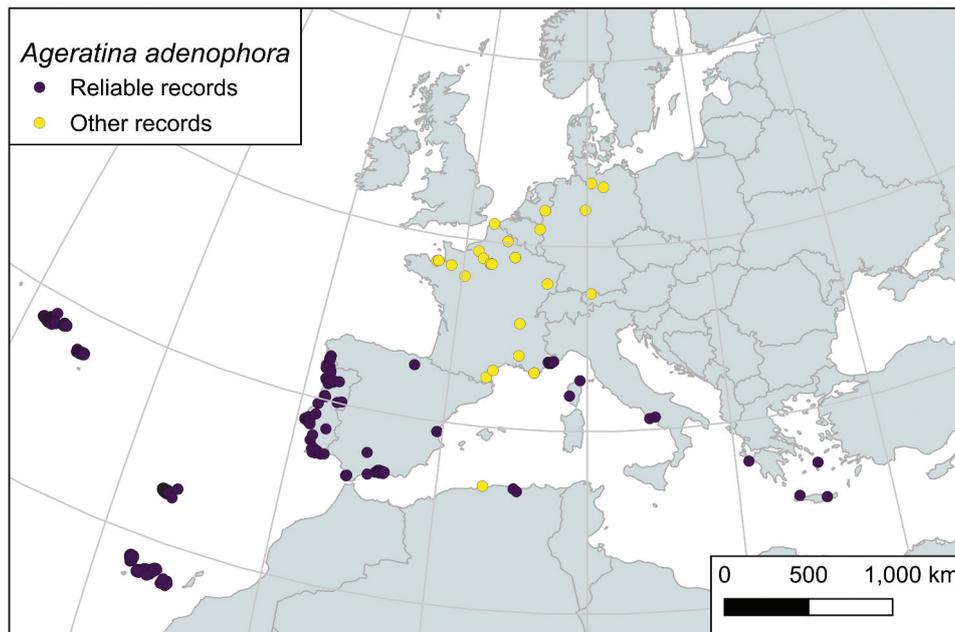


Figure 4. Map showing occurrence records of *Ageratina adenophora* in Europe obtained by the expert working group performing the EPPO Pest risk assessment (PRA) for the species (EPPO 2023). The map distinguishes records they considered as reliable established populations, from those considered most likely to be unreliable records or casual populations. Data were primarily obtained from GBIF.org (2022) though some other sources also contributed records (EPPO 2023).

Zealand in 1931 (Webb 1987), Nepal in 1937 (Herbarium of Forest Research Institute, Dehradun, India, voucher no: 74161), Algeria in the 1870s (Battandier and Trabut 1878) and South Africa in 1958 (Henderson 2006). We provide a more detailed account of its spread history across Europe, the Mediterranean, and the Macaronesian regions below.

3.1. Algeria

Ageratina adenophora appears in the seed catalogue of the Test Garden of Hamma in Algiers (1874–1875), which suggests that the plant was cultivated in botanical gardens. The plant is considered to have naturalized as early as the 1870s (Battandier and Trabut 1878). It is also indicated in the flora of Battandier and Trabut (1902) as present in the ravines of Bab-el-Oued, a district in the northwest of Algiers. In the mid-20th century, *A. adenophora* was still reported as naturalized in Algiers by Quézel and Santa (Quézel and Santa 1962–1963). However, Faurel (1959) noted that the species was “endangered by the transformations and expansions of the Algiers urban area.” Subsequently, no further records of this species were documented in Algiers. More recently, between 2007 and 2021, *A. adenophora* has been repeatedly observed as well naturalized by Errol Vêla, Heddad Moussa, Dries Fatsah, and Khellaf Rebbas in the Gouraya National Park and Souk El Thenine in the Bejaia province (R. Meddour, pers. com., 2023).

3.2. France

Ageratina adenophora has been cultivated in botanical gardens since the 19th century. Records exist from Jardin botanique de la Villa Thuret (Sauvaigo 1899), Jardin Exotique de Monaco (Jeannel 1890), Jardin des plantes de Montpellier (L’Indépendant 1848), and Jardin des Plantes Joséphine Baker in Grenoble (Verlot 1857). It was also probably cultivated in private gardens as it is also mentioned in horticultural books which give advice on cultivation and maintenance (Dupuis and Hérincq 1884). The first dated mention goes back to 1846 where Rantonnet (1847) indicates that the plant died during a harsh winter in Hyères. Sauvaigo (1899) seems to say that at the end of the 19th century the species was much less widely cultivated in gardens “where it once had a good place” among cultivated species. However, he also notes that the species was already naturalized in some gardens in Nice at that time (Sauvaigo 1899). The first record of the species outside a garden dates back to 1910. In his inventory of the *Colline du Château* (Castle Hill), Mader (1910) lists *A. adenophora* among the naturalized species and indicates it as very common on the western side of the hill near the waterfalls. A few years later, Chevalier (1918) found it “abundantly naturalized on the grounds dominating the Pont Saint-Louis in Menton, and in Monaco, along the ravine of Sainte-Dévote”. In the 1930s it was noted in a stone gutter in front of the railway station in Villefranche-sur-Mer (Muséum national d’Histoire naturelle, Paris (France),

Collection: Plantes vasculaires (P), Specimen P04185072). Despite these observations of the first naturalizations, it seems that the plant remained uncommon and was only known by local botanists; the flora of France of the beginning of the XXth century (Coste 1906; Fournier 1936) does not mention this species. In the mid-1980s, Alziar (1984) noted that the species had become much more common. The author observed that *A. adenophora* was now present everywhere between Menton and Monaco: on walls, unkempt stairs, in abandoned gardens and among rubble. He also observed that the plant was more vigorous in cooler places but that it also managed to establish very well in between rocks. More recent records in the 2020s confirm this expansion trend, with several new locations covering the area between Monaco and Nice (Cap-d'Ail, Beausoleil, Roquebrune-Cap-Martin, Eze, Beaulieu-sur-Mer, Saint-Jean-Cap-Ferrat, Nice). The species now occupies the entire Riviera coastline between Nice and Menton (Fried 2023).

3.3. Corsica

A. adenophora was first reported in 1952 from Lupino, near Bastia, by Professor Th. Marchioni who observed the species on the banks and in the bed of the Lupino stream. The species had already invaded a 1-km long stretch of the stream (Conrad 1961b). In 1961, Conrad (Conrad 1961a) found it in Ajaccio where it invaded the banks of the Gravona canal near the “Château des Anglais” at Carrosaccia.

3.4. Greece

Based on GBIF data, the first record in Greece dates back to 1915 in Chania, on the island of Crete (GBIF.org 2022). Alien Plants in Greece (2023) details that *A. adenophora* is distributed in East Aegean Islands, Ionian Islands, Kiklades, Kriti and Karpathos north central and northeast. The database mentions that the species is non-invasive.

3.5. Italy

Ageratina adenophora has a long history of cultivation in Italian botanical gardens; the first record of the species in cultivation was from the botanical garden of Palermo (Sicily) in 1858 and in the mainland of Italy at the botanical garden of Genova in 1890. The species was first reported as growing in the wild in 2013 by Del Guacchio (2013). This author detailed two established populations in southern Italy (Campania), one in Sorrento, which had been present for 7 years, and one in Salerno, which had been present for 5 years.

3.6. Portugal

Plantas invasoras em Portugal (2020) reports that *A. adenophora* is distributed in the coastal provinces of the mainland, in the Azores archipelago (islands of São Miguel, Terceira, S. Jorge, Pico, Faial) and Madeira archipelago (islands of Madeira, Porto Santo and Desertas islands). In his flora of Madeira, Lowe (1868) explains in detail the introduction and establishment of the plant: “Introduced into Madeira scarcely before 1840, and first noticed on the walls of the Ribeira de Santa Luzia in Funchal below the house of a former British Consul, Mr. Veitch, from whose garden, supplied with plants and seeds occasionally by the Horticultural Society of London, it was probably thus at first a straggler; this plant had even in 1855 already spread in vast profusion over all the neighbourhood of Funchal and elsewhere, even in the north of the island, up to an elevation of 600 or 900 m or more; forming, in some places, hedges about cottage gardens, and in ravines (as up the Ribeira de Santa Luzia almost to the foot of the great waterfall) thickly clothing the wet dripping perpendicular cliffs in many places as if perfectly indigenous. Unfortunately, it seems inapplicable to any use but litter and is entirely unfit for fodder. The Portuguese have given it a very appropriate name, “Inqa muito,” – equivalent to Spread-much, or literally (as applied to insects) Swarm-much.

3.7. Spain

The plant is known from Andalusia, where it was first mentioned near Malaga (Burton 1979). It is well established and abundant there along field ditches near Motril. More recently, it has been recorded near Huelva, again in ditches along the N-472 road towards San Juan del Puerto (Sánchez Gullón et al. 2006). *Ageratina adenophora* has also been found in Galicia. The first mention dates to the end of the 1980s (Rodríguez-Oubiña and Ortiz 1989) in the locality of Redondela (Pontevedra). Later, Gómez Vigide et al. (2005) mention it from Lourizán, in the same province. In both cases, the plant is reported in human-modified environments. More recently, it has been found in A Pobra do Caramiñal, where it is relatively abundant and shows clearly invasive behaviour (González-Martínez and González-Martínez 2017). It is distributed over a stretch of about 800 m long on slopes and ditches on both sides of a road (oriented N and S) and its immediate surroundings, in more or less human-modified environments, and especially in cool and shaded areas on wet soil.

4. Ecology

Ageratina adenophora is highly adaptable and can tolerate a wide range of biotic and abiotic conditions.

Throughout the invasive range of the species, plants are found in a diversity of habitats which can be explained by epigenetic variation as experimentally demonstrated in populations from China which show cold tolerance (Xie et al. 2015; Le Roux 2021).

4.1. Response to abiotic factors

4.1.1. Climate

4.1.1.1. Temperature. In the native range of *Ageratina adenophora* in Mexico, mean annual temperatures – based on CHELSA climate data (Karger et al. 2017) associated with GBIF occurrence records (GBIF.org 2022) – average around 17°C, with a minimum of 7°C and a maximum of 27°C; notably, 50% of the values fall between 15°C and 19°C. In general, *A. adenophora* prefers to grow in warm, moist and frost-free areas of Europe. In China, the mean annual air temperature of known localities of *A. adenophora* ranges from 4.4°C to 23.1°C (Zhu et al. 2007). In South Africa, *A. adenophora* appears to prefer temperatures in the range from 10°C to 25°C and low temperature seasonality (Tererai and Wood 2014). Lu et al. (2006) conducted laboratory and greenhouse studies to determine the effect of several environmental factors on seed germination and seedling emergence. Seeds germinated over a range of 10–30°C, with optimum germination at 25°C. High temperature markedly restricted germination, with no germination occurring at 35°C and similarly, low temperature (5–10°C) has also been shown to limit germination (Lu et al. 2006; Li and Feng 2009). Cold temperatures are reportedly not required for seed stratification (Wang et al. 2012). Li et al. (2008) details that populations in China show different responses to low temperatures. Some populations are able to withstand low temperatures more than others where freezing injury was less in plants from Huangguoshu at an elevation of approximately 900 m (in the province of Guizhou, in southwestern China, with a humid subtropical climate) compared to other populations. The authors suggest that freezing tolerant populations would have a greater chance to invade more northeastern areas.

Marginal populations at high elevations in the Himalayas (India and Nepal) and Yunnan province (China) can experience freezing temperatures during the winter. One population in Lijiang Yunnan has been reported to experience the lowest temperature of –10°C at an elevation of 2600 m (Xie et al. 2015). However, continuous exposure to sub-zero temperature damages the aerial parts of the plant and reduces the reproductive output drastically. Reciprocal transplant experiments carried out in western Himalaya demonstrated the absence of local adaptation and population differentiation in response to low temperature and the populations exhibited very high mortality due to freezing temperatures at high elevation (>

2200 m) during the winter. However, due to microclimatic variations populations can be found growing at higher elevations (Datta et al. 2017). Higher cold tolerance in some populations have been reported from China and has been attributed to epigenetic modifications of cold tolerance genes (Xie et al. 2015). In cultivation, *A. adenophora* can endure short periods of cold, at least immediately above freezing temperature by night (Del Guacchio 2013).

4.1.1.2. Precipitation. According to CHELSA climate data (Karger et al. 2017) combined with occurrence records from GBIF (GBIF.org 2022), annual precipitation within the native range of *Ageratina adenophora* in Mexico averages approximately 1200 mm, with values ranging from 400 mm to 4300 mm and an interquartile range between 800 mm and 1300 mm. Precipitation of the driest month was the most important factor explaining *A. adenophora* distribution in southwest China (Zhang et al. 2022). The known localities of *A. adenophora* in China were distributed in areas with annual precipitation ranging from 698 mm to 2254 mm (Zhu et al. 2007). Summer precipitation has been considered to be crucial for seed germination and establishment in the dry lower Himalayan belt (Datta et al. 2017).

In a niche modelling study, Zhu et al. (2007) showed that the most likely areas for future invasion in China, were associated with increased levels of moisture-related variables, especially mean annual precipitation and precipitation in the driest month.

In Italy, clones cultivated near Salerno show considerable drought resistance, enduring up to 3 weeks without water. After the aerial parts of the plant mainly dried up due to drought, the plants could readily regenerate from the base or rootstock; however, after just 1 week without water, signs of drought stress become apparent (Del Guacchio 2013).

The species is capable of absorbing water in multiple ways depending on the availability of water in diverse habitats. For example, plants growing on volcanic lava fields with limited soil water retention capacity (e.g. Hawaii) utilize atmospheric moisture, whereas plants growing in Mediterranean-type climates (e.g. France, Italy and South Africa) benefit from moisture from streams (Fried 2023).

4.1.1.3. Substratum. If water retention capacity is sufficient for growth, *A. adenophora* can grow in a wide range of soil types in terms of texture and pH ranging from dry sands to wetland clay soils (Queensland Government 2022). It can tolerate some salinity and can persist in nutrient-poor soils (CABI 2022). In addition to growing in soil, *A. adenophora* can establish on stone surfaces, concrete walls, and within cracks of buildings or monuments, highlighting

its high stress tolerance and capacity to colonize diverse substrates, including culturally significant sites.

4.1.1.4. Light. *Ageratina adenophora* exhibits moderate shade tolerance, though light is essential for seed germination (Lu et al. 2006). Auld and Martin (1975) demonstrated under experimental conditions that seedlings can tolerate shading to 10% daylight. They considered this trait advantageous for competing with other colonizing plants. In the Western Himalayas, the species can grow under the canopy of broadleaf as well as coniferous forests (Khatri et al. 2024). Redlight promotes germination, whereas far red light prevents germination (Wang and Niu 2016). Zheng et al. (2009) demonstrated the plastic response of *A. adenophora* to irradiance. They found that as irradiance increased, the light-saturated photosynthetic rate and root mass fraction (which peaked at 40% irradiance) increased, while the leaf area to root mass ratio, leaf area ratio, and specific leaf area decreased. These changes facilitate light capture, efficient use, and water balance across different irradiance levels. Invasive populations in China have higher light-saturated photosynthetic rates and therefore higher growth rates than native populations (Y-L et al. 2011).

4.1.1.5. Species distribution modelling. As part of an EPPO Pest Risk Assessment for *A. adenophora*, a species distribution model was developed to estimate the climatic suitability for its potential establishment in Europe and the Mediterranean region, under

current and projected future climatic conditions (EPPO 2023). The model predicted climatically suitable areas currently occur around the Mediterranean, Black Sea, Atlantic and Macaronesian coastlines (Figure 5). Frost-free inland areas in Portugal, southern France, and Italy (Sardinia and Sicily) were also predicted to be climatically suitable. These results align with the species' observed preference for oceanic climates in its secondary range, where mild winters and relatively stable temperatures prevail. The model suggests that low winter temperatures, especially in more continental or colder inland areas, are the strongest limiting factor preventing establishment elsewhere in Europe. This reflects the species' sensitivity to freezing conditions and its reliance on oceanic climatic conditions for successful establishment.

The model predicts that for the 2041–2070 period, under both moderate (SSP1–2.6) and more extreme (SSP3–7.0) climate scenarios, reduced frost will allow some range expansion of the species into inland western Europe, particularly southern France, Italy, and northwest Spain. However, increased summer drought is expected to decrease suitability along the Mediterranean coast. By mid-century, suitability is projected to remain stable in Macaronesia and the Black Sea, decline in the Mediterranean, and increase significantly in the Atlantic region.

4.2. Response to biotic factors

Ageratina adenophora flourishes in disturbed environments, taking advantage of reduced competition and increased light availability in gaps created by

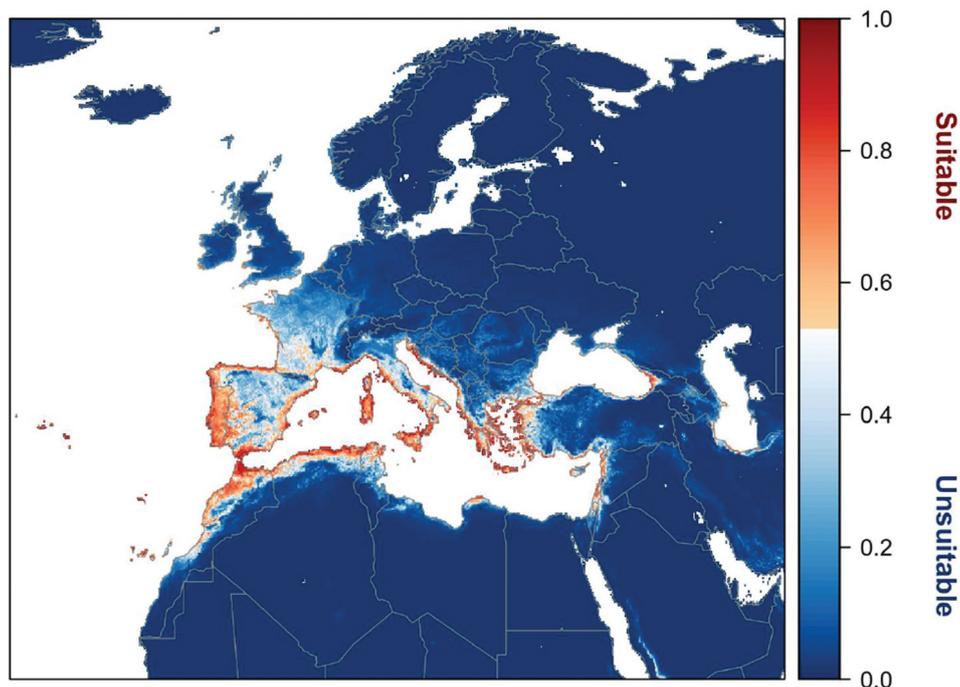


Figure 5. Projected current suitability for *Ageratina adenophora* establishment in Europe and the Mediterranean region from a recent pest risk assessment (EPPO 2023).

natural or anthropogenic disturbances. Disturbances such as road construction, deforestation, and agricultural activities have facilitated the spread and formation of large dense stands (Zhang et al. 2023). Its competitive success is more often associated with environments where water and nutrient stress are mitigated. Conversely, in more constrained regions where native species are well established, the growth of this species can be limited, particularly by drought conditions and competition for nutrients (Fried 2023). However, in contrast to plants that are more dependent on light, *A. adenophora* demonstrates a moderate tolerance to shade, enabling it to survive in partially covered environments during the early stages of development (Auld and Martin 1975). Once established, *A. adenophora* can outcompete other plants by forming dense mats and inhibiting the growth of surrounding species through allelopathy (Darji et al. 2021; Kumar and Garkoti 2022). Furthermore, interactions with beneficial soil microbes, such as arbuscular mycorrhizal fungi, enhance its competitive ability by improving nutrient uptake in disturbed soils.

4.3. Habitats and syntaxonomy

Ageratina adenophora is found in several habitats, including dry to wet forests, riverbanks, swampy sites, grassland but also disturbed sites (Weber 2003). Its habitat preferences vary depending on the region of the world (and the associated climate).

4.3.1. Native range

Herbario Nacional de México (2015) notes that in the native range, *A. adenophora* occurs in different types of forest habitats. For example, just to cite a few, some northern records (Las Cebollitas) are located in “*Pinus*, *Quercus*, *Pseudotsuga*, *Picea*, and *Abies* mixed forest, on shallow stony soils”; more in the centre and close to coast (La Guaynera) on “rocky, oak covered slopes”. Close to the area of the *Reserva de la Biósfera de Serra Gorda*, the records are located in a riparian habitat (*Platanus* gallery forest) and in *Alnus* forest. In the area of Tehuacán, the records are located in “xerophytic shrubland”, in Chiapas in “tropical subcaducifolious forest” and in “tropical evergreen forest” close to the “Parque Natural El Triunfo”. There is also a high variability in the altitudinal data for example, one sample collected in the municipality of “Donato Guerra” reports an elevation of 2980 m a.s.l. (Herbario Nacional de México (2015), Plantas Vasculares; more in general this on-line herbarium database reports about 100 records with an altitudinal range of 170–2980 m a.s.l.

4.3.2. Introduced range

4.3.2.1. North America. In California, *A. adenophora* is found on “stream margins, ditches, road embankments, and hillsides” (Nesom 1993+). For the same area, the Jepson eflora listed also “disturbed places, streambanks, canyons, hillslopes” (Jepson Flora Project 2022). It is also recorded in coastal scrub, riparian forests, riparian woodlands, riparian scrub including dry riverbeds, and coniferous forests (CAL-IPC 2022).

4.3.2.2. Africa. In South Africa, *A. adenophora* has been described as a “weed of waste places, particularly partly shaded and damp roadsides” (Flora of South Africa). In the Western Cape, it is restricted to riparian habitats (Nel et al. 2004; Meek et al. 2013) and along irrigation canals in urban areas (D.M. Richardson, pers. obs.). In eastern South Africa, it invades grasslands and forest margins, especially where these habitats are disturbed (Tererai and Wood 2014).

4.3.2.3. Asia. In the *Flora of China*, the description of the habitats of *A. adenophora* includes the main environments where the species is found: “wet places or roadsides on slopes, forest margins” between 900 and 2200 m (Wu and Raven 1994). In more specific research articles, the species is noted in a variety of habitats. First, it is regularly recorded along linear habitats (corridors) such as roadsides or riverbanks (Lu and Ma 2006; Zhao et al. 2013). Second, several publications report it colonises farmland (Lu et al. 2006, 2008; Zhao et al. 2013) where it has become a “problem weed” in grassland, pastures, plantations, and in cultivated croplands (Lu et al. 2008). Among other man-made habitats, it also colonized wastelands and rubbish dump edges (Zhao et al. 2013). Finally, it is found in a variety of forest types, including broadleaf forests, pine forests, mixed coniferous and broadleaf forests (Lu et al. 2006; Wu et al. 2020), as well as evergreen and broadleaf-deciduous mixed forests (H-B et al. 2007; Wu et al. 2020). *Ageratina adenophora* also invades the understorey of *Eucalyptus globulus* plantations (Yu et al. 2014).

In India, in the Western Himalayas, *A. adenophora* can be found at elevations ranging from 400 m to 2300 m a.s.l. with a preferred elevation of 1300 m (Datta et al. 2017). In these areas, the species grows in moist regions along the slopes of hills or mountains and forest understorey, but also grows in diverse conditions ranging from the flat floodplains of the lower Himalaya to steep and dry rocky slopes, to ruderal habitats. It also grows along roads, streams, and gullies. In Nepal, this species can be found at elevations up to 3280 m a.s.l. in habitats similar to India (Siwakoti et al. 2016).

4.3.2.4. Oceania. In Australia, *A. adenophora* grows in wet shaded areas of fringing forest and along streams. It prefers south-facing damp slopes and is also found along roadsides and overgrazed pastures (Queensland Government 2022). This species commonly occurs along roadsides, railway lines, pastures, fence boundaries, and in disturbed areas, including wastelands and riverbanks in subtropical and warm temperate climates. It is also frequently observed in urban green spaces, open woodland habitats, forest edges, and clearings within rainforests.

In New Zealand, the species grows in lightly shaded frost-free areas, e.g. forest edges, shrublands, wetlands, banks of stream, open forest, inshore and offshore islands, gumlands (shrub-covered, flat to rolling land) in northern New Zealand which has deposits of *Agathis australis* (kauri), slips (land slip), alluvial flats, coast and estuaries (New Zealand Plant Conservation Network 2023). In Hawai'i, this species can be found in a variety of habitats, from relatively dry areas to wet forest, from around 600–2,000-m elevation on the islands of O'ahu, Moloka'i, Lāna'i, and Maui. Invaded areas include lava fields on the slopes of Haleakalā volcano, the edges of mesic native forest, stream sides, fallow pastureland, and trail and roadsides (Wagner et al. 1999).

4.3.2.5. Macaronesia. On the Azores archipelago, *A. adenophora* grows on cliffs, water stream margins, roadsides, *Pittosporum* scrubland (non-native woodland dominated by *Pittosporum undulatum*) and waste places (Silva et al. 2008). In Madeira, it is found on rocky shores, cliffs, thermo-Mediterranean scrubland, heath substituting Apollonias laurel forest, heath substituting Ocotea laurel forest, Madeira olive micro forest, Apollonias laurel forest (Mediterranean laurel forest), *Ocotea* laurel forest (temperate laurel forest), riparian laurel forest (*Sambucus* woodland, *Persea* laurel forest, *Salix* woodland), cultivated and human-modified vegetation, urban areas, abandoned land, degraded natural habitats (Silva et al. 2008). On the Canary Islands, *A. adenophora* grows in a variety of habitats, including cultivated and human-modified areas, mid-elevation scrubland, humid mountain woodlands (such as hygrophytic and mesophytic types, heathlands, and *Morella* scrubland), as well as inland wetlands (including water springs, infiltration areas, ponds, reservoirs, and ditches), and urban environments (Silva et al. 2008).

4.3.2.6. Europe. In France, Tison et al. (2014) reported *A. adenophora* on “wet or fresh rocks and old walls, rubble” but the species is most abundant on the banks of streams and in coastal wetland valleys (Fried 2023). In mainland Portugal, *A. adenophora* is established on “cliffs, banks of water lines and roads, including disturbed and

agricultural areas” (Plantas invasoras em Portugal 2020). It is also found along wet rocky coasts or on riverbanks in Italy (Del Guacchio 2013). In Spain, it is listed as occurring in riparian environments (artificial conduction systems, springs, seeps and other wet enclaves and ponds), moist montane “forests” (heaths, hygrophytic tree thickets and mesophytic tree thickets), scrubland, urbanised areas, cultivated land and man-made green spaces (Catálogo Español de Especies Exóticas Invasoras 2013). Table 1 summarizes information on habitats the species may establish in and habitats which the species is currently established in Europe and Macaronesia.

4.4. Ecological interactions

4.4.1. Herbivory

According to Niu et al. (2010), more than 30 phytophagous insect species have been found in the native range of *A. adenophora* in Mexico (Fritz Heystek, pers. comm. in Niu et al. 2010). A much smaller number of species attacking *A. adenophora* have been recorded in China (Niu et al. 2010), including *Acrydium japonicum* Bolívar (Orthoptera: Tettigidae), *Callimorpha albipuncta* Wileman (Lepidoptera: Arctidae), *Agriolimax* sp. (Stylommatophora: Agriolimacidae), as well as species from the families Limacodidae (Lepidoptera), Tortricidae (Lepidoptera), and Geometridae (Lepidoptera). Niu et al. (2010) also reported significant damage caused by the ant *Dorylus orientalis* Westwood (Hymenoptera: Formicidae) which feeds on the roots and stems of the plant, damaging the epidermis, cortex, phloem, cambium, and xylem tissues, and leading to the local death of several individuals. However, this ant species is also considered a crop pest in China, India, Nepal, Bhutan and Thailand and is not being considered for use in biological control.

In Europe, generalist natural enemies may potentially attack the plant, but these are unlikely to cause enough damage to influence establishment and further spread. Biological control has been practiced against the species in Macaronesia. The biological control agent, *Procecidochares utilis* Stone (Diptera: Tephritidae) was released in Madeira in 1962 to control *A. adenophora* (Marchante et al. 2023). However, it has achieved a negligible degree of control on the island (Vieira RMD 2002). *Procecidochares utilis* has also been accidentally introduced into the Canary Islands. Biological control has been used with varying degrees of success in other regions where the species is invasive (see section 8.2; Winston et al. 2014).

4.4.2. Fungi, bacteria, viruses

A recent study by Chen et al. (2020), highlights the role of *A. adenophora* as a reservoir for local

Table 1. Summary of habitats where *Ageratina adenophora* has been recorded, based on the EUNIS habitat classification 2021, with details on the species' presence in specific habitats in Europe.

Habitat groups (EUNIS)	Habitat types	Is <i>A. adenophora</i> present in the habitat in Europe (Yes/No)	References
Q Wetlands	Periodically exposed shores (Q6): riverbanks, streambanks	Yes	Tison et al. (2014), Plantas invasoras em Portugal (2020), Del Guacchio (2013), Catálogo Español de Especies Exóticas Invasoras (2013)
R Grasslands and lands dominated by forbs, mosses or lichens	Lowland moist or wet tall-herb and fern fringe (R55) Mediterranean grasslands on alluvial river banks (R554): stream margins	Yes	Tison et al. (2014), Plantas invasoras em Portugal (2020), Del Guacchio (2013), Catálogo Español de Especies Exóticas Invasoras (2013)
S Heathland, scrub and tundra	Heaths (hygrophytic tree thickets and mesophytic tree thickets), scrubland (S7)	Yes (Canary Islands)	Catálogo Español de Especies Exóticas Invasoras (2013)
T: Forest and other wooded land	Mediterranean and Macaronesian riparian forest (T14) Coniferous forests (T3) Broad-leaved forests (T1-T2) Eucalyptus plantations (T291)	Yes No No No	Catálogo Español de Especies Exóticas Invasoras (2013) Lu et al. (2006); Wu et al. (2020) Lu et al. (2006); Wu et al. (2020) Yu et al. (2014)
U Inland habitats with no or little soil and mostly with sparse vegetation	Mediterranean wet inland cliffs (U3D1): cliffs, wet or fresh rocks, wet rocky coast	Yes	Tison et al. (2014), Plantas invasoras em Portugal (2020), Del Guacchio (2013)
V Vegetated man-made habitats	Artificial grasslands and herb dominated habitats (V3): roadsides, old walls, rubble, urbanized areas, man-made green spaces, pastures Bare tilled, fallow or recently abandoned arable land (V15) Recently abandoned garden areas (V23)	Yes No Yes	Tison et al. (2014), Plantas invasoras em Portugal (2020), Catálogo Español de Especies Exóticas Invasoras (2013)

pathogens, many of which persist asymptotically as endophytes. They identified 293 fungal operational taxonomic units across 44 families and 73 genera, highlighting *A. adenophora* as a highly competent host. Taxonomically, the dominant genera included *Alternaria*, *Colletotrichum* (see also 5.2. ii), *Clonostachys*, *Diaporthe*, *Epicoccum*, *Gibberella*,

Irpex, *Nemania*, *Neofusicoccum*, *Nigrospora*, *Pestalotiopsis*, *Schizophyllum* and *Xylaria*. The species harboured diverse necrotrophic pathogens, but its endophyte and leaf spot pathogen communities were compositionally distinct, with little species overlap. Notably, 21% of the fungal taxa found in local plant hosts (native wild plants in China as well as crops) also occurred as endophytes or pathogens in *A. adenophora*. An inoculation experiment revealed that local pathogens (from native wild plants) could infect *A. adenophora* asymptotically, while its own pathogens and endophytes were also capable of infecting native plants. These findings suggest that *A. adenophora* facilitates the persistence and transmission of local pathogens. The fungi most frequently shared were pathogenic generalists found on crops, such as *Colletotrichum*. However, many of these fungi were endophytic in *A. adenophora*.

5. Biology

Ageratina adenophora is a triploid plant with $n = 51$ (Noyes 2007; Bala and Gupta 2014; Liu et al. 2025). It reproduces primarily by seeds that are produced by apomixis (clonal asexual reproduction through seeds), in particular by gametophytic diplosporous apomixis

without fertilisation (Holmgren 1919; Parsons and Cuthbertson 2001). Under favourable conditions, individual plants can produce 7 000–10 000 seeds. The plant also reproduces vegetatively by stem and root fragments if the plants are broken (Parsons and Cuthbertson 2001). The life span of plants is 12–15 years (Sun et al. 2005).

5.1. Phenology

The flowering of *A. adenophora* in its native range in Mexico is heavily concentrated from February to May, with a peak in March (based on 128 herbarium records, Universidad Nacional Autónoma de México (UNAM), 2025). The phenology of *A. adenophora* is generally consistent across its introduced range, although some regional variations have been observed. Flowering typically begins in late winter or early spring and continues through summer, depending on local climatic conditions. Seeds ripen rapidly following flowering, usually from mid-spring to mid-summer, and are dispersed by wind, animals and water. Germination often coincides with the rainy season, enabling seedlings to establish quickly under favourable conditions.

In Australia, flowering occurs from August to December (late winter to summer), with seeds ripening between October and mid-January (Auld and Martin 1975). In India (Himalayas), flowering begins in February–March (early spring), with seeds ripening in late spring and early summer (Datta 2018). In China, flowering starts as early as February, with seed set in April and May (X-Y et al. 2004; Sun et al.

2005). Across these regions, *A. adenophora* takes advantage of optimal growth conditions in the rainy season, forming dense thickets and propagating both by seed and vegetative means, such as adventitious roots in moist soils (Negi et al. 2025).

In California (USA), flowering occurs from March through August, occasionally extending into September (CAL-IPC 2022), while in Hawaii, flowering is observed year-round due to the tropical climate (D. Frohlich, pers. comm., 2023). Similarly, seed germination in Hawaii aligns with the rainy season but can occur throughout the year in wet habitats.

In Europe, the life cycle appears similar to that in Australia. In Mediterranean France, flowering begins in early spring (April), with seeds ripening from mid-May through summer (Fried 2023). In southern Spain, flowering can start as early as March.

5.2. Physiological data

5.2.1. Tolerance to frost and cold stress

The ability of *A. adenophora* to endure lower temperatures is largely attributed to its production of specific biochemical compounds, including antioxidants and osmolytes, which mitigate cellular damage during cold exposure. A study in China showed that nine populations exhibited a range of physiological changes in response to freezing stress, including increases in malondialdehyde (MDA) and total soluble protein contents, reductions in total soluble sugar and chlorophyll contents, and fluctuations in superoxide dismutase (SOD) activity (Li et al. 2008). Cold-tolerant populations showed only a moderate increase (0.8 to 5.3-fold) in malondialdehyde (MDA) content, an indicator of lipid peroxidation due to cold stress, indicating better protection against oxidative damage. Moreover, cold-tolerant populations displayed an increase in total soluble protein content, which can enhance stress resistance by stabilizing cellular structures and enzymes. Superoxide Dismutase (SOD) is an enzyme that helps neutralize reactive oxygen species generated during cold stress. In the sensitive population, SOD activity decreased by 36% of the control, whereas in the cold-tolerant population, it reduced only to 70% of the control, indicating better oxidative stress management. Finally, the cold-tolerant population experienced a smaller reduction (29%) in soluble sugar content, which acts as osmoprotectants during stress, compared to the sensitive population. These physiological traits explain the ability of certain populations of *A. adenophora* to maintain high photosynthetic efficiency in environments with occasional frost, though prolonged exposure to freezing temperatures severely limits its growth and expansion (Xie et al. 2015; Datta et al. 2017). The invasive success of this species in temperate regions is partly due to its capacity to recover from cold stress during milder winters,

allowing for continued vegetative growth once temperatures rise. However, the plant tends to be less competitive in regions with persistent sub-zero temperatures, as freezing-induced cellular dehydration compromises its metabolic processes (Li et al. 2008).

5.2.2. Tolerance to drought and heat stress

Distribution models have shown that prolonged drought is one of the key factors limiting the expansion of *A. adenophora*, particularly in Mediterranean regions with dry summers. However, the species exhibits significant plasticity (Khatri et al. 2024) and can tolerate a certain level of drought (Del Guacchio 2013). The study by Yang et al. (2024) highlights the important role of foliar endophytic *Colletotrichum* fungi in enhancing the drought tolerance of *Ageratina adenophora*. Specifically, the researchers examined the effects of three genetically distinct *Colletotrichum* strains (AX39, AX115, and AX198) under abiotic stress conditions, including drought and nutrient limitations. Their findings revealed that under drought stress, strain AX198 significantly increased stem length and chlorophyll content, suggesting improved plant vigour and photosynthetic efficiency. The presence of *Colletotrichum* endophytes also boosted biomass production in *A. adenophora* under both drought and nutrient stress, indicating a potential role in stress mitigation. Environmental stress appeared to amplify the positive effects of these endophytes, shifting their role from slightly parasitic under normal conditions to beneficial when conditions became challenging.

Chen et al. (2016) examined the heat tolerance of different *Ageratina adenophora* populations and found significant variation in their ability to withstand high temperatures. Populations from hotter regions exhibited greater heat tolerance, suggesting that *A. adenophora* can adapt to extreme temperatures over time. Heat stress mainly affected photosystem II (PSII), with tolerant populations showing less damage to their photosynthetic capacity compared to sensitive ones.

5.2.3. Responses to light availability

Ageratina adenophora exhibits strong phenotypic plasticity in response to light availability, which significantly influences its growth, biomass allocation and reproductive success in different forest types (Khatri et al. 2024). In open-canopy forests, such as cypress (*Cupressus torulosa* D. Don) and sal-mixed forests (*Shorea robusta* Gaertn. f.), the species reaches greater heights, allocates more biomass to shoots, and shows increased leaf area and seed production. This suggests a strategy to maximise carbon assimilation and reproductive output in high light environments. In contrast, in closed-canopy forests such as Banj oak (*Quercus oblongata* D. Don) and Kharsu oak (*Quercus*

semecarpifolia Smith), *A. adenophora* tends to have smaller leaves, lower biomass and reduced reproductive effort, reflecting its adaptation to shady conditions. The high plasticity of traits such as specific leaf area (SLA), and stem/root biomass ratio allows the species to optimise resource use and successfully invade a range of habitats.

By measuring various leaf traits along an altitudinal gradient in Kumaon Himalayan region, Khatri et al. (2022) showed that *A. adenophora* populations growing in high-elevation ranges exhibited lower leaf length, leaf width, mean leaf area, leaf area, specific leaf area, and leaf area ratio, and found more generally a negative correlation of these trait values with elevation rise. As posited by Zheng et al. (2009), the presence of small leaves serves to diminish the absorption of sunlight and evapotranspiration rate, thereby affording the plant a degree of protection from UV radiation and water loss at higher elevations. These findings indicate that *A. adenophora* employs specific adaptations to survive in the harsh climatic conditions of high elevations.

5.2.4. Response to nutrient availability

Ageratina adenophora exhibits remarkable plasticity in its response to varying nitrogen levels, adjusting key physiological and morphological traits to optimize growth under different nutrient conditions. According to Feng et al. (2009), compared to native populations in Mexico, invasive populations from China and India, allocate a greater proportion of nitrogen to photosynthesis rather than structural components like cell walls, enhancing photosynthetic efficiency and biomass accumulation. The authors suggest that *A. adenophora* may have undergone selection favouring greater nitrogen allocation to photosynthesis while reducing investment in defence structures like cell walls. This shift likely contributed to its invasive success by promoting genotypes with higher specific leaf area, enhanced photosynthetic rates, and improved nitrogen-use efficiency. This nitrogen-use strategy allows *A. adenophora* to sustain rapid growth even in resource-limited environments.

Furthermore, Feng et al. (Y-L et al. 2011) found that invasive populations of *A. adenophora* exhibits a higher nitrogen-use efficiency, characterized by greater photosynthetic rates (photosynthetic energy-use efficiency) and a faster return on energy investment (i.e. time needed to pay back leaf construction cost through photosynthesis) compared to native populations. This adaptation enables the species to maintain high relative growth rates (RGR) across a range of nitrogen conditions. Under elevated nitrogen availability, the plant enhances carbon assimilation by increasing chlorophyll content and leaf area, further boosting its competitive advantage.

5.3. Reproductive biology

5.3.1. Floral biology

Despite having androecia and gynoecia, *A. adenophora* does not reproduce sexually because the plant is triploid in nature, inducing abnormalities during meiosis. Instead, the plant produces seeds apomictically (without fertilization). Although this appears to be disadvantageous, this increases invasive success as the species does not have to depend on successful pollination and fertilization for producing viable seeds (Noyes 2007; Bala and Gupta 2014).

5.3.2. Hybrids and cultivars

No hybrids or cultivars are known to exist, probably because it is a sexually sterile plant and produces seeds only by apomixis.

5.3.3. Seed production and germination

Seed production of *A. adenophora* is very high and it forms a large soil seed bank. Dense populations can produce up to 60 000 viable seeds per square metre (Muniappan et al. 2009). Seed density is reported to be higher in the upper layer of the soil seed bank, but varies depending on the depth. Shen et al. (2006) reports that seed density in the 0–10 cm soil layer varied from 47 to 13,806 seeds m⁻², and averaged 2,199 seeds m⁻². Fifty-seven percent of the seeds of *A. adenophora* were in the 0–2 cm soil layer, 24 % in the 2–5 cm layer and 19% in the 5–10 cm layer.

Seed viability varies with the depth the seed is buried and time. The species forms a persistent seed bank. Shen et al. (2011) showed that 90% of seed on the soil surface died. Forty percent of seeds were viable at depths of 5 cm and 10 cm after 2 years, and 20% of seeds germinated after 3 years. After 4 years, survival rates at 5 and 10 cm decreased to less than 10%. Similar observations were made in India (Yadav and Tripathi 1982).

5.3.4. Dispersal

Natural spread. *Ageratina adenophora* propagates primarily by means of seeds that are equipped with pappus hairs for wind dispersal. Individual plants are capable of producing 7,000 to 10,000 seeds each year under optimal conditions (Parsons and Cuthbertson 2001). Seeds can float on water and can be spread with water movement. It is also plausible that seeds are spread by animals when they become attached to muddy fur, skin, or feathers (CABI 2022). Vegetative reproduction by stem or rhizome fragments also occurs in the presence of moisture. The establishment of stem fragments is assumed to be very successful, as the species can grow vegetatively from small cuttings (Wang et al. 2011). This may act to facilitate short-distance spread and the expansion and increased density of the local population. Broken stem fragments

can root when pieces are in contact with the soil. However, for natural spread, stem fragments are not considered as important as the spread of seed. Wang et al. (2011) note:

A large number of stem fragments or broken rhizomes can be produced and float downstream with a flood event. Flooding can act to amplify the vegetative dispersal ability of *A. adenophora*. Following the destruction or disturbance of other riparian vegetation, large openings are available and favourable for colonisation.

Natural spread is promoted via transportation networks (roads and railways) and rivers in China (Lu and Ma 2006; Wang and Wang 2006; Wang et al. 2011; Horvitz et al. 2014). The invasion of *A. adenophora* expressed as cover, abundance, and number of clusters has been shown to decline significantly with distance from roads and streams in Southwest China (Lu and Ma 2006). When modelling the mechanisms for spread in China, Horvitz et al. (2014) estimated that rivers have played an important role in the rapid spread of the species over time. Its biological traits, favouring dispersal by water and wind, coupled with local spatiotemporally heterogeneous geography and ecology, promote invasion downstream and upstream along river valleys, while other factors associated with human activities facilitate its invasion over high mountains and across river valleys, providing new scope for progressive invasions (Wang et al. 2011).

In Sikkim (India), *A. adenophora* spread rapidly from sites at 1800 m elevation to sites at 2700 m elevation in 3 years (Verma et al. 2023). In Europe, *A. adenophora* is present along riparian systems where it spreads, and on the banks of streams and rivers (Plantas invasoras em Portugal 2020; Fried 2023). In Corsica, when the plant was first discovered in 1952, it already occupied 1 km along a riverbank (Conrad 1961a). In Portugal, clusters of distribution along urban watercourses suggest spread by natural means (Plantas invasoras em Portugal 2020). Although this does not allow us to deduce a rate of spread, it nevertheless shows that the species has a very good capacity to colonise along the river corridors.

Human-assisted spread. A number of human-assisted mechanisms can act to spread *A. adenophora*. The species may be spread via the deliberate movement of seeds or plants for ornamental purposes (CABI 2022; CAL-IPC 2022). Seeds can also be spread as contaminants of plants for planting. The small seeds can be contaminants of soil which can facilitate the spread and potential establishment as soil may be placed in suitable conditions to facilitate seed germination.

Other potential means of spread detailed in the literature include via mud attached to clothes and equipment (e.g. agricultural workers as well as tourists, hikers, etc.), and spread via contaminants of machinery (CABI 2022). Seeds may also contaminate stockfeed (grain) (CABI 2022). An important means of spread of *A. adenophora* is movement as an impurity in agricultural produce, mainly cereals, forage and other seeds, also in sand and gravel used for road construction (CABI 2022).

Disturbance of existing populations, through direct management or habitat restoration can spread seeds and stem fragments. The dumping of contaminated garden waste can also spread the plant if it contains viable propagules.

In Europe, established populations have not shown significant spread to-date. Due to the wind dispersal of the seed, a greater rate of spread would have been expected than has been observed currently. It seems that, for most existing populations and cultivated individuals in Europe, seed rains land in habitats or conditions (both biotic and abiotic) that are unsuitable, and therefore the invasive potential of the species has not yet been fully realised. With climate change, and the potential increase in established populations, spread is likely to increase within Europe. If climate change promotes establishment, populations may exhibit higher propagule pressure, leading to increased spread (see section 3.1).

6. Economic importance and impacts

6.1. Uses and positive impacts

The species was originally grown in many parts of the world as an ornamental plant, but it has declined in popularity, as evidenced by its absence from nursery catalogues (Auld and Martin 1975). Biomass of this weed has been also used for the preparation of compost by small-holder

farmers in Nepal (Shrestha et al. 2019). Phytochemical research has led to the discovery of bioactive chemicals with antibiotic properties, cytotoxic activity, antioxidant activity and wound healing properties. *A. adenophora* has been used as a medicinal plant in China, India and Nigeria for multiple purposes such as hemostatic agent, to treat diabetes, jaundice, ulcer and skin disorders (Giri et al. 2022).

6.2. Negative impacts

6.2.1. Effects on biodiversity and ecosystem functioning

6.2.1.1. Impacts on plants and vegetation.

Competition. Once *A. adenophora* invades an area, it can rapidly produce dense monospecific stands that displace native plant species and alter local nutritional

cycles and hydrological conditions to produce a regime shift (Gaertner et al. 2014). Dense *A. adenophora* stands reduce biodiversity and endanger native plant species, particularly rare species, ultimately causing ecosystem degeneration and altering the local natural landscape (Wan et al. 2010). Studies carried out in Yunnan and Sichuan provinces, China, revealed that *A. adenophora* invasion led to significant declines of species richness, ranging from 7% to 53% across all affected habitats (Ding et al. 2007). Plant communities dominated by annual herbs showed a more significant declining trend than those with perennial herbs (Ding et al. 2007).

Ageratina adenophora has been reported to negatively impact the composition and structure of understory communities, as well as the growth of *Pinus yunnanensis* Franch. seedlings under pine stands in Yunnan (Fu et al. 2018). According to Fu et al. (2018), *A. adenophora* altered species and functional diversity by modifying species composition and abundance in the understory due to its higher specific leaf area, leaf nitrogen concentration (LNC), and leaf phosphorus concentration compared to native species. Their study also found that species with lower LNC were the first to disappear as invasion intensity increased.

In Nepal, *A. adenophora* is locally known as “Kalo Banmara” which means “black forest killer plant”. Thapa et al. (2017) demonstrated that seedlings of the native tree species *Schima wallichii* had reduced root length and dry weight when grown in the presence of *A. adenophora* leaf litter.

In Hawaii, *A. adenophora* spread rapidly after its introduction in the late 1800s to dominate large areas by 1913, forming monotypic stands up to 1.5 m tall, and crowding out desirable plants and overtaking pasturelands (Loope et al. 1992). Despite the release of the biological control agent *Procecidochares utilis*, the species remains along streams, in native-dominated forests where, along with a suite of other introduced species, it has been found to inhibit the growth of native plants (Loope et al. 1992). In Europe, along the streams of the French Riviera (between Nice and Menton), *A. adenophora* forms dense, monospecific stands (Figure 6) in several wet ravines and valleys, but over smaller areas of only a few hundred square meters (Fried 2023). It is likely to have a negative impact on the abundance of native species characteristic of these habitats such as *Allium triquetrum* L., *Carex pendula* Huds., *Eupatorium cannabinum* L., *Hypericum androsaemum* L., *Oloptum miliaceum* (L.) Röser & Hamasha, *Parietaria Judaica* L., *Sambucus nigra* L., *Samolus valerandi* L. or *Sanicula europaea* L (Fried 2023). In drier ruderal habitats (roadsides) or on old walls and cliffs, populations are sparser and impacts are less likely (Fried 2023).

In Italy, Del Guacchio (2013) notes that in Campania, *A. adenophora* may compete with native species both in stillcidious rocky coasts and along rivers. In Sorrento, several endemic species were observed to grow alongside with *A. adenophora*. It competes with these endemic plants, which often disappear from sites where ecological conditions are less challenging for alien competitors. For instance, *A. adenophora* can outcompete *Centaurea tenorei* Guss. ex Lacaita and *Helichrysum litoreum* Guss. growing in the same locations, depriving them of space and light. Recent sightings, supported by images (see invasoras.pt), revealed dense stands of *A. adenophora* along the banks of large rivers through urban areas in Portugal (Leiria, Lisbon and Coimbra), indicating a suppression of native vegetation. In Northwest Spain (A Pobra do Caramiñal), *A. adenophora* is relatively abundant and shows clearly invasive behaviour (González-Martínez and González-Martínez 2017). On the coast of Eastern Andalusia *A. adenophora* invades riparian environments and ruderal habitats, but it is also present in the Natural Park of the Sierras de Tejada, Almirajara and Alhama.

In Madeira, a high density of the plant can negatively impact native plant communities such as the temperate laurel forest (Silva et al. 2008). Historically, Lowe (1868) describes its behaviour as invasive “spread[ing] in vast profusion”, “forming, in some places, hedges [. . .], and in ravines, thickly clothing the wet dripping perpendicular cliffs in many places as if perfectly indigenous”. In the Canary Islands, it is present on four of the seven main islands: La Palma, La Gomera, Tenerife and Gran Canaria (García Gallo et al. 2008). According to Sanz Elorza et al. (2004), the presence of *A. adenophora* is particularly concerning in the National Park of Caldera de Taburiente, on the island of La Palma where it has been reported in 80% of the park’s territory, although it is not present above 1,800 m elevation. It is located also in the Garajonay National Park, in La Gomera, where it invades *Pinus canariensis* forests and degraded Laurisilva (Macaronesian laurel forests). Importantly, in the National Park of the Caldera de Taburiente, at the beginning of the decade of the 1990s, a control plan for *A. adenophora* was adopted. This involved uprooting the plants and then reintroducing native taxa for 3 years in a row. However, after 2 years, the areas where the control operations were carried out were colonized again by *A. adenophora*, leading to the abandonment of this control method.

Allelopathy. *Ageratina adenophora* can reduce the growth of other species by releasing allelopathic compounds (Kaul and Bansal 2002; Darji et al. 2021) which also alters the soil microbial communities (H-B et al. 2007). Laboratory trails demonstrated that chemicals from the plant, such as cadinenes and β -sitosterol,



Figure 6. Populations of *Ageratina adenophora* in wet ravines of the French Riviera. A) 05 February 2022, Eze, B) 15 April 2022, Eze, France. Photos by Guillaume Fried.

inhibit the germination of crop seeds, including *Allium cepa* L., *Raphanus sativus* L., and *Cucumis sativus* L. seeds (Baruah et al. 1994). In a pot experiment, leachates from fresh leaves and roots of *Ageratina adenophora* were found to be phytotoxic, inhibiting the growth and development of two native Nepalese shrubs, *Osbeckia stellata* Buch.-Ham. ex D. Don and *Elsholtzia blanda* (Benth.) Benth (Darji et al. 2021). Similarly, another pot experiment demonstrated that *A. adenophora* plant litter collected at different growth stages strongly inhibited the survival and growth of *Lantana camara* L. cuttings, with the greatest suppression caused by litter from the post-flowering stage (Kaul and Bansal 2002).

6.2.1.2. Impacts on soil properties and microbial communities. Shrestha et al. (2022) highlighted that *A. adenophora* invasion alters soil chemistry by increasing nitrogen content and enhancing microbial processes. These impacts are shared with species like *Chromolaena odorata* (L.) R.M.King & H.Rob., *Parthenium hysterophorus* L., and *Leucanthemum*

vulgare Lam., which also enrich soil nutrients and promote active nutrient cycling. A study by Balami et al. (2017) found that soil fungal species richness is lower in invaded soils compared to uninvaded ones. *Ageratina adenophora* also alters soil fungal composition by replacing saprophytic fungi with an increased presence of pathogenic fungi (Balami et al. 2017). Soil in *A. adenophora*-invaded areas tends to have lower pH but higher levels of organic matter, total nitrogen, phosphorus, and potassium compared to uninvaded soil. No studies on allelopathic effects of *A. adenophora* and its effects on the soil microbiota have been conducted in Europe. However, EPPO (2023) noticed that similar effects to those seen in other regions where the species is established are very likely to occur in Europe.

6.2.1.3. Impacts on animals. Gu et al. (Gu et al. 2008) studied the impact of *A. adenophora* on Carabidae (Coleoptera) in Yunnan Province, China. They found that the abundance of Carabidae was lower in areas dominated by *A. adenophora* compared

Table 2. Summary of the impact of *Ageratina adenophora* on provisioning, regulating, supporting and cultural services.

Ecosystem service (ES)	Short description of impact	References
Provisioning	Reduction in productivity of pastureland/reduced yields in crops (maize, rice, eggplant and banana) in China/negative impacts on forest regeneration in China and Nepal; reduction in natural flow of water along streams and water bodies in India.	Lu et al. (2008); Fu et al. (2018); Malla et al. (2021); Datta (2018)
Regulating	Increases the potential for natural fires by increasing the amount of fuel material.	Wang and Niu (2016)
Supporting	Modifies nutrient cycling in soils	Poudel et al. (2019)
Cultural	Loss of land for amenities. In Australia for example, it has become problematic along the eastern coast invading habitats such as public reserves (State forests, national parks and nature reserves). <i>A. adenophora</i> is toxic to horses.	Department of Primary Industries A (2022)

to native grasslands (dominated by *Echinochloa* sp. or *Setaria* sp.), although species richness was higher. The study indicated that the invasion of *A. adenophora* altered the structure of carabid communities, with some habitat specialists found exclusively in either invaded vegetation or native pastures. However, this did not necessarily result in a reduction in the alpha-diversity of carabid assemblages. Some carabid species, such as *Hyphaereon masumotoi* (N. Ito) and *Cosmodiscus* sp., appear to be favoured by the deep litter layer associated with vegetation dominated by *Ageratina adenophora*.

6.2.1.4. Impacts on ecosystems. The impact of *A. adenophora* on ecosystem services in the current area of distribution is significant, as it affects provisioning, regulating, supporting and cultural services (Table 2). In China, the main negative impact of the species is on the ecosystem functions of grassland (Xu et al. 2006).

6.2.2. Colonization of high conservation value habitats and effects on rare or vulnerable species

6.2.2.1. Presence in habitats of high conservation value. *A. adenophora* is invasive in several regions across the world that are of high conservation value including biodiversity hotspots. For example, in South Asia it is invasive in the Himalayas, the Indo-Burma region and the western Ghats, all of which are biodiversity hotspots (Shrestha et al. 2022). In South Africa, it is present in the Cape Floristic Region which is important from a conservation perspective due to the high level of endemism. The mountains of South-West China is a biodiversity hotspot and have been aggressively invaded by *A. adenophora*. In Spain, it occurs in two national parks: National Park of Caldera de Taburiente (La Palma), Garajonay National Park (La Gomera) and one Natural Park (the Sierras de Tejeda, and Almirajara and Alhama). In the Canary Islands, it invades a priority habitat under the EU Habitats Directive -the Macaronesian laurel forests (*Laurus*, *Ocotea*) HD 9360—particularly the vegetation formations *Myrico-Ericetum*, *Lauro-Perseetum*, and *Visneo-Arbutetum* (García Gallo et al. 2008). According to these authors, *A. adenophora* alters the structure of

potential vegetation, threatening numerous protected natural areas and the Natura 2000 Network, where control and eradication measures are needed. Its presence in high-conservation-value habitats is a significant concern, especially given the sensitivity of island ecosystems to biological invasions and the disproportionate impact such species can have on native biodiversity.

6.2.2.2. Impact on species of high conservation value. There is no clear evidence of impact of *A. adenophora* on rare or protected plant species. However, several studies suggest an existing or potential impact. *A. adenophora* has been noted as a threat to native Hawaiian ecosystems, where it invades forests and outcompetes native plant species, some of which are endangered (Danielle Frohlich, pers. com. 2025). Its spread alters soil chemistry and light availability, further disadvantaging native plants. In Canary Islands, García Gallo et al. (2008) indicates that *A. adenophora* competes for space with endemic and native species typical of laurel forest communities. In one site, in the French Riviera, it has been found co-occurring with *Symphytum bulbosum*, a nationally protected species (Conservatoire botanique national méditerranéen 2023).

6.2.3. Agriculture and other economic impacts

Ageratina adenophora can be a serious weed in some agricultural systems, especially in perennial crops, in pastureland and rangelands and in forests (Sharma and Khatri Chhetri 1981).

6.2.3.1. Impacts on crop yield. In China, ZhiHong et al. (2004) report annual yield losses of 18% in maize (*Zea mays* L.) and 9% in rice (*Oryza sativa* L.) in Tianlin County. They also note that banana plants can experience a reduction of 2–3 leaves and a height decrease of 4–8%, potentially impacting yield. However, these figures should be interpreted with caution, as EPPO (2023) highlights that the methodology used by ZhiHong et al. (2004) to assess yield losses is unclear. Further data from China documented effects of various densities of *A. adenophora* in cotton (*Gossypium hirsutum* L.) and eggplant (*Solanum melongena* L.). AoCheng et al. (2013) showed that fruit

branches and bolls per plant decreased by 22 % and 57 % at a density of 60 plants/m² of *A. adenophora* compared to the untreated control, and loss of lint yield was up to 57%. WenDa et al. (2011) demonstrated that height, fruit number and yield of *S. melongena* were not affected when the densities of *A. adenophora* ranged from 1–2 plants/m², while these parameters decreased significantly when the density was >5 plants/m². The primary cause of eggplant yield loss may be attributed to the height of *A. adenophora*, which interferes with light penetration and affects the accumulation of water and nutrients.

When *A. adenophora* grows near crop fields, it may release leachates through rainwater, which can then be mixed into the paddy field. Shrestha et al. (2021) studied the impact of leaf extracts of *A. adenophora* on the growth and development of rice (Khumal-11). In controlled studies, fresh and dry leaf extracts of *A. adenophora* were shown to have a negative impact on root shoot growth and the number of roots of rice.

7.2.1.2. Impact on rangeland. In Australia, *A. adenophora* reduces the value of bush land (Department of Primary Industries A 2022), reduces animal carrying capacity, and restricts livestock movement (Parsons and Cuthbertson 2001). Dense stands of *A. adenophora* reduce species diversity, biomass and productivity of grasslands in Western Himalaya (Balami et al. 2017).

Xu et al. (2006) report that *A. adenophora* and *Chromolaena odorata* are the two main invasive plants in China that threaten grassland ecosystem functions through the loss of forage. Wan et al. (2010) detail that *A. adenophora* has caused 989-million-yuan (133 million Euros) losses to livestock production and 2.6 billion yuan (338 million euros) annual losses to the production of grassland in China. These high figures are supported by data that suggests that each hectare of grassland invaded by this toxic species produces no more than 1 kg of grass compared to 78,000 kg of Crofton weed (Lu et al. 2008). According to Sun et al. (X-Y et al. 2004) only 3 years after invading a natural pasture, the coverage of *A. adenophora* can reach 85% to 95% and reduce yield by 70% to 79%.

7.2.1.3. Impacts on livestock. *Ageratina adenophora* is poisonous to domestic animals such as horses and cattle (Ren et al. 2021). This toxicity is mainly due to the presence of numerous sesquiterpenes, most of which share a cadinene-type molecular structure. Among these compounds, the most harmful are 9-oxo-10,11-dehydro-agerophorone (commonly known as euptox A), 2-deoxo-2-(acetyloxy)-9-oxo-agerophorone (DAOA), and 9-oxo-agerophorone (OA) (Ren et al. 2021; Huang et al. 2023). *Ageratina adenophora* has been shown to cause liver inflammation, disrupt cellular function,

and negatively impact both metabolism and the nervous system (Huang et al. 2023). Additionally, it can impair spleen function, as studies in mice have demonstrated damage through oxidative stress and inflammation-related cell death (pyroptosis) (Sun et al. 2019).

The plant is more toxic in its flowering than in its juvenile stages (O’Sullivan 1979). It causes respiratory disease in horses that may result in death, if horses continue to feed upon it for prolonged periods (O’Sullivan 1979). It causes the “blowing disease” in Hawaii and “Numinbah disease” or “Tollebudgera horse disease” in Australia. Symptoms such as coughing, difficulty in breathing, and violent blowing after exertion are the result of acute lung edema leading to haemorrhage (Swarbrick and Skarratt 1994). Verma et al. (1987) found that *A. adenophora* reduced digestive function and causes photosensitive reaction in cattle (Parsons and Cuthbertson 2001).

7.2.1.4. Impacts on forestry. A survey in Guangxi, China in 2003, reported that *A. adenophora* infestations caused annual economic losses of around 5% in forest-related sectors, though the exact nature of these losses (e.g. timber yield, forest services) was not specified (ZhiHong et al. 2004). Above sections already detailed the effects of *A. adenophora* on biodiversity and soils in forest systems. *A. adenophora* has been shown to have a negative effect on the growth of *Pinus yunnanensis* seedlings under pine stands (Fu et al. 2018). The impacts on the regeneration capacity of other tree species appear to vary depending on the context. For instance, in Nepal, when *A. adenophora* invades plantation forest (*Pinus roxburghii* Sarg., *P. patula* Schiede ex Schltdl. & Cham. and *P. wallichiana* A.B.Jacks.) regenerated by seeds, there is a negative impact on forest regeneration and a cost for the management of the suite of invasive plants (Malla et al. 2021). In contrast, in a study assessing the impacts of *A. adenophora* on vegetational attributes and regeneration status across three forest types in Kumaun, Central Himalaya, India, Negi et al. (2023) found no significant difference in the regeneration of *Quercus oblongata*, *Pinus roxburghii*, and *Cupressus torulosa* between invaded and uninvaded sites. The authors, however, caution that tree species with poor or no regeneration status require special attention and management strategies, including the control of invasive species, to support forest ecosystems. There is the potential for further negative impacts in managed forests in Spain and Portugal (where moisture levels may be more suited to its establishment).

7.2.2. Control costs

Quantitative data on the control costs of *A. adenophora* are limited. ZhiHong et al. (2004) report that *A. adenophora* can have impacts on infrastructure as plants block drainage ditches which can have a negative effect on irrigation. In this context, the authors estimate it can cost around 450–1200 RMB (61–162 Euros) per hectare in management costs. There are no studies and few monetary figures on the economic impact of *A. adenophora* in Europe. To our knowledge, there are no management actions and therefore no costs in France and Italy. The only known figures in Europe are from Andreu et al. (2009) who detail management costs in Spain to be 23 109 Euros over the last decade.

8. Legislation and management

8.1. Legislation

In China, *A. adenophora* is considered as a quarantine pest since 2021 (EPPO 2025). In the USA, *A. adenophora* is listed as a federal noxious weed and is thus prohibited from import or interstate commerce unless under permit. It is also listed as a noxious weed in several states including Alabama, Florida, Hawaii, Minnesota, North Carolina, and Vermont, as a prohibited weed in Massachusetts, and as a plant pest in South Carolina (USDA NRCS 2022). The species is a U.S. Federal noxious weed seed and is also a prohibited noxious weed seed in Hawaii (USDA AMS 2022). In South Africa, it is a category 1b plant prohibited from planting or commerce (National Environmental Management: Biodiversity Act listing). In Australia it is regulated in two states. In New South Wales, it is listed as a Class 4 species, i.e. a locally controlled weed. This means that the “growth and spread of this species must be controlled according to the measures specified in a management plan published by the local control authority and the plant may not be sold, propagated or knowingly distributed (in a large number of local authority areas)” (Australian Government 2014). In Western Australia, it is on the prohibited species list and not permitted entry into the state (Australian Government 2014). In New Caledonia, where it is not present, it is listed in the *Code de l'environnement de la province nord de Nouvelle-Calédonie : Article 261-1 relatif aux espèces envahissantes* (Délibération n° 2012-236/BPN du 12 octobre 2012) ». In Europe, the species has been included on the A2 List of pests recommended for regulation as quarantine pests of the European and Mediterranean Plant Protection Organization (EPPO) in 2023 (EPPO 2025).

It is also listed as invasive species in Portugal in the Decreto-Lei n° 92/2019, 10 July, as well as in Spain where it is listed as invasive species in the Real Decreto 630/2013, de 2 de agosto. The Regulation applies to the Canary Islands.

8.2. Management

8.2.1. Preventive strategies

In rangelands threatened by invasion of *A. adenophora*, maintaining a high diversity of competitive and desirable pasture plants can help suppress this invasive species. For example, in southwest China, researchers identified 38 pasture cultivars from 16 extensively cultivated species as effective competitors against *A. adenophora*. These plants were selected based on traits such as tolerance to allelopathic chemicals, rapid growth rates, and dense canopy cover, which reduces light availability – a key factor since *A. adenophora* germination is dependent on light. The most suitable species for planting included *Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. ex Moss, *Dactylis glomerata* L., *Medicago sativa* L., *Macroptilium atropurpureum* (DC.) Urb., *Vicia sativa* L., and *Vicia villosa* var. *glabrescens* W.D.J.Koch (Zhong et al. 2007). More generally, this can be extended to natural environments, where ecological approaches can be applied to manage biological invasions. An ecological approach refers to the use of fundamental ecological principles in landscape management. For example, maintaining high native plant diversity can enhance ecosystem resistance and reduce the competitive advantage of invasive species.

8.2.2. Chemical control

A number of herbicides have been effective in controlling *A. adenophora*. Control of *A. adenophora* can be performed by spraying herbicides such as glyphosate, fluroxypyr, 2,4-D amine, picloram + 2,4-D, picloram + triclopyr, dicamba + MCPA and metsulfuron-methyl (Parsons and Cuthbertson 2001; DiTomaso et al. 2013). They are most effective when the plant is in the vegetative stage and growing actively. However, the use of herbicides should be considered as a last resort and must be carefully evaluated due to their potential impact on non-target species and the environment, particularly water quality. Additionally, in the European Union, herbicide use is strictly regulated and prohibited in natural habitats to prevent ecological harm. Recently, Methyl 4-Hydroxyphenylacetate has been reported to be an effective growth inhibitor of *A. adenophora* by downregulating the levels of plant hormones. This compound is a derivative of benzoic acid and is claimed to be less toxic compared to traditional herbicides (Yang et al. 2025).

8.2.3. Physical control

Mechanical control, such as hand-pulling and digging, can be applied where the plant is accessible. However, plants often grow on steep slopes, making hand removal difficult. Cutting a plant may not control it, but over time it will reduce the seedbank and reduce the population.

In some cases, the biomass left after slashing is burned to prevent resprouting following rainfall. After slashing, the soil is ploughed, and seeds of competitive species are sown to minimize the risk of reinfestation (Parsons and Cuthbertson 2001; Poudel et al. 2019). Incomplete mechanical control efforts can prove to be counterproductive since the plant has potential to resprout vigorously after mechanical injury. Given that *A. adenophora* is primarily invasive in mountainous landscapes, implementing mechanical control methods is often impractical.

8.2.4. Biological control

A number of biological control agents have been released worldwide against *A. adenophora*, with varying levels of success (Poudel et al. 2019). Early efforts of biological control dates to 1924 when a host-specific shoot-gall causing fly, *Procecidochares utilis*, was reported (Osborn 1924). This biological control agent was initially introduced in Hawaii and later it was introduced from Hawaii to seven invasive ranges viz. New Zealand, South Africa, India, Nepal, China and Thailand (Winston et al. 2014). It has now been introduced in most of the invasive ranges including Portugal in 1962.

Procecidochares utilis can reduce the vigour and fitness of the plant and in some cases can also result in mortality (Erasmus et al. 1992; Muniappan et al. 2009). However, the efficacy of this shoot-gall causing fly depends on the climatic conditions of the range. For instance, in Hawaii, it has performed relatively well under moderate to low precipitation conditions compared to other ranges with high precipitation (Bess and Haramoto 1972). In the Himalayas, infestation of gall can still be found abundantly in populations of *A. adenophora* but it has little effect on the invasiveness of the plant. Poudel et al. (2020). investigated the effectiveness of *P. utilis* along an elevation gradient in central Nepal. Results showed that gall abundance and size peaked at mid-elevations (1940–2000 m), where galls acted as nutrient sinks and reduced stem diameter, suggesting that elevation significantly influences biocontrol success. The reduced efficiency has also been attributed to high abundance of several parasitoids of *P. utilis* that were most likely co-introduced (Heystek et al. 2011).

The Agricultural Research Council-Plant Protection Research Institute of South Africa (ARC-PPRI) carried out special surveys in Mexico from 2007 to 2009 (Heystek et al. 2011). The efficacy of biological control agent has been investigated in a quarantine research facility at Pretoria where more than 20 insect species have been screened as potential biocontrol agents (Heystek et al. 2011). A comprehensive list of natural enemies of *A. adenophora* has been documented in a recent review (Poudel et al. 2019).

The leaf spot fungus *Passalora ageratinae* Crous & A.R. Wood has been introduced into several countries and has established. The rust fungus *Baeodromus eupatorii* (Arthur), a native of Mexico, was released in Australia in 2014. *Xanthaciura connexionis* (Diptera) Benjamin, native to Mexico, was released in Hawaii in 1955.

It appears that there is no single biological control agent that can act as a panacea for the invasion of *A. adenophora*. Indeed, a synergistic approach has been the focus of recent research (Buccellato et al. 2012).

8.2.5. Cultural control

Cultural control refers here to modifications in existing agricultural practices, livestock farming and novel utilization of the target invasive plant. These practices are often associated with some kind of economic benefit that acts as incentives for local people. In the case of *A. adenophora*, local people in Nepal use the above-ground part for cattle bedding and composting (Tiwari et al. 2005; Baral et al. 2017; Shrestha et al. 2019). Additionally, the biomass has also been used for making cost-effective bio-briquettes in Nepal (Baral et al. 2017). The plant has found novel utilization in China in the form of substrate for producing a domestic fungus (X-Y et al. 2004). These cultural practices seem to have promise but need to be applied with caution as the seeds might get transported to new locations leading to new invasion foci.

Ageratina adenophora exemplifies the ecological and economic challenges posed by invasive species. Originally introduced as an ornamental plant, its adaptability, reproductive strategies, and competitive dominance have enabled it to invade diverse ecosystems across the globe. The species disrupts native biodiversity, alters soil chemistry, and poses serious risks to agriculture and livestock, making it a significant concern for land managers and conservationists. While efforts to control its spread have included biological control, chemical management, and ecological restoration, its persistence highlights the importance of proactive measures to prevent future invasions.

At the same time, the spread of *A. adenophora* in Europe has so far remained moderate despite its strong reproduction and adaptability. This is possibly due to climatic restrictions and unsuitable habitats. This situation is likely to change, and further observation of the species is needed, and awareness should be raised among municipalities and other relevant authorities. Systematic monitoring should be carried out in areas where the species is already present, combined with rapid response strategies such as pulling, cutting or other appropriate management techniques, to prevent its establishment and/or limit its spread. This also applies to areas

where the species is not currently present but are considered climatically suitable for the species. In addition, future studies should investigate the biology of the species in Europe, including life cycle, genetic variation and cold tolerance, in order to assess its further spread and derive efficient control options. To better understand the species' capacity to adapt and thrive in new environments, studies focusing on the diversity of different populations should be undertaken. Furthermore, the effectiveness of different biocontrol agents should be tested under controlled environments. Citizen science initiatives in invaded as well as vulnerable areas should be undertaken for public awareness and participation in control measures.

Note

1. This account presents information on all aspects of the biology and ecology of *Ageratina adenophora* (Spreng.) R.M.King & H. Rob. that are relevant to understanding its invasive behaviour. The main topics are presented within the framework of the monograph series of *Botany Letters on Invasive Plant Species in Europe: taxonomy, distribution, history of introduction and spread, ecology (including preferred climate and habitats, responses to abiotic and biotic factors, ecological interactions), biology (including physiology, phenology, and reproductive biology), impacts and management.*

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Authors' contributions

Guillaume Fried drafted the full review, initially developed as an EPPO Pest Risk Analysis. Arunava Datta contributed to several sections, notably those on management. Giuseppe Brundu, Swen Follak, and Johan van Valkenburg reviewed the manuscript. Daniel Chapman contributed as an expert on *Ageratina adenophora* distribution modelling. Daniele Frohlich and David M. Richardson reviewed and helped improve the final version. Rob Tanner reviewed the manuscript and coordinated the EPPO Pest Risk Analysis. All authors contributed their expertise as participants in the EPPO Pest Risk Analysis and provided input throughout the preparation of the manuscript.

Data availability interest

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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