

Biology of Invasive Plants

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Biology of Invasive Plants 6. *Parthenium hysterophorus* L.

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Scientific Classification

Kingdom: Plantae

Subkingdom: Tracheobionta

Division/Phylum: Magnoliophyta/Tracheophyta

Class: Magnoliopsida/Angiospermae

Subclass: Asteridae

Category: Campanulids

Order: Asterales

Family: Asteraceae

Subfamily: Asteroideae

Tribe: Heliantheae

Subtribe: Ambrosiinae

Genus: *Parthenium*

Species: *hysterophorus* L.

Synonyms: *Argyrochaeta bipinnatifida* Cav.; *Echetrosis pentasperma* Phil; *Parthenium lobatum* Buckley; *Parthenium pinnatifidum* Stokes.

EPPO code: PTNHY

Name and Taxonomy

Parthenium weed (*Parthenium hysterophorus* L.) belongs to the Asteraceae family and Heliantheae tribe. It was initially classified under the Melampodiinae subtribe but later reassigned to the Ambrosiinae subtribe; the same subtribe under which other genera such as *Ambrosia*, *Xanthium*, *Iva*, and *Parthenice* belong (Stuessy 1973). However, the exact phylogenetic relationships among these genera remain uncertain (Panero 2005).

Parthenium hysterophorus is recognized by a multitude of names around the world, reflecting its widespread distribution and impact (Table 1).

Importance

Parthenium hysterophorus is a weed of global significance because of its widespread distribution, its aggressive invasive nature, and its detrimental impacts on agricultural production, animal and human health, and the environment (Chippendale and Panetta 1994; Jayachandra 1971; Navie et al. 1996). Initially, in its invaded range, *P. hysterophorus* was primarily seen as a weed of rangeland settings (Adkins and Shabbir 2014), but more recent reports indicate its proliferation in agricultural systems as well, with one study reporting up to 97% of sorghum [*Sorghum bicolor* (L.) Moench] yield losses attributed to *P. hysterophorus* infestation in Ethiopia (Tamado et al. 2002). In India, one of the worst *P. hysterophorus*-affected countries in the world, yield losses have been reported to be as high as 40% in rice (*Oryza sativa* L.), 63% in tomato (*Solanum lycopersicum* L.), and 90% in sorghum (Kumar 2012; Oudhia 2000). In Pakistan, *P. hysterophorus* infestation in maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) crops have caused regional food shortages (Khan et al. 2013). *Parthenium hysterophorus* is known to outperform crops when competing for resources such as light, water, space, and nutrients (Zimdahl 2004); and under competition, crop growth, reproduction, and ultimately crop yields are all negatively affected. It also competes indirectly through its powerful allelopathic mechanisms (Bajwa et al. 2020; Shi and Adkins 2020) or by serving as an alternate host to pests and diseases (Shabbir 2014b; Sharman et al. 2009). *Parthenium hysterophorus* also causes

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Table 1. International and local names for *Parthenium hysterophorus* around the world.

Country	Name	Reference
English-speaking countries	Barley flower, bastard feverfew, bitterweed, broomweed, carrot grass, dog flea weed, false ragweed, featherfew, feverfew, mugwort, quinine-weed ragweed parthenium, star weed, whiteheads, white top, white top weed, wild wormwood, wormwood	Saha et al. (2018); Weyl (2022)
Belize	coriente, siiu, silantro	Weyl (2022)
Brazil	Coentro-do-mato, fazendeiro, losna-branca	Adkins et al. (2018); Gazziero et al. (2006); Weyl (2022)
China	Yin jiao ju	Weyl (2022)
Cuba	Artemisilla, cofitillo, escoba amarga	
Dominican Republic	Baille lame, escoba de puerco, escobita amarga, yerba mala	
Ethiopia	Arama-kuba, arama-sorgo, biyabassa, chebchabe, terekabi	
France	Fausse camomille, matricaire, parthenium matricaire	
Guatemala	Hauay, tacana	
Haiti	Absinthe marron, balai amer, parthene multifide	
Honduras	Ajenjo, escobilla	
India	bhoothkeda, carrot weed, chatak chandani, coimbatore chedi, congree grass, congress grass, congress pacha, gajar ghas, gazar ghas, keepa geda, osadi	Adkins et al. (2018)
Jamaica	dog-flea weed, whitetop	Weyl (2022)
Mexico	altamisa cimarrona, altamisa del campo, altamisilla, arrocillo, chaile, cicutilla, cola de ardilla, confitillo, falsa altamisa, hierba amargosa hierba del burro, hierba del gusano, huachochole, jihuete amargo, manzanilla del campo, romerillo, yerba de la oveja, zacate amargo	Adkins et al. (2018); Martínez (1979); Rzedowski and Rzedowski (2004); Villarreal (1983); Weyl (2022)
New Caledonia	Fausse camomille	Weyl (2022)
Nicaragua	Manzanilla monterá	
Portuguese	Mentruz	
Puerto Rico	Ajenjo cimarron, artemisa cimarrona, yerba amarga	
Pakistan	Baby-flower, gajar booti, gandhi booti, speen gulai, lewanai bhang	Adkins et al. (2018); Bajwa (2019)
Saint Lucia	Matnitjen, whitehead	Weyl (2022)
South Africa	Famine weed	Adkins et al. (2018); Weyl (2022)
Spain	Ajenjo cimarron, amargosa, camalote, escoba amarga, hierba amargosa, istafiate, requeson	Weyl (2022)
Sweden	Flikparthenium	
Zimbabwe	Demoina weed	Adkins et al. (2018)

indirect yield losses when its pollen grains fall onto the floral structures of various crops (Kanchan and Chandra 1980), which then causes poor seed set of the crop.

Apart from crop production losses, livestock production is the second major agricultural system affected by *P. hysterophorus*. Competition with fodder crops directly impacts the quality and yield of fodder, which in turn jeopardizes livestock health, milk and meat production, and meat quality. For example, in Australia, livestock that consume *P. hysterophorus* have been reported to produce a bitter-tasting milk, and the meat from sheep (*Ovis aries* Linn.) is said to emit a strong odor that spoils the taste and market value of the meat (Tudor et al. 1982). Additionally, the invasion of *P. hysterophorus* into a given habitat is known to alter grazing community composition and diversity by reducing the richness and abundance of species, both in the above- and belowground communities (Belgeri et al. 2014; Boja et al. 2022; Khatri-Chettri et al. 2022; Mutua et al. 2022; Paneru et al. 2023). *Parthenium hysterophorus* invasion also affects the physical and chemical properties of soil, such as its texture, pH, organic matter, nitrogen (N), phosphorus (P), and potassium (K) content (Karki 2008; Osunkoya et al. 2017; Timsina et al. 2011), as well as soil invertebrates (Jeyalakshmi et al. 2011), faunal diversity (McClay et al. 1995), and water systems (Ashraf et al. 2010; Patel et al. 2008).

Parthenium hysterophorus is also a serious threat to public health due to its ability to cause allergies and dermatitis as well as internal respiratory diseases like allergic asthma, bronchitis, and rhinitis (hay fever). Contact dermatitis is a common allergy caused by personal contact with *P. hysterophorus* (Allan et al. 2019; Muddebihal et al. 2023), and 40% of cases of plant dermatitis in

India are related to *P. hysterophorus* (Agarwal et al. 2021). Various allergies due to the pollen of *P. hysterophorus* have been recorded in almost all countries where the plant has been introduced (Goldsworthy 2005; Gupta and Chanda 1991; Lonkar et al. 1974; Nadeem et al. 2005).

The socioeconomic losses caused by *P. hysterophorus* infestations are significant in some parts of the world. In India, Kumar and Varshney (2010) reported *P. hysterophorus* infestation of over 35 million ha of land and predicted that the cost of manual and chemical control would be around US\$36.2 million yr⁻¹. Additionally, the predicted costs for the treatment of *P. hysterophorus*-induced health problems were estimated to be US\$1.06 million yr⁻¹ (Kumar and Varshney 2010). In Pakistan, the combined cost of the negative impacts of *P. hysterophorus* on crops, fodder, and animal and human health for a single rural household was estimated to be ca. US\$3,244 yr⁻¹ (Bajwa et al. 2019a). In Australia in the 1970s, the infestation of *P. hysterophorus* had reached ca. 600,000 km² of rangelands and was predicted to be causing beef production losses of US\$11.03 million (Chippendale and Panetta 1994). Adamson (1996) estimated that if the rate of *P. hysterophorus* spread continues in Australia until the year 2050, the economic losses would reach US \$72.2 million yr⁻¹. This is one of the reasons that *P. hysterophorus* has been designated as a Weed of National Significance in Australia along with only 31 other invasive plant species.

Parthenium hysterophorus spread and impacts are predicted to be further aggravated by climate change, as its growth and reproduction traits are known to tolerate increasing temperature and drought conditions and to respond positively elevated

atmospheric carbon dioxide (CO₂) levels (Bajwa et al., 2019e; Belgeri 2013; Navie 2002; Nguyen et al. 2017a). Because many grain crops are grown on marginal, less-fertile, and nonirrigated lands, the ability of *P. hysterophorus* to grow under water-stress conditions is a threat to dryland crop production. Under current and future climate scenarios with a temperature increase of +3 C, *P. hysterophorus* is likely to significantly expand into much larger areas that are under irrigation (Shabbir et al. 2023).

Parthenium hysterophorus is known to cause significant negative impacts on the biodiversity of natural areas, such as natural reserves, national parks, forests, and other protected areas (Witt and Belgeri 2019). Once it has invaded an area, *P. hysterophorus* reduces the native plant diversity and abundance and alters the soil nutrient dynamics (Osunkoya et al. 2017; Shabbir and Bajwa 2006; Etana et al., 2011; Timsina et al. 2011). For instance, in Ethiopia, *P. hysterophorus* was reported to change the species composition and had significantly reduced the grass species diversity in a grassland (Nigatu et al. 2010). Another study in southeastern Ethiopia reported lower biomass and diversity of grasses across *P. hysterophorus*-invaded sites. The species diversity and evenness in aboveground vegetation were significantly lower in *P. hysterophorus*-invaded sites compared with uninvaded sites (Ayele et al. 2013).

Despite negative impacts of *P. hysterophorus*, it also has beneficial uses (Chandrasena and Rao 2019), including use in traditional medicine for alleviating skin inflammation, rheumatic pain, diarrhea, urinary tract infections, dysentery, and malaria (Patel 2011); as a bioherbicide (Saha et al. 2018); in making compost (Devi and Khwairakpam 2021); in phytoremediation to clean contaminated soil; in biogas production due to its high biomass content; and as a natural dye for fabrics (Saini et al. 2014).

Description

Parthenium hysterophorus is a rapidly growing annual or short-lived perennial herb that often grows in dense stands at an average height of 1.5 m, or up to 2.0 m in field conditions under adequate soil moisture conditions (Adkins and Shabbir 2014; Haseler 1976; Navie et al. 1996). It is a dicotyledonous plant and produces cotyledons measuring 3 by 6 mm in size that are hairless and exhibit a short petiole (Figure 1A). Following the cotyledonary stage, the first true leaves appear pale green in color and often form a basal rosette of leaves that measure ca. 15 cm in length and 2 to 4 cm in width. The leaves are alternately arranged onto the main stem and are deeply lobed with petioles of up to 2 cm in length. *Parthenium hysterophorus* forms a rosette growth habit under specific environmental conditions such as when the plant is under environmental stress or heavy competition. Upon stem elongation, leaves that are smaller and narrower are produced in the upper branches, while relatively larger leaves, measuring about 20-cm long and 4- to 8-cm wide are produced in the lower branches. Leaves are covered with small, stiff hairs called trichomes, which appear more frequently on the lower surface than on the upper surface, and trichomes also cover the stem. Stems are longitudinally grooved, and succulent in the early growth stages but become hard and inflexible as the plant matures. The plant produces a deep taproot with many small root hairs that help with nutrient and water extraction from greater depths within the soil profile (Navie et al. 1996). The plant can withstand mild winter frosts, normally while in the rosette stage, and can regrow following moderate chilling injury, but cannot survive severe frost (Shabbir 2012). The

chromosome number of *P. hysterophorus* is $2n = 34$ (Adkins et al. 2019).

Flowering begins as early as 28 d after seedling emergence (Jayachandra 1971; Figure 1). The flower structure is arranged into flower heads, or capitula, which are produced in numerous clusters on the terminal panicles. Each capitulum is creamy-white in color, measures about 4 mm across, and consists of five ray florets or occasionally six to eight ray florets, to which two sterile disk florets and a bract or phyllary are attached to form a complex cypsela (Rollins 1950). Inside each cypsela is a single black achene (hereafter referred to as a seed), which is obovate, 2.0- to 2.5-mm long, light in weight, and crowned by persistent corolla appendages and a style, measuring about 2- to 3-mm long by 1- to 2-mm wide, without a pappus (EPPO 2014). The cypsela is light brown in the early stages of development but turns dark brown when mature (Figure 1).

Geographic Distribution

Parthenium hysterophorus is known to be present in at least 70 countries. The native range of this plant includes 30 countries from the United States to Mexico and throughout Central America and South America (Rollins 1950). The non-native global distribution, or introduced range of *P. hysterophorus*, spans 40 or more countries and islands that are part of Africa, Asia, Oceania, and Europe (Adkins et al. 2019; Bajwa et al. 2016; Mao et al. 2021b). The Global Biodiversity Information Facility (GBIF 2024) lists 26,297 occurrences. This includes a non-native distribution in Australia (3,696 occurrences), India (2,120 occurrences), Taiwan (1,351 occurrences), and Ethiopia (1,196 occurrences), and these rival the lists for its native range, which includes the southern region of the United States (3,988 occurrences), Mexico (4,529 occurrences), Central America (213 occurrences), and South America (2,468 occurrences) (Figure 2).

United States

Established populations of *P. hysterophorus* occur mainly south of 35°N and include the states of California, Oklahoma, Kansas, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Texas, and Florida (Dale 1981; GBIF 2024; Rollins 1950). Populations are most common in Texas, Oklahoma, Florida, Louisiana, and Mississippi (Boyd and Reuss 2022; Dale 1981; Fernandez et al. 2015; GBIF 2024; Reddy et al. 2007) and have an allelopathic chemical composition, particularly sesquiterpene lactone (secondary metabolite), similar to those of populations found in Mexico and Central America, which suggests the plant's native range encompasses the southern United States (Picman and Towers 1982; Rollins 1950). Increased occurrences have been observed since the early 2000s in Alabama and Georgia, since the mid-2010s in California, and most recently in South Carolina in 2021 and 2022 (GBIF 2024; Reddy et al. 2007).

Parthenium hysterophorus was introduced into Hawaii in the 1960s, most likely from the continental United States and has since been naturalized on the islands of Hawai'i, Kaua'i, Maui, Molokai, and O'ahu (PIER 2023; Wagner et al. 1990). It has been reported northward of 35°N in the continental United States in New Mexico in 1904, Missouri in 1948, Illinois in 2007, Ohio in 1890, Michigan in 1917, Connecticut in 1908, Delaware in 2011, New York in 1921, and New Jersey in 1931 (GBIF 2024; Rollins 1950; USDA-NRCS 2023; Wiegand and Eames 1925). There are no records beyond the initial observation of *P. hysterophorus* in any of these locations in



Figure 1. Growth stages of *Parthenium hysterophorus*: (A) cotyledon stage; (B) early seedling stage; (C) rosette stage; (D) flowering stage; (E) a close-up of a flower head; (F) cypselae, each containing a single achene; and (G) achenes (seed).

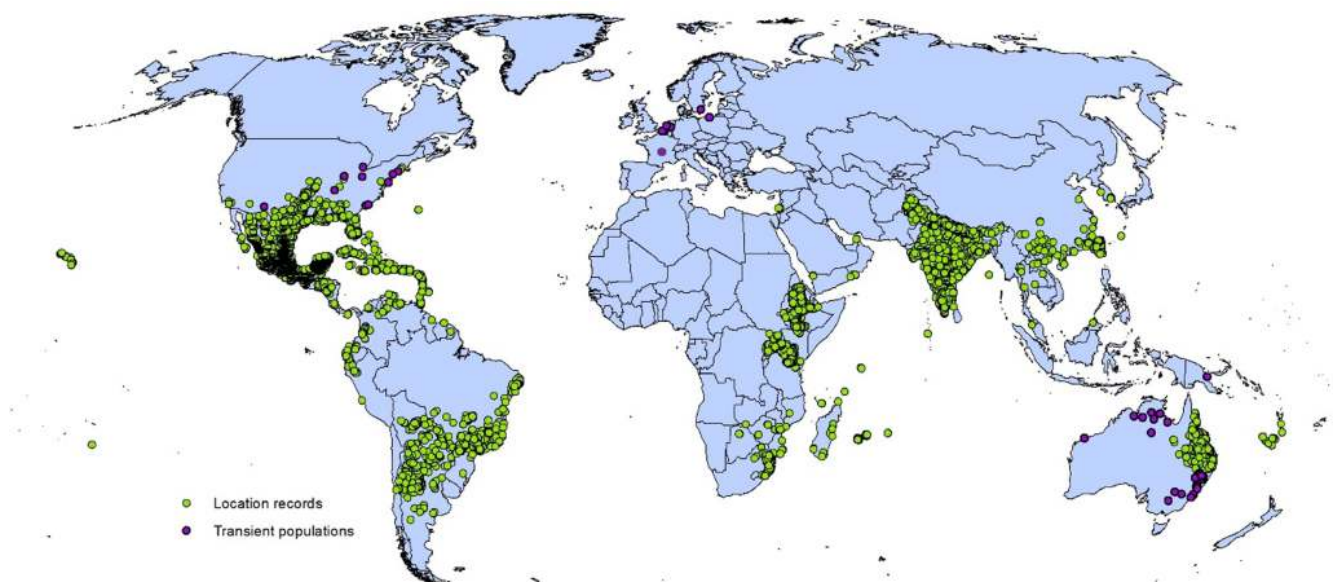


Figure 2. The occurrences of *Parthenium hysterophorus* around the world showing established (green dots) and transient populations (orange dots). Sources: GBIF (2024), REMIB database (2024), and survey data.

the United States, and they therefore should be considered transient.

Mexico

The majority of the *P. hysterophorus* populations in Mexico are to be found in lower-elevation areas of the Tamaulipas and Yucatán provinces that border the Gulf of Mexico and the Tamaulipas and Sierra Madre Oriental provinces in the northeast (Adkins et al. 2019). *Parthenium hysterophorus* has a limited naturalized presence in the temperate parts of central Mexico but has become more concentrated in recent decades around the Federal District of Mexico and the surrounding Guanajuato, Morelos, and Querétaro provinces, as well as the Sonora and Chihuahua provinces in the northwest provinces (Adkins et al. 2019; GBIF 2024). Mexico and the region around the Gulf of Mexico are central to the distribution of the genus *Parthenium* and contain the highest diversity of its natural enemies (Bennett and McClay 1979; McClay et al. 1995; McFadyen 1979).

Central America

Populations of *P. hysterophorus* occur throughout Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama (GBIF 2024). Several populations from these countries have been shown to have a composition of sesquiterpene lactone, an allelopathic chemical, similar to populations in Mexico and United States, suggesting the plant's native range encompasses the region (Picman and Towers 1982; Rollins 1950).

South America

Parthenium hysterophorus is recorded from virtually all countries in South America, but most occurrences are concentrated in two disjunct ranges: one throughout Paraguay, northern Argentina, southern Brazil, and southern Bolivia, and the second spanning the northern range of Venezuela, Columbia, Ecuador, and Peru (Adkins et al. 2019; Dale 1981). Differences in the composition of sesquiterpene lactone, an allelopathic chemical, have been identified, with most plants in the South American range containing hymenin and having cream or yellow flowers (Picman and Towers 1982), while parthenin is the dominant sesquiterpene lactone for the white-flowering biotypes in Central America, Mexico, the Bahamas, and the southern United States (Dale 1981). Interestingly, the yellow-flowering biotype of *P. hysterophorus* is only found in southern Brazil, Bolivia, and northern Argentina (Adkins et al. 2018; Dale 1981). The white-flowering form is also found in Brazil and is hypothesized to be a more recent introduction to the area (Adkins et al. 2018). The high diversity seen in populations in this region of South America is likely due to polyploidy or hybridization with the closely related species *P. bipinnatifidum* (Ortega) Rollins and *P. confertum* A. Gray (Picman and Towers 1982; Rollins 1950).

In Uruguay, the distribution of *P. hysterophorus* is irregular, and it has not established widely based on survey data collected in 2010 (Belgeri 2011) and from herbarium records made in the 1930s and 1960s (GBIF 2024). Three unverified records of *P. hysterophorus* have been made from near Saul, French Guiana, in 2021, with one further account represented by a herbarium record from 1883 (GBIF 2024). Like the records in French Guiana, the occurrence of *P. hysterophorus* in Guyana and Suriname should be considered transient based on the limited number and age of the

herbarium records made in Guyana (1883) and Suriname (the mid- to late 1800s, 1936, and 1997) (GBIF 2024).

Bermuda to the Caribbean

Parthenium hysterophorus is widespread in all Commonwealth Caribbean countries and dependent territories, from the Bahamas to other countries in the region that include Cuba, Haiti, Antigua and Barbuda, Trinidad and Tobago, and the Federation of Saint Christopher and Nevis (Hammerton 1981; Rollins 1950). The plant is predominantly found along roadsides, forests, and agricultural areas, with large and persistent infestations near the towns of San Juan, Puerto Rico, and Santo Domingo, Dominican Republic, and across the north coast of Jamaica (GBIF 2024; Wunderlin et al. 2024). A recent survey indicated *P. hysterophorus* has spread to Dominica and Saint Kitts as recently as 2018, with observations in urban areas within both countries (A Witt, personal communication, 2023). Whether the West Indies are within the native range is difficult to determine, but *P. hysterophorus* is argued to have been introduced to this region from Mexico (Navie et al. 1996) due to there being no other species of the genus *Parthenium* there or the insects that exclusively target the weed (Adkins et al. 2018).

South Asia

The main *P. hysterophorus* infestation was introduced into India from a U.S.-based food grain shipment delivered in 1955 (Shabbir et al. 2019c). This infestation spread aggressively across India and then to Pakistan, Nepal, Bangladesh, Bhutan, and Sri Lanka, in multiple introductions, as indicated by genetic and ecological studies (Bambaradeniya 2002; Jabeen et al. 2015; Shabbir and Bajwa 2006; Shrestha et al. 2015; Tomasello et al. 2019). *Parthenium hysterophorus* is estimated to have invaded 35 million ha in India (Kohli et al. 2006; Sushilkumar 2012) and 1.3 million ha of vegetable production in a northern province of Sri Lanka (Kirshanthan et al. 2016; Kishojini et al. 2018). The most severe infestations in Pakistan occur in the northeastern parts of the Punjab Province (Dhileepan and Senaratne 2009; Shabbir 2013; Shabbir and Bajwa 2007), but a southward range expansion is becoming more prevalent in agricultural land, especially in irrigated cropping systems (Shabbir et al. 2012, 2019c).

East and Southeast Asia

In southern and southeast China, *P. hysterophorus* is found in 9 of the 12 provinces and districts situated between 18°N to 25°N (Li and Gao 2012; Tang et al. 2009), with Chongqing being the most recent introduction (Chen et al. 2016; Mao 2018). In Zhejiang Province, a population was found in Ningbo, ca. 166 km northeast of the Wenzhou population (Mao 2018; Wei et al. 2021). In northern China, a population found in 2004 in Junan County of the Shandong Province (Wang and Hou 2004) rapidly expanded to more than 400,000 ha by 2010 (Li and Gao 2012). This northern population in Shandong Province was shown to be a unique chloroplast haplotype, different from the southern population and considered to be a separate introduction into China (Tang et al. 2009). Apart from mainland China, populations of *P. hysterophorus* are also known in the island of Taiwan (Peng et al. 1988), Vietnam (Nguyen 2011), Japan (Tachikake and Nakamura 2007; Tominaga 2013), South Korea (Kim 2013), Malaysia (Maszura et al. 2018; Shi et al. 2019; Sukumaran 2015), and Christmas Island (Dodd et al. 2012). In 2016, *P. hysterophorus* was reported in

Lampoon Province, northern Thailand, within an agricultural area (Shabbir 2017), and has since been reported in Chiangmai Province in northern Thailand, Nakhon Phanom and Nakhon Ratchasima provinces in the northeast, and in central Thailand near Kanchanaburi (S Zungsontiporn, personal communication, 2024).

Africa

In Southern Africa, *P. hysterophorus* is found in the countries of South Africa, Eswatini (formerly Swaziland), Mozambique, Zimbabwe, Botswana, and the western Indian Ocean islands such as Madagascar, Mauritius, Réunion, and the Seychelles (McConnachie et al. 2011; Nath 1988; Strathie and McConnachie 2019). *Parthenium hysterophorus* thrives in the subtropical climate of South Africa and occupies about 4.4 million ha, with the most severe infestations in the KwaZulu-Natal Province (McConnachie et al. 2011; Terblanche 2015). Populations have also been reported from Egypt in North Africa and the East African Countries of Ethiopia, Eritrea, Djibouti, Kenya, Rwanda, Somalia, Tanzania, and Uganda (Strathie and McConnachie 2019; Witt et al. 2017). There is a widespread occurrence in Uganda from the eastern and southern to southwestern regions and in Ethiopia throughout in the south, central, and northern regions (Adem 2010; McConnachie et al. 2011; Million et al. 2021). The immediate origins of most of the *P. hysterophorus* populations in central and southern Africa are from the United States, but secondary transfer to South Africa has occurred from Mozambique (Picman and Towers 1982; Towers and Mitchell 1983; Wise et al. 2007) and from there into Botswana (Strathie and McConnachie 2019).

Eastern Mediterranean and Persian Gulf

Parthenium hysterophorus has a limited naturalized presence in the Arabian Peninsula, with populations found mainly along roadsides and on wastelands in Yemen (Kilian et al. 2002) and the United Arab Emirates (Mahmoud et al. 2015) and, most recently, in agricultural areas and fallow fields in Oman (Shammas 2022) and Saudi Arabia (Thomas et al. 2015). *Parthenium hysterophorus* is thought to have been introduced into the Arabian Peninsula from populations in eastern Africa or South Asia (McConnachie and Witt 2019) and from Yemen into Saudi Arabia, as populations are close to the border (A Witt, personal communication, 2023). In Israel, the first establishment of *P. hysterophorus* was found near the banks of several fishponds. It is thought that *P. hysterophorus* was introduced into Israel through contaminated low-grade grain that was subsequently used to make fish meal (Dafni and Heller 1990). Since then, the weed has rapidly expanded into agricultural areas in the Beit Shean Valley, Jezreel Valley, and Jordan Valley (Matzrafi et al. 2021).

Oceania

Parthenium hysterophorus is widely naturalized in Queensland, Australia; occasional populations found in Western Australia, Northern Territory, and New South Wales (AVH 2023; Blackmore and Johnson 2010; GBIF 2024; Navie et al. 1996) are immediately targeted for eradication. The weed was introduced into Queensland on two occasions, to Toogoolawah in the 1940s and into Clermont in the 1950s. The origin of both populations (biotypes) was the United States, as confirmed by genotypic studies (Graham and Lang 1988; Hanif 2014) and characterized by plants containing parthenin as the major sesquiterpene lactone (Picman and Towers

1982; Rodriguez et al. 1971). In Queensland, it was estimated that *P. hysterophorus* occupied 2.9 million ha by 1980, 17 million ha of rangelands by 1991, and 52 million ha by 2003, then effective control measures reduced the area of infestation to 36.9 million ha by 2013 (Chippendale and Panetta 1994; McFadyen et al. 2019). Vanuatu eradicated the first introduction of *P. hysterophorus* in 1971, but a new population has been reported in 2009 and has expanded into several islands, with the most severe infestations occurring on the Efate and Tanna islands (Day and Bule 2016; McFadyen et al. 2019). A recent population in Port Vila shares morphological characteristics with populations from both Vietnam and China (Mao et al. 2021b). *Parthenium hysterophorus* was introduced in 2001 in Papua New Guinea, near the city of Lea, but seems to be one of the few successful eradication efforts, with no plants found during annual surveys since 2006 (Kawi and Orapa 2010; McFadyen et al. 2019). Populations are also known in New Caledonia and Tahiti (Florence et al. 2007; Gargominy et al. 1996).

Europe

Parthenium hysterophorus was found in Poland in 1938 and 2022 (GBIF 2024; Mirek et al. 2002), Belgium in 1999, 2003, 2013, 2017, and 2023 (GBIF 2024; Verloove 2006), Sweden in 1937 and 1967 (GBIF 2024), and the Netherlands in 1938 and 2014 (GBIF 2024), but this species has not persisted or established in these countries.

Habitat

According to a global Köppen-Geiger climate zone map, *P. hysterophorus* occurs across 16 global climate subtypes within a wide range of tropical (Group A), arid (Group B), temperate (Group C), and continental (Group D) climate groups. In the northern portion of the native distribution of *P. hysterophorus*, from the southern United States to Mexico, populations are predominately in temperate areas of humid subtropical (Cfa) and lowland (Cwa) climates, with additional occurrences in tropical savanna (Aw) regions along the Mexican Gulf Coast and the Yucatan Peninsula (Structured Appendix, Figure A1). Most populations in Mexico are found at elevations <1,500 m asl within regions with mean annual temperatures above 4 C or mean annual precipitation exceeding 600 mm (Adkins et al. 2019). Its northern native range is considered to extend into the arid regions of the southwestern United States to the Sonora and Chihuahua states of Mexico, where the BSh (steppe, hot) and BSk (steppe, cold) are dominant, with a few occurrences in hot (BWh) and cold (BWk) desert areas likely due to a long, dry winter season (Adkins et al. 2019). In Central America (native range) and Bermuda to the Caribbean (likely introduced range), *P. hysterophorus* occurs mainly in tropical climate subtypes Am, As, Aw (monsoon and savannah with dry summer or winter, respectively), apart from Honduras in the temperate climate subtype Cwa. In South America, the temperate areas of humid subtropical (Cfa) and lowland (Cwa) climates are dominant, followed by tropical savanna (Aw) regions, to some tropical rainforest (Af) regions in the north and warm-summer Mediterranean (Csb) regions in the southwest, and less commonly, in equatorial savanna (As) and steppe (BSh) climate subtypes in the east. Its distribution extends south of the 34th parallel in Argentina to the cold, steppe (BSk) regions, where it is commonly found around 1,500 m above sea level (asl) and as high as 3,580 m asl (Dale 1981; GBIF 2024).

Globally, *P. hysterothorus* predominately occurs in one of five diverse climate types. It is most commonly present in areas of the world with a subtropical savanna biome with distinct wet and dry seasons (Aw; East Africa, central India, northern Australia) or humid subtropical climates (Cfa; central and southeastern China, Japan, eastern Australia). It thrives in these habitats with regular and abundant summer rains (Aw, Cfa), such as the major agricultural regions in Australia (McFadyen et al. 2019), east Africa (McConnachie and Witt 2019), and in limited areas of China that receive at least 500 mm of annual rainfall (Shi et al. 2019; Structured Appendix, Table A1). The tropical savanna (Aw) and humid subtropical climates (Cfa) with average monthly temperatures exceeding 18 °C in the tropical savanna (Aw) and humid subtropical climates (Cfa) promote optimal germination rates within temperature ranges of 15 to 25 °C and 22 to 25 °C for biotypes in Israel (Matzrafi et al. 2021) and Australia (Navie et al. 1996), respectively, with flowering occurring more rapidly at warm temperatures (27/22 °C; day/night) as compared with cooler temperature regimes (Adkins et al. 2019). The desert subtropical climate (Cwa) is the next most common climate type where *P. hysterothorus* is found, from south-central Africa to the majority of south Asia and eastern Australia.

Parthenium hysterothorus has a lesser, but significant presence in climate types such as the hot semiarid (Sh) regions of central and southern Africa, India, and parts of Australia (Structured Appendix, Figure A1). The hot (BSH) and cold (BSK) semiarid climates with dry winters or prolonged drought may limit the range expansion of *P. hysterothorus* (Doley 1977; Royimani et al. 2019). Based on global populations that can germinate over a wide range of temperatures from 9 to 36 °C in Australia (Navie et al. 1996), 10 to 30 °C in Israel (Malka et al. 2023), and 12 to 35 °C in Ethiopia (Tamado et al. 2002), seeds of *P. hysterothorus* are likely adapted to both the hot (BSH) and cold (BSK) semiarid climates. Populations are limited, but still often found, in areas of the world having a Mediterranean climate with cool, dry summers (Csb; parts of Kenya and Ethiopia) or hot, dry summers (Csa; Israel), and mainland coastal areas with hot, dry summers (Cfb; coastal South Africa and southeastern Australia). *Parthenium hysterothorus* tolerates subtropical highland climates (Cwb) but is likely restricted by dry winters in these regions of Mexico, South America, South Asia, and Africa. Nonetheless, this species is invading the high-altitude grasslands of Cwb climates in Bhutan, where it is mostly limited up to 1,700 m asl but reported as high as 2,320 m asl (Tshering and Adkins 2012), from 1,500 to 2,400 m asl in the northwestern Indian Himalayas (Dogra et al. 2011; Kohli et al. 2004), up to 1,935 m asl in the northern highlands of Nepal, and up to 2,500 m asl in Lalibela, Ethiopia (Shrestha et al. 2015; Tamado and Milberg 2000). Known occurrences of *P. hysterothorus* are confirmed to tropical rainforest (Af) and monsoon (Am) climate types in parts of Madagascar and southern Thailand and solely tropical rainforest (Af) climates in parts of Hawaii, central Africa, Sri Lanka, and Papua New Guinea. Isolated populations in continental hot (Dsb) and warm (Dwa) summer climates are known to occur in northeastern Pakistan and South Korea, respectively.

Parthenium hysterothorus grows best on black, alkaline, cracking clay soils with high fertility (Adkins and Shabbir 2014). It is typically found in a wide range of soils textures, from sandy loams to clay loams and, in its native range, specifically, on eutric vertisols (base-rich cracking clays) or calcic leptosols (shallow, rocky, or gravelly soils) (Adkins et al. 2018; Adkins and Shabbir 2014; Dale 1981). *Parthenium hysterothorus* can tolerate a wide

range of soil types with various nutrient contents but is known to invade and thrive in nitrogen- and phosphorus-rich environments in its native range of Mexico and South America (Dale 1981) and globally in areas such as Nepal (Timsina et al. 2011), China (Shi et al. 2019), and Tanzania (Ojija and Manyanza 2021). Soil disturbance in fallow areas promotes its range expansion within its native range, regardless of soil type (Dale 1981). A single soil disturbance in an Australian cropping system promoted the germination and persistence of a *P. hysterothorus* stand for a 4- to 6-yr period (White 1994), and similarly, in Mexico, dense infestations have been observed to persist for ≥1 yr in frequently disturbed sites (Adkins et al. 2018).

Soil disturbance, anthropogenic activity, and waterways are important influences on seed distribution and establishment of this species. *Parthenium hysterothorus* inhabits waste areas and fallow lands to urban areas, roadsides and railway tracks, and field edges and agricultural land; it occurs along rivers and waterways and, less commonly, in open forest and shrub areas (Figure 3). In most invaded countries, *P. hysterothorus* spreads rapidly from small, isolated patches on roadsides, then into wastelands or fallow areas, and then into agricultural areas (Shi et al. 2019). The trans-border and long-distance movement of vehicles promotes seed dispersal of *P. hysterothorus* seed along road networks in southern Africa (Strathie and McConnachie 2019); East and North Africa (McConnachie and Witt 2019; Mutua et al. 2022; Ojija and Manyanza 2021); and in the Persian Gulf, including Oman, Yemen, and the United Arab Emirates (Mahmoud et al. 2015). Road maintenance practices of grading gravel-surfaced road networks and grass cutting along roadsides in a survey in southern Africa were found to have exacerbated the spread of *P. hysterothorus* seed along roadsides (Strathie and McConnachie 2019). A survey in Mexico attributed *P. hysterothorus* populations along roadways to increased moisture availability provided by water runoff from the road surface (Dale 1981). For example, in the savanna climate of Kenya, *P. hysterothorus* was initially limited since its introduction in the early 1970s (McConnachie and Witt 2019), but a 2022 survey in Nakuru County reported high densities alongside Kenyan roads following construction (Mutua et al. 2022). Unlike many plants, *P. hysterothorus* has strong mechanisms to tolerate environmental pollution in roadside communities (Adkins et al. 2019). Similarly, in wasteland areas, *P. hysterothorus* utilizes high bioaccumulation and translocation rates to tolerate soils contaminated with heavy metals of nickel, lead, copper, cobalt, chromium, and zinc (Hadi and Bano 2009; Irshad et al. 2015).

Waterways and irrigation channels are known to promote the transport of *P. hysterothorus* seeds; such movement has been reported from Pakistan, with seed being moved along the irrigation canal networks in the Punjab Province and the Indus River basin in south Pakistan (Anwar et al. 2012; Shabbir et al. 2012), from the Mahaweli River body in Ethiopia by irrigation networks (Horo et al. 2020), and in many parts of India along waterways (Adnan et al. 2015). *Parthenium hysterothorus* is frequently found along riverbanks and the edges of water channels in the otherwise inhospitable and seasonally dry (BWh/BSH) regions across the globe, such as central Pakistan (Shabbir et al. 2012), and parts of Australia (Auld et al. 1982; McFadyen et al. 2019), Saudi Arabia (Thomas et al. 2015), Kenya (Njoroge 1986), Ethiopia (Horo et al. 2020; Seta et al. 2013), and the Shandong and Guangxi provinces in China (Huang et al. 2012; Mao 2018; Tang 2012). For example, the invasion of *P. hysterothorus* in southern Pakistan is supported by moisture made available from irrigation canals and groundwater

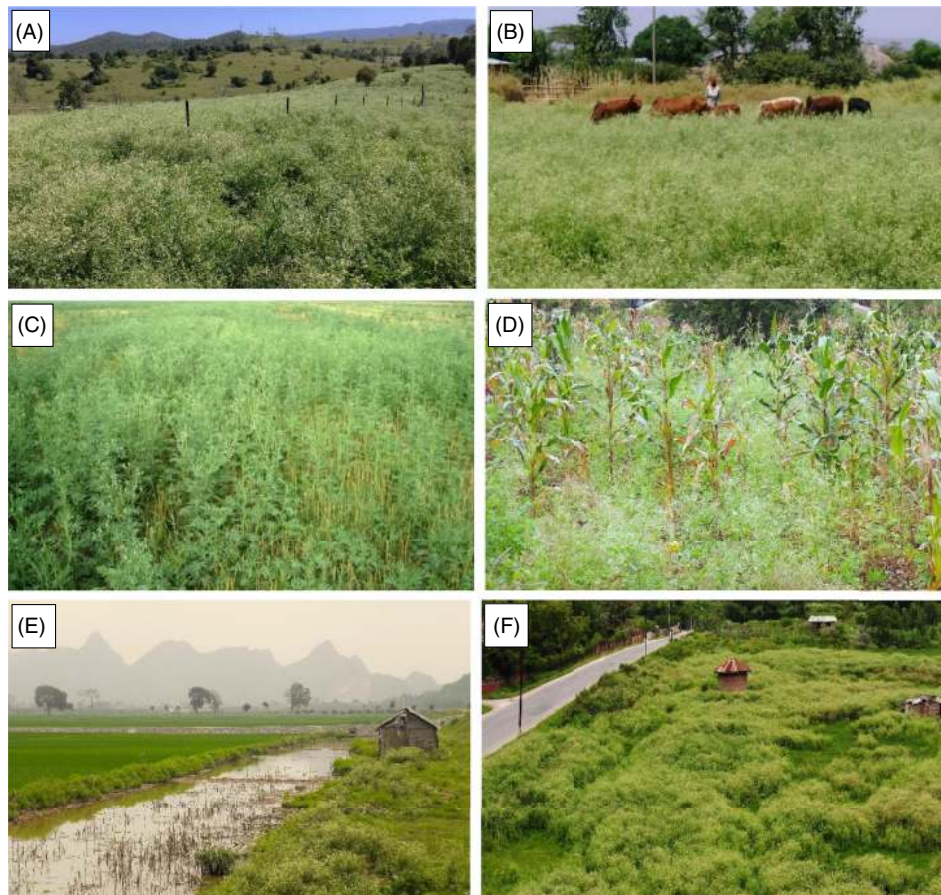


Figure 3. *Parthenium hysterophorus* infestations in pasturelands in Queensland, Australia (A) and Ethiopia (B), wheat fallow in Lahore, Pakistan (C), and maize crop in Arusha, Tanzania (D), along a water channel in Vietnam (E), and on campus of Tribhuvan in Nepal (F).

pumping when the climate conditions of hot summers and 250 mm of annual rainfall would otherwise be limiting (Shabbir et al. 2023).

A comparison of the global distribution map of *P. hysterophorus* and the United Nations land-use assessment map (FAO 2013) shows its distribution is predominately associated with croplands and grasslands or sparse areas in both unmanaged systems and with livestock stocking rates from low to high densities. Shrub cover areas and forests having either agricultural activities or various stocking rates in areas in the southern United States, Mexico, southern and central Africa, and Australia are also correlated with known occurrences but likely limited to open shrub and forest areas with adequate light intensities that support the growth of *P. hysterophorus* (FAO 2013; Navie et al. 1996). *Parthenium hysterophorus* being found in low-rainfall climates that overlap with low- and high-intensity irrigation areas indicates increased water availability is promoting range expansion and that nearby non-invaded irrigated areas should be monitored.

Invasion History

The history of invasion, as far as is known, began with an accidental introduction to the island of Mauritius in the 18th century (Fusée-Aublet 1775). This and other early introductions were sporadic in nature but were usually associated with maritime trading (Binggeli 2003). Thus, the global distribution of *P. hysterophorus* initially

comprised island populations or locations close to large ports, including those of Kolkata, India (1810), Reunion in the Mascarenes (1878), Natal in South Africa (1880), the islands of New Caledonia (1881), the Seychelles (1908), and French Polynesia (1909) (Mao et al. 2021b). The pace of invasion never flagged and has increased dramatically in recent years. By the 1940s, *P. hysterophorus* was established in only about a dozen countries outside its native range, but since the 1950s, the speed of invasion has accelerated considerably (Mao et al. 2021b). A second and major introduction was made to India in 1955, which then spread over the entire country by the 1970s (Batish et al. 2012), and into most neighboring countries by the early 2000s (Chhogyel et al. 2021; Jayasuriya 2021; Shabbir et al. 2012; Sushilkumar 2014). Similarly, a second major introduction in 1958 established the weed in Queensland, Australia. During the next 20 yr, only local spread occurred, followed by dramatic spread in the late 1970s, with invasions covering almost one-third of the state by 2000 (McFadyen et al. 2019), and repetitive incursions in New South Wales and other bordering states and territories (Blackmore and Johnson 2010). The fastest spread in recent years has occurred in Asia and Africa, with new invasions taking place at a rate of ca. 10 countries per decade, a threefold rate of new introductions as compared with the 1950s (Mao et al. 2021b). Several countries of the Middle East (e.g., United Arab Emirates, Saudi Arabia) have recently been invaded by *P. hysterophorus* (McConnachie and Witt 2019; Shabbir et al. 2019c). Its spread is also increasing within already invaded countries, such as Oman (Shammas 2022).



Figure 4. Road signs are erected in Queensland, Australia to assist in the prevention of further seed spread of *Parthenium hysterophorus*.

Many attempts have been made to eradicate *P. hysterophorus* after invasion has occurred; however, this has proven to be extremely difficult. So far, eradication has only been successful in countries and regions where early detection of small populations was made. Eradication of such populations has been achieved in Papua New Guinea (Kawi and Orapa 2010), the state of New South Wales, Australia (Blackmore and Johnson 2010), and on Espiritu Santo Island, Vanuatu (McFadyen et al. 2019). In locations where the weed has become well established, containment, rather than eradication, is applied (Khan et al. 2018; McFadyen et al. 2019; Shabbir et al. 2019d; Figure 4). When used together with chemical and biological control and applied at the invasion front, containment can bring about local eradication, as has been achieved in regions of Australia (Blackmore and Johnson 2010; Thorp 2001) and South Africa (Terblanche et al. 2016). Sadly, eradication as well as containment of *P. hysterophorus* are still challenging to achieve on most occasions, especially in the countries of Asia and Africa, where the weed is spreading fast.

Life-Form and Life History

The life history of this annual forb commences from seed present in the soil seedbank on the soil surface (Figure 5). Fast germination, as well as rapid early seedling growth, enables this weed to enter the reproductive stage within 2 mo of germination under ideal conditions and then to live for up to 8 mo (Adkins et al. 2019) or, rarely, after regrowth in a subsequent season to more than 14 to 16 mo (Hassan 2011). When under stress, however, the weed can tolerate adverse effects by entering a rosette stage (Figure 5). Further rates of vegetative, then reproductive, growth vary under different environmental conditions (Kaur et al. 2017, 2019), thus phenotypic plasticity facilitates its survival under a wide range of conditions. Although plants do not survive in freezing temperatures, the soil seedbank serves as a reservoir for future generations, with seeds able to survive for more than a decade in the soil (Navie et al. 1998; Nguyen et al. 2017b; Osunkoya et al. 2014).



Figure 5. The life stages of *Parthenium hysterophorus*: seed containing cypselas, seedling, rosette, mature plant, and seed.

The weed gains precedence in the long term by having a flexible life history: fast germination, excessive vegetative growth, prolonged reproduction, and tolerance of unfavorable conditions. When conditions allow, interspecific competition against other plants (Vehra and Khan 2011) and crops (Bajwa et al. 2019b, 2019c) is significant, especially when environmental disturbances are present (Cowie et al. 2020a). With residues returned to the soil (Batish et al. 2005), the weed also displays a moderate allelopathic effect (Shi and Adkins 2018), improving its chances of survival against other plants in the community.

Dispersal and Establishment

In an unmanaged population, *P. hysterophorus* is spatially dispersed by means of natural elements, such as wind and water.

The structure of its cypsela, which contains a single mature achene, includes a winged assembly, consisting of two “air sacs” originating from two sterile florets, that assists its movement by wind or water (Auld et al. 1982; Nguyen 2011). The wind-assisted dispersal of the cypsela is thought to be only locally important (Auld et al. 1982; Mao et al. 2021b), although the distance traveled could be considerable in the event of a whirlwind or storm (Haseler 1976; McConnachie et al. 2011). Water dispersal, on the other hand, could be over much longer distances and times. After 7 d of simulated water movement, 20% of the treated seeds remained floating, while still able to germinate (Mao et al. 2019). These floating seeds provide an excellent opportunity for the weed to spread long distances downstream. Lawes and Grice (2008) found *P. hysterophorus* growing along the entire Burdekin River catchment in Queensland, Australia, especially on the lower levels of the riverbanks. In addition, the Darling River catchment in New South Wales, Australia, was infested by *P. hysterophorus* along the edges of the watercourses and an eradication effort is underway (Shabbir et al. 2019c). Thus, flooding in such areas could be suspected as the major opportunity for the dispersal of *P. hysterophorus* seeds.

Native animals, livestock, and feral animals are also believed to be involved in the dispersal of *P. hysterophorus* seeds over short distances (Parsons and Cuthbertson 1992). The spread of *P. hysterophorus* seeds by cattle from infested to un-infested land has been observed in southern Queensland and in dung in southeast Queensland (Khan 2012). The human spread of seeds is mainly by vehicles as well as by agriculture machinery (Blackmore and Johnson 2010). These pathways for seed spread can be over very long distances and are thought to be the most important pathways in most countries. Blackmore and Johnson (2010) reported that 73% of all the *P. hysterophorus* populations appearing in New South Wales arrived as seed carried on vehicles from Queensland. *Parthenium hysterophorus* seed can also be spread within fodder or within crop and feed seed lots (Gupta and Sharma 1977). All these various means of seed dispersal play a role in the overall spread of the weed within invaded countries, making management more difficult. Other mechanisms of spread of *P. hysterophorus* are also known, including when the weed is used as an ornamental plant in floral bouquets, when its vegetative and reproductive parts are used as packaging for small items in crates, and when it is used as a green manure (Chandrasena and Rao 2019).

When seed arrives in a new location by means of dispersal, plant establishment requires additional environmental support. Once germination takes place, growth and reproduction are commonly completed in 2 to 6 mo when temperature, water and light conditions are adequate (Bajwa et al. 2017; Navie et al. 1998; Pandey and Dubey 1989). However, not all seeds germinate while support is in place; dormancy can ensure multiple germination events can occur over time, thus creating overlapping generations, which are commonly seen in field populations (Navie et al. 1998). In tropical India, three cohorts of *P. hysterophorus* seedlings are observed in a single growing season (Pandey and Dubey 1989), and consecutive seedling cohorts were observed in the Middle Mountain region in Nepal (Shrestha et al. 2024), while in Australia, with lower annual rainfall, only two cohorts are generally found in one growing season (Mao 2020). In India, the highest survival rate of plants was found from the first cohort of the growing season, with mortality increasing in the later cohorts (Pandey and Dubey 1989). Such mortality could be due to a water shortage later in the season, as well as greater competition from within the population (Pandey and Dubey 1989). Successful sexual

reproduction is vital to sustain a field population under unfavorable conditions, although new populations can be reestablished from the arrival of just a few seeds via biotic and abiotic vectors (Mao et al. 2021b).

Temporally, the new frontier of the weed's invasion will be extended by seed dispersal. In a simulated spatial and temporal dispersal model (Mao 2020), a typical wind condition was predicted to disperse the population by 1.4 m yr⁻¹ when the plant height attained was 1 m and when 40 seeds wk⁻¹ were released during an 8-wk growing period. Under such an assumption, the population front may move by up to 14 m in a 20-yr period without other assistance (Mao 2020).

Invasion Risk

Predictive modeling can be used to assess *P. hysterophorus*'s potential global distribution, as well as the distribution of its biological control agents. Continental model predictions in Australia (Adkins et al. 1996; Thorp 2001), Asia (Ahmad et al. 2019; Dhileepan and Senaratne 2009; Dorji et al. 2022; Masum et al. 2022), Africa (Dorji et al. 2022; McConnachie et al. 2011; Terblanche et al. 2016), and Europe (Brunel et al. 2014; Kriticos et al. 2015) have already been used to estimate the potential distribution of *P. hysterophorus* based on climatic data from the environments where the weed has shown sustained growth (Figure 6). These mapping activities show *P. hysterophorus* is already present in some of the projected high-risk areas that are dominated by humid subtropical and savanna climates and warm temperate areas (Mao et al. 2021b; Structured Appendix, Figure A1).

Mapped areas, classified as medium- to low-risk in the current climate, are expected to be invaded over time based on the ability of *P. hysterophorus* to persist under wide temperature ranges and soil moisture conditions (Kriticos et al. 2015). Of great concern in Africa is the continued spread into sub-Saharan Africa, such as from southwest Kenya to northern Tanzania, where some farmers in neighboring subsistence and pastoral agricultural areas have already been forced to abandon land heavily infested by *P. hysterophorus* (Mainali et al. 2015; McConnachie et al. 2011). East Africa is at great risk for invasion, with climatically suitable areas spanning from Ethiopia to Mozambique, beyond which *P. hysterophorus* is already considered the most problematic weed in croplands and grazing areas (Tamado and Milberg 2000), but the dry season may be a limiting factor for germination for part of the year (Tamado et al. 2002).

Irrigation networks aiding seed distribution of *P. hysterophorus* and increasing soil moisture availability in cropping lands are expected to expand the invasion territory of *P. hysterophorus* into the large fertile areas of Australia, such as the Murray-Darling Basin, as well as throughout sub-Saharan Africa, and into southern Pakistan and other parts of the Middle East (Kriticos et al. 2015; Shabbir et al. 2019c, 2023).

A change in climate can alter the habitat suitability boundaries for *P. hysterophorus* distribution (Guan et al. 2020; Mushtaq et al. 2021). Using the maximum entropy (MaxEnt) modeling approach, Adhikari et al. (2023) suggested the current distribution of *P. hysterophorus* between 35°N and 35°S of the Equator would be retained in a future climate scenario, while its habitat suitability range would also extend as far as 65°N of the Equator. Currently uninhabited areas such as those in central China would face an increasing risk of invasion (Mainali et al. 2015; Wang et al. 2023). Land-use systems of crop production, livestock production, and

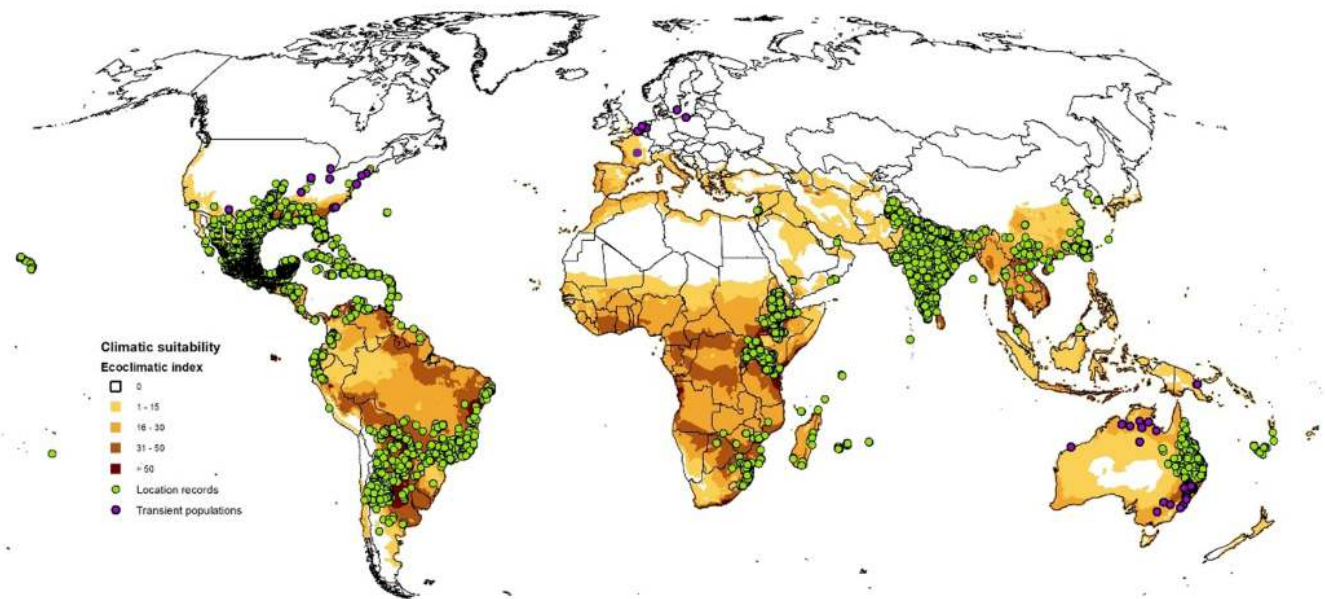


Figure 6. Global climatic suitability with occurrence records (green dots) of *Parthenium hysterophorus* using CLIMEX (Shabbir et al. 2023).

forestry were predicted by Kriticos et al. (2015) to have the greatest potential for colonization by *P. hysterophorus*. The northern range expansion of *P. hysterophorus* into the southern and central-western parts of Europe and most Mediterranean countries under a climate change scenario may occur due to an increased habitat suitability in riparian zones, agricultural landscapes, and actively managed forests of this region (Brunel et al. 2014; Kriticos et al. 2015). Within its native range in the United States, isolated weed populations in the semiarid West and Southwest are at risk of expanding along the West Coast and into parts of the Midwest, with these important agronomic systems commonly under irrigation being particularly at risk due to increased soil moisture availability (Kriticos et al. 2015; Shabbir et al. 2023). Conversely, *P. hysterophorus* is expected to spread to the arid and hot southern parts of Pakistan through irrigated areas where the excess moisture will allow the weed to tolerate the predicted climate change conditions (Shabbir et al. 2012). The effect of the irrigation network, allowing incursions of *P. hysterophorus* beyond its normal range, would be a threat to the cotton (*Gossypium hirsutum* L.) industry of Pakistan (Shabbir et al. 2012).

Many climatic models indicate a trend of a northerly shift of *P. hysterophorus* populations alongside a decrease in the area of habitat suitability due to temperature increases and more variable precipitation patterns in some regions of India (Ahmad et al. 2019), Bhutan (Chhogyel et al. 2021; Thiney et al. 2019), Sri Lanka (Kariyawasam et al. 2019), Oman (Al-Ruheili et al. 2022), and South Korea (Adhikari et al. 2023). Rising temperatures may drive the distribution limit into higher latitudes and altitudes in parts of the world (Ziska and McConnell 2016), as is predicted to occur in Asia (Dhileepan and Senaratne 2009; Masum et al. 2022). For example, population densities are projected to increase in Nepal and northeast India to the western Himalayas due to more suitable climatic conditions of cooler temperatures and moisture availability compared with the surrounding regions (Ahmad et al. 2019; Mainali et al. 2015; Shrestha et al. 2019). *Parthenium hysterophorus* may move ca. 240 km northward in China (Guan et al. 2020) and

may gain greater altitude in mountainous areas such as Nepal (Maharjan et al. 2019; Shabbir et al. 2019c) and Bhutan (Thiney et al. 2019), shifting ca. 753 upward to 2,931 m asl (Dorji et al. 2022). McConnachie et al. (2011) determined that among the indicators used for CLIMEX on climatic suitability, altitude acted poorly when modeling range limits of *P. hysterophorus*. The plant's range limits being minimally influenced by altitude agrees with survey data in Ethiopia by McConnachie et al. (2011), who reported most populations to occur between 1,500 to 2,000 m asl, with some infestations reaching up to 2,627 m asl. Such shifts to higher altitudes may also be accelerated by the elevation of atmospheric CO₂ concentration, as the weed becomes more competitive under such conditions (Cowie et al. 2020b; Mao et al. 2021a; Nguyen et al. 2017a; Rice et al. 2021).

Based on CLIMEX models, it appears that *P. hysterophorus* has the capacity to spread into the midwestern and coastal regions in the United States and further into the central region of South America (Kriticos et al. 2015; Figure 6), but there are no specific studies in its native range to understand the extent of natural competition and enemies keeping populations in check. Cold winter temperatures in the midwestern United States may limit the establishment of *P. hysterophorus* in this area. Large areas of southern, eastern, and western Australia are indicated by climate models to be suitable for *P. hysterophorus* (Mainali et al. 2015; McConnachie et al. 2011), but on-ground reports indicate *P. hysterophorus* growth and establishment are limited in environments with precipitation mostly occurring in the winter months followed by a hot and dry summer (McFayden et al. 2019). Although there are gaps in the known occurrences of *P. hysterophorus* in regions in Asia and Africa with climatic suitability, it is probable that known populations have established in neighboring countries such as Afghanistan (Khan et al. 2014a), Myanmar and Brunei (Shi et al. 2019), and several countries in sub-Saharan Africa (Mainali et al. 2015; McConnachie and Witt 2019; McConnachie et al. 2011) but such occurrences have not yet been adequately reported (Shabbir 2012).

Table 2. Key morphological features of *Parthenium hysterophorus* and their role in its resilient growth habit^a.

Attribute	Function and its role in the plant's success
Taproot system	Helps deep penetration in a range of soils, facilitating anchorage and efficient water uptake.
Rosette growth stage	A growth stage supported by C ₄ photosynthesis, which helps with efficient resource use and stress tolerance.
Erect, angular woody stem	Upright vertical growing stature facilitates seed dispersal and competition with other plants. Suppression of understory plants and better light interception.
Trichomes on leaves	Help avoid herbivory and reduce transpiration, which improve physiological efficiency, especially under stress conditions.
Multiple branching	Improved plant canopy structure, helping with physical competition and seed production.
Attractive, clustered flowering/ inflorescence	Distinct, shiny, multiple flowers enable efficient reproduction. Floral structure enables both self-pollination and insect-induced pollination.
Single-seeded cypselsae with special features	Many compact cypselsae, equipped with appendages to help easy dispersal by wind, and to provide flotation on water,

^aThe information presented here is adopted and modified from Bajwa (2019) and Bajwa et al. (2016).

Invasion Pathways

Parthenium hysterophorus spreads through various pathways. The small-sized, lightweight seed can disperse seeds unnoticed through many local activities, while new populations can establish easily from the arrival of just a few seeds. Regionally, road networks were responsible for most population spread (36%), while direct cross-border travel contributed to more than half (51%) of the incoming sources of new populations into a country (Mao et al. 2021b). Other pathways of spread at the local or regional scale include by wind, water, contaminated machinery, and agricultural produce (Khan et al. 2018; Mao et al. 2019; Shabbir et al. 2019c). These pathways can provide multiple conduits for spread to allow local establishment. For example, in Australia, ca. 6,000 *P. hysterophorus* viable seeds were found in every ton of material washed off vehicles at a roadside cleaning facility near a heavily infested region of central Queensland (Nguyen 2011); an infestation found along Eley Creek, in the Northern Territory of Australia, is thought to have originated from the Roper Highway 8 km upstream, where the weed was first observed (DENRNT 2017); a report suggested that a major flooding event in 2010 to 2011 brought new populations of the weed from Queensland in to New South Wales, Australia, and this event caused local outbreaks of the weed in that state (Blackmore and Charlton 2011). These events are believed to occur in all invaded regions, although many of them go undocumented.

Conversely, the pathway through international trade is thought to have contributed the most to the spread of the weed on a larger scale (Mao et al. 2021b; Shabbir et al. 2019c). A third of all new introductions have been traced back to the importation of contaminated seed lots and other plant commodities (Mao et al. 2021b). For example, seed imports from the United States, especially as part of USAID programs, were the source of *P. hysterophorus* establishments in Israel (Dafni and Heller 1982), Mozambique (Wise et al. 2007), and Ethiopia and India (Adkins and Shabbir 2014). Used vehicles carried weed seeds from Queensland, Australia, into Papua New Guinea (McFadyen et al. 2019), while the weed itself was first brought into Australia from United States through contamination of a shipment of aviation parts (Adkins and Shabbir 2014). In addition, trading ports have been sites of unintentional introductions, both in the early 20th century and in recent years. The Republic of Korea reported *P. hysterophorus* populations present in the export zone of Masan City (Kim 2013), while China experienced a second introduction into the northern province of Shandong, following the discovery of a plant in the busy port of Lianyungang a year before (Mao 2018).

However, seeds may still manage to slip into new countries without invasive populations being formed. Such events have occurred in Belgium and Poland, where the local climate was not suitable for establishment (Mirek et al. 2002; Verloove 2006). Fewer introductions are now being observed due to improved border control and quarantine procedures in many countries.

Growth and Development

Morphology

Parthenium hysterophorus displays an upright growth pattern and a robust taproot that firmly anchors it in the soil (Adkins et al. 2018). Its invasiveness can be attributed to a distinct set of morphological features (Table 2).

These features contribute to competitive ability, invasiveness, and adaptability (Adkins and Shabbir 2014; Bajwa et al. 2016). The rosette stage in the growth cycle of *P. hysterophorus* can play a critical role, influencing the timing of subsequent stages based on the prevalent environmental conditions. This adaptive flexibility in growth stages aids in the plant's successful invasion (Adkins et al. 2018).

Eco-physiological Responses to Climate Change

Parthenium hysterophorus has an extraordinary ability to emerge, compete, and reproduce under different climatic conditions (Mao et al. 2021a). It has evolved morphological and physiological adaptations to sustain its growth while completing its life cycle under climate change conditions. *Parthenium hysterophorus*'s response and adaptive biology under major climate change elements are discussed in the following sections.

High Temperature

Parthenium hysterophorus has demonstrated an impressive ability not only to germinate but also to grow vigorously and reproduce across a wide range of temperatures. The weed has evolved phenological flexibility, allowing it to adapt to variations in temperature. This adaptability is a key factor in its successful establishment in regions with vastly different average temperatures, ensuring its presence throughout the year in certain countries. In India, Kaur et al. (2017) reported changes in ambient temperature and relative humidity to have a significant impact on the phenology of *P. hysterophorus*. However, crucially, these

changes do not inhibit its ability to germinate or flower. In a controlled-environment study, Nguyen et al. (2017a) found that *P. hysterophorus* plants grown at warmer day/night temperatures (35/20 °C) grew faster and taller and produced more seed with a high seed-fill rate and predicted longevity than plants grown at cooler day/night temperatures (30/15 °C). However, the life span of plants grown under warmer temperatures was shorter compared with those exposed to the lower-temperature regime. These adaptive responses underline the resilience and invasiveness of *P. hysterophorus*, which enable it to thrive in diverse climatic conditions and to successfully reproduce, even in challenging and fluctuating climatic conditions.

In addition to phenological adaptations, *P. hysterophorus* displays impressive physiological adaptations to high temperatures. Plants grown under high, summer temperatures (ranging from 35 to 45 °C) exhibited enhanced growth rates, increased chlorophyll content, higher levels of soluble sugars, and increased protein quantities compared with plants grown at cool temperatures (22 to 30 °C) within a greenhouse (Kapoor 2014). Conversely, these attributes are not expressed when plants are exposed to low temperatures (7 to 15 °C) during winter. Another study conducted by Sharma et al. (2014) reported a substantial upregulation of antioxidant and heat shock-related stress-tolerant biochemicals in response to high temperatures. These heightened levels of heat-induced proteins are associated with the effective capturing of reactive oxygen species, leading to improved regulation of plant physiological functions (Sharma et al. 2014). Such adaptive physiological changes play a vital role in the success of *P. hysterophorus* in harsh tropical and subtropical environments.

Drought

Parthenium hysterophorus demonstrates remarkable adaptability to low soil moisture conditions by modifying its morphology, growth phases, and life cycle. For instance, the cuticle (14.0 µm) and palisade layers (145.6 µm) of *P. hysterophorus* leaves growing in Yunnan Province, China, were the thickest among nine weed species, and presumably are helpful to reduce water loss (Pu et al. 2023). Studies have shown that when grown at 50% of soil water-holding capacity (WHC), *P. hysterophorus* plants adjust their life cycle, flowering ca. 17 d earlier and producing seeds about 18 d earlier than those grown under normal moisture conditions. This adaptation results in a shortened life span by ca. 32 d under drought conditions (Nguyen et al. 2017a). Interestingly, while drought negatively affects seed fill, it does not significantly reduce total seed production or predicted seed longevity (Nguyen et al. 2017a).

Moreover, under drought conditions, *P. hysterophorus* plants produced significantly higher amounts of antioxidants such as superoxide dismutase, glutathione reductase, catalase, glutathione S-transferase, ascorbate, and proline compared with normal moisture conditions (Ahmad et al. 2017). The plants also upregulate various defense proteins in response to oxidative stress, enhancing their ability to tolerate the adverse effects of drought stress (Ahmad et al. 2017). Similar findings have been reported for Australian biotypes of *P. hysterophorus* under moisture-stress conditions (Bajwa et al. 2017). These physiological adaptations underscore the resilience and invasive potential of *P. hysterophorus*, which allow it to thrive and spread even in arid and drought-prone environments.

Soil Constraints

Parthenium hysterophorus exhibits a notable tolerance to elevated salinity levels, enabling its invasion of salt-affected and coastal

areas. Research by Khurshid et al. (2012) demonstrated that *P. hysterophorus* can withstand high salinity levels both in controlled conditions (up to 30 mM NaCl) and in field conditions (10 dS m⁻¹). However, it is important to note that, comparatively, *P. hysterophorus* was found to be more sensitive to salinity stress than to drought (Ahmad et al. 2017).

Moreover, *P. hysterophorus* has the capacity to uptake and accumulate a variety of heavy metals, including cadmium, copper, cobalt, lead, nickel, chromium, and zinc, from soils contaminated with industrial waste (Ajmal et al. 2006; Lata et al. 2008; Malik et al. 2010). This ability to cope with phytotoxic stress induced by heavy metals makes it feasible for *P. hysterophorus* to establish itself in disturbed environments. The weed thrives in roadside communities that are heavily polluted with vehicle emissions, dust, and dirt, indicating a strong tolerance mechanism toward air, soil, and water pollution (Adkins et al. 2018; Strathie and McConnachie 2019).

Elevated CO₂

The rise in atmospheric CO₂ concentration profoundly influences the morphology and physiology of plants, a phenomenon extensively investigated in *P. hysterophorus* (Mao et al. 2021a). As a C₃/C₄ intermediate plant species, in its C₃ adult form *P. hysterophorus* enhances its photosynthetic activity in response to elevated atmospheric CO₂ levels. This results in a significant improvement in its growth, biomass accumulation, competitive ability, allelopathic ability, and seed production (Adkins et al. 2018; Khan et al. 2018; Moore et al. 1987; Shi and Adkins 2020). Rice et al. (2021) showed that *P. hysterophorus* has already reaped benefits from the historical increase in atmospheric CO₂ concentrations over the past century. An invasive biotype of *P. hysterophorus* from Australia grown under modern-day CO₂ concentrations (400 ppm) exhibited close to a 50% increase in size and produced 50% more parthenin (a major allelochemical/allergen) compared with when it was grown under preindustrial-era CO₂ concentrations (300 ppm).

Various studies have consistently reported substantial increases in growth, competitive ability, and reproductive output of *P. hysterophorus* plants when exposed to elevated atmospheric CO₂ concentrations, like those predicted to prevail in the coming decades (Bajwa et al. 2019e; Khan et al. 2015; Navie et al. 2005). For instance, Shabbir et al. (2014) observed a significant increase in height (52%), biomass (55%), branching (62%), leaf area (120%), photosynthesis (94%), and water-use efficiency (400%) of *P. hysterophorus* plants at an elevated atmospheric CO₂ concentration (550 ppm) compared with plants at an ambient CO₂ concentration (380 ppm).

Interactive Effects

The interactive effects of different climate change elements are more important given the fact that all these factors coexist under natural conditions. Nguyen et al. (2017a) studied the growth and fecundity of *P. hysterophorus* plants at normal (100% WHC) and low (50% WHC) soil moisture in combination with high (35/20 °C) and low (30/15 °C) day/night temperatures. The plants had significantly higher growth and seed production under a combination of normal moisture and low temperature compared with those grown at low moisture in combination with high temperature (Nguyen et al. 2017a). Bajwa (2019) reported that *P. hysterophorus* plants grown under elevated CO₂ better tolerated moisture stress condition than their counterparts grown under ambient CO₂. Similarly, *P. hysterophorus* plants better tolerated

soil salinity when grown in a CO₂-enriched environment (Saravanane et al. 2023). These compensatory improvements were attributed to enhanced metabolic activity and better growth regulation. This demonstrates that the interaction of different climate change elements could have a significant impact on the morphology, physiology, phenology, and reproductive capacity of *P. hysterophorus*.

Reproduction

Floral Biology

Flower initiation can start as early as 28 d after seedling emergence from the soil (Jayachandra 1971), while others report that flower initiation will take up to 42 to 63 d (Navie et al. 1996). The flower head or capitulum consists of a conical receptacle surrounded by an outer involucre of five persistent bracts, five (sometimes six to eight) peripheral fertile ray florets, and 12 to 20 central cylindrical staminate disk florets, each bearing four connate anthers (Navie et al. 1998). The appearance of reddish-brown spots on the stigmas of the ray florets indicates successful pollination has taken place. Pollen grains are mostly spheroidal, 12 to 20 µm in size, and have short to medium-length spines often permeated with micropores (Lewis et al. 1991). On average, 150,000 to 350,000 pollen grains are produced in each of thousands of capitula, so pollen production by an average plant is extremely large, ca. 850 million pollen grains plant⁻¹ (Kanchan and Jayachandra 1979; Lewis et al. 1988) or more than 10 billion pollen grains m⁻² in a typical stand of the weed. Large amounts of airborne pollen from *P. hysterophorus* plants have been detected both in the United States and India at various altitudes (2 to 915 m asl) and at considerable distances from *P. hysterophorus* populations (Lewis et al. 1991).

There are conflicting reports as to whether *P. hysterophorus* is self- or cross-pollinated, and what the actual mechanism of pollination is. Esau (1946) reported that apomixis did not occur in *P. hysterophorus* and that the species was only known to produce seed after pollination. Lewis et al. (1988), working on plants from the native range, considered the species to exhibit a high degree of self-pollination (95% of seeds produced in this way were viable) with little or no insect pollination. They concluded that wind or self-pollination accounted for most seed produced. In later studies, Lewis et al. (1991) advanced the notion that the mechanism of wind pollination in *P. hysterophorus* was less developed than that seen in many other wind-pollinated species, indicating that self-pollination was probably the most common form of pollination in this species. However, Gupta and Chanda (1991) noted that *P. hysterophorus* plants in the invaded range of India appeared to be insect pollinated or, at least, pollen was dispersed mainly by insects. The main pollinating agents were thought to be honey bees (*Apis* Spp.), ants (*Lasius niger* Linn.), house flies (*Musca domestica* Linn.), and other dipterans that frequently visited its flowers. They concluded that *P. hysterophorus* is not normally self-pollinating, but ants may occasionally induce the process of self-pollination after visiting flowers from the same plant. More recently, Hanif (2014) has raised the very interesting idea that in certain parts of the invaded range, where the plants are extremely invasive, they are mainly cross-pollinating plants, while less invasive plants are self-pollinated.

Seed Production

Parthenium hysterophorus is a very prolific seed producer and will continue to flower and fruit profusely until senescence (Haseler

1976). Seed (retained within the cypsela) is shed gradually throughout the latter stages of growth, while other seed is retained in the flowers until after senescence (Parsons and Cuthbertson 1992). Each flower head produces up to five blackish achenes, occasionally six to eight, of uniform size and weigh (Auld et al. 1982; Lewis et al. 1988), which are individually enclosed in the straw-colored cypsela along with two lateral attached sterile florets (Navie et al. 1996). While there have been a range of estimations of *P. hysterophorus* seed production per plant in the field (ca. 15,000 [Haseler 1976] to ca. 156,000 [Dhileepan 2012]), the most recent and accurate counts for glasshouse-grown plants is between ca. 18,000 to 26,000 filled seeds per plant (Nguyen et al. 2017b). In India, Kanchan and Jayachandra (1979) found that there was an average of 15 plants m⁻² in a typical stand of *P. hysterophorus*. Such data indicate that more than 300,000 seeds m⁻² could be produced in many field situations. These figures for seed production are only applicable when sufficient moisture and warm temperatures are available to produce vigorously growing stands of plants, as Nguyen et al. (2017a) have shown that filled seed production will be reduced (from ca. 20,000 to ca. 9,000) when plants are grown under cool/dry conditions compared with warm/wet environmental conditions. Pandey and Dubey (1988) reported *P. hysterophorus* to produce polymorphic seeds that vary in size and weight. They suggested that the variation in seed morphology may be due to differences in the maturation time of the capitula produced at different positions on the parent plant. They also found that small seeds were more commonly produced at lower latitudes (i.e., in southern India) compared with the larger seeds produced at higher latitudes (i.e., in northern India). Therefore, it seems that the climatic conditions have a bearing on both seed production and seed size (Dubey and Pandey 1988).

Seedbanks, Seed Viability, and Germination

Little is known concerning the longevity of *P. hysterophorus* seeds, either on the soil surface or in the soil seedbank. Navie et al. (1998) reported more than 70% of seed buried 5 cm below the soil surface could live for at least 2 yr, with a half-life of 7 yr. Tamado et al. (2002) reported more than 50% of soil-buried seed remained viable for up to 2.5 yr, with an anticipated life span of 3 to 4 yr. One additional study (Nguyen 2011) using a controlled ageing test suggested that the quality of the seed at the time of burial may also affect longevity, with higher-quality seed predicted to live longer in the soil seedbank than poor-quality seed. The longevity of surface-lying seeds seems to be quite short, with most dying within 6 mo (Navie et al. 1998). In Australia, Navie et al. (2004) determined the size of the germinable *P. hysterophorus* soil seedbank to range from 3,200 to 5,100 seed m⁻² in a black clay soil to 20,500 to 44,700 seed m⁻² in a sandy loam soil. At these two sites, the *P. hysterophorus* seedbank accounted for 47% to 73% and 65% to 87%, respectively, of the total seedbank present. In a riparian habitat invaded by *P. hysterophorus* near Lahore, Pakistan, a soil seedbank of 4,400 m⁻² has been reported (Shabbir 2015). In other locations, much larger seedbanks have been recorded; for example, Joshi (1991) estimated an Indian *P. hysterophorus* soil seedbank in an abandoned field to be 200,000 m⁻².

Parthenium hysterophorus seeds have a very high rate of fill, and those seeds have a high viability of 85% or greater when collected directly from the adult plant (Pandey and Dubey 1988; Williams and Groves 1980). Research has demonstrated that water-soluble germination inhibitors (i.e., parthenin and certain phenolic acids) are present in the layers surrounding the seed and that these

inhibitors need to be leached out before maximum germination can be attained (Picman and Picman 1984). *Parthenium hysterophorus* seed may also be induced into a state of quiescence by certain ambient environmental conditions, such as deep burial (White 1994). Recently, Nguyen et al. (2017a) have shown that the proportion of dormant seeds produced by a *P. hysterophorus* plant is determined by the maternal environment in which those seeds matured, with a warm/wet environment producing up to ca. 2,000 dormant seed plant⁻¹, while a cool/dry environment producing only ca. 100 dormant seeds plant⁻¹. This result is supported by Shrestha et al. (2024), who found the germination of summer-produced seed to be significantly lower than that of winter-produced seed.

Navie et al. (1996) found that the optimal temperature for germination of Australian seeds was between 22 and 25 C, but with a much wider range of temperatures over which some seed would germinate (9 to 36 C). Bajwa et al. (2018a) reported superior germination ability of the highly invasive Australian biotype of *P. hysterophorus* compared with its non-invasive counterpart, Toogoolawah biotype, across a range of temperature, pH, salinity, and osmotic stress levels under laboratory conditions. According to Tamado et al. (2002), fluctuating temperature regimes of 12/20 C to 35/20 C (day/night) were all suitable for the germination of Ethiopian seed. Williams and Groves (1980), working with Australian seed, reported that the maximum germination (88%) could be achieved in the dark, while Pandey and Dubey (1988), using seed of Indian origin, found the highest germination to occur in both continuous light and continuous dark, suggesting that this species does not have a strict light requirement for germination. Soil germination decreased from 91% when the soil was at field capacity, to just 50% when the soil moisture was reduced to -0.07 MPa, and to 0% when the soil moisture was reduced to -0.90 MPa. This demonstrates that *P. hysterophorus* seed germination depends on high moisture availability (Williams and Groves 1980). According to Tamado et al. (2002), the depth of seed burial can have a significant impact upon germination and/or seedling emergence. A depth of 0.5 cm seems to be ideal for this weed's germination, while 5.0 cm or more will result in slow or no germination. In one germination study conducted in India, the percentage of seeds germinating gradually increased as their seed size increased (Pandey and Dubey 1988).

Vegetative Reproduction

Parthenium hysterophorus does not reproduce vegetatively from plant parts or by apomixis. However, it has been observed that *P. hysterophorus* can regrow from an overwintering stem base created by either grazing or physical weed management (G Hassan, personal communication, 2010).

Population Dynamics

In some climates where *P. hysterophorus* occurs, it can grow at any given time of year due to its ability to germinate, grow, and flower over a wide range of photoperiod and temperature conditions (Haseler 1976). Its main season of growth, however, is the rainy season during the summer months in regions such as North and Central America, Mexico, and Australia, or during the wet season in India, Pakistan, and Nepal (Adkins et al. 2019). A field season with sufficient moisture and warm temperatures typically supports *P. hysterophorus* stands of 15 to 25 plants m⁻² in India (Kanchan and Jayachandra 1979; Joshi 1991), 315 plants m⁻² in eastern

Ethiopia (Tamado and Milberg 2004), to field reports of 800 plants m⁻² in central Queensland (Dhileepan 2003, 2012). It has been estimated that *P. hysterophorus* may produce more than 300,000 seeds m⁻² within a season under these conditions (Adkins et al. 2019). A season with frequent and abundant rainfall may allow the emergence of three or more successive cohorts (Pandey and Dubey 1989), with each cohort having variable life spans depending on seasonal conditions and the prevailing competition for light, water, or other resources (see "Life-Form and Life History"). For example, field observations made in India show three successive cohorts of *P. hysterophorus* to be recruited after the first rains of the new season, and the average recruitment over the 2-yr study was 110 plants m⁻², of which 14 plants m⁻² (13%) achieved maturity (Pandey and Dubey 1989). The study found seedling density and survivorship declined over successive cohorts until the third cohort had very few plants surviving past the seedling stage, which indicated the first, well-established cohort adversely affected the growth, and probably the survivorship, of the latter cohorts through resource competition (Pandey and Dubey 1989) and possibly allelopathy (Belz et al. 2009; Shabbir and Javaid 2010a, 2010b). Late-emerging cohorts in the autumn months in northeastern Mexico are known to produce large rosettes and overwinter in this form from October to March (Adkins et al. 2019), likely as a response to cooling temperature, shortening photoperiods, or water stress (McClay 1983).

As *P. hysterophorus* often grows in pure stands, only a few studies have been conducted on its population dynamics in relation to competition with other species in the field. A field report from Nepal has shown *P. hysterophorus* to outcompete native vegetation as quickly as 1 to 2 yr after agricultural land has been abandoned (Shrestha et al. 2015). Also, *P. hysterophorus* populations in Australia and Texas have been shown to remain dominant over native populations for more than 15 yr following soil disturbance (Dale 1981). These interactions may, in part, be attributed to direct or indirect soil-based allelopathic activity through phytotoxic effects that suppress root growth of neighboring plants (Belz et al. 2009). Parthenin-containing leaf leachates are also known to stimulate chlorophyll content (Kumari and Kohli 1987) and may be a self-stimulatory allelopathic mechanism that helps form pure, dense stands of *P. hysterophorus* (Belz et al. 2009). *Parthenium hysterophorus* is also known to indirectly manipulate plant communities by inhibiting the growth of beneficial microorganisms (Belz et al. 2009; Osunkoya et al. 2017). A field study undertaken in the Yucatán, Mexico, reported the microorganism population was much different in non-invaded soils compared with invaded soils. The study showed 5.2% of *P. hysterophorus* plants to be colonized by arbuscular mycorrhizal fungi, suggesting the microbial community could aid its invasion and establishment in certain edaphic regimes (Jeyalakshmi et al. 2011).

The density and fecundity of *P. hysterophorus* stands are based on competition dynamics and habitat factors as well as climatic conditions. Frequent and abundant rainfall events have been reported to help *P. hysterophorus* quickly colonize fallow areas and bare soils (Royimani et al. 2019). For example, a field survey in the province of Kwazulu-Natal, South Africa, indicated a correlation between low rainfall events from 2006 to 2012 with a decline in *P. hysterophorus* population size, followed by a high rainfall event in 2016 that rapidly expanded the area occupied by *P. hysterophorus* (Royimani et al. 2019). Flooding events exacerbate the spread of *P. hysterophorus* seed into new areas, as indicated by heavily infested areas in the wetlands of Sri Lanka

(Jayasuriya 2005) and Mozambique (Bandeira et al. 2006) and the establishment of large colonies over floodplains and waterways in central Queensland, Australia (Parsons and Cuthbertson 1992), Tanzania (Wabuye et al. 2014), and Shandong Province, China (Shi et al. 2019). Severe weather events are also known to aid *P. hysterophorus* seed dispersal and have subsequently increased population densities in Ethiopia (Ayele 2007) and Oman (Ghazanfar 2017).

Detection and Recognition

Using a field spectroscopy approach, Iqbal et al. (2021) discriminated *P. hysterophorus* from co-occurring native and introduced species in a protected reserve forest in Pakistan. Of various spectral indices, the Normalized Difference Vegetation Index (670- and 830-nm wavelengths) best discriminated *P. hysterophorus* from the rest of seven plant species. In contrast, Kganyago et al. (2017) found that the subset of two red-edge (685 and 707 nm), one near-infrared (1,115 nm) and seven short-wave infrared bands (1,971, 1,982, 1,990, 1,966, 2,003, 2,005, and 2,013 nm) showed the greatest discrimination ability of *P. hysterophorus* from its co-occurring species in South Africa. In another study, different growth stages (seedling, rosette, and flowering) of *P. hysterophorus* were detected and discerned from two grasses, kangaroo grass (*Themeda triandra* Forssk.) and desert bluegrass [*Bothriochloa ewartiana* (Domin) C.E. Hubb.], using images collected on glasshouse-grown plants with RGB and hyperspectral cameras (Costello et al. 2022). Similarly, Ullah et al. (2021) performed spectral discrimination of *P. hysterophorus* from four co-occurring plant species using hyperspectral data, using a combination of spectral angle mapper and genetic algorithms to successfully classify training and testing datasets, both with an accuracy of more than 90%. In summary, *P. hysterophorus* can be detected and classified using remote sensing and machine learning approaches. Further investigation is needed to scale up the data from distinct spectral bands to airborne and satellite sensors. This will facilitate the comprehensive documentation of *P. hysterophorus* distribution at the landscape level.

Management Options

Legislative Measures

Effective legislation addressing prevention and containment of weed is for weed management. In Australia, *P. hysterophorus* is classified as a declared pest plant in all states and territories. Each state and territory authority has its own legislation to prevent the entry and spread of *P. hysterophorus* based on the perceived level of risk (Campbell et al. 2019). For instance, in New South Wales, specific legislative requirements outline the requirement of interstate movement of agricultural machinery such as harvesters and other equipment. The regulation mandates that equipment needs to be thoroughly cleaned to remove any weed seeds and to be checked by the state border inspector (Campbell et al. 2019). Similarly other countries such as South Africa, Kenya, and Sri Lanka have implemented legislation to contain the spread of *P. hysterophorus* into un-infested areas (Adkins and Shabbir 2014). However, in many other countries where *P. hysterophorus* has invaded, effective legislation does not exist; thus the weed continues to spread within invaded areas and into new regions (Dorjee et al. 2021).

Phytosanitary Measures

Phytosanitary measures play a crucial role in the prevention, introduction, and further spread of weeds into new areas. In New South Wales, Australia, 59% of *P. hysterophorus* outbreaks on new properties were attributed to contaminated harvesters coming from the state of Queensland, where this weed is a significant problem (Blackmore and Johnson 2010). Establishment of road-side vehicle wash-down facilities in weed-infested areas and along the state border crossings has proven effective in removing *P. hysterophorus* seeds and minimizing its further spread (Bajwa et al. 2018b).

Phytosanitary measures are essential to minimize the spread of *P. hysterophorus* to new regions and countries. Within the Euro-Mediterranean region, *P. hysterophorus* is only established in Israel. To prevent the potential risk of *P. hysterophorus* spreading to other countries in the region, the European and Mediterranean Plant Protection Organization performed a pest risk analysis on this weed (Brunel et al. 2014) and recommended it be regulated as a quarantine pest for the member countries (EPPO 2014). Similar measures are required to prevent seed spread at the local level, for instance, the state of Queensland has developed a weed hygiene declaration form that require providers to include the weed seed status in any grain, feed, or animals being purchased (Chamberlain and Gittens 2004).

Chemical Control

Chemical control of *P. hysterophorus*, as for most weeds, is the most effective, quickest, and most economical weed control method, especially in agroecosystems (Bajwa et al. 2019d). A range of pre- and postemergence herbicides have been used to control *P. hysterophorus* in non-cropped and cropped areas (Table 2). In non-cropped areas, glyphosate and 2,4-D have been the major herbicides used to suppress *P. hysterophorus* growth and biomass production (Tanveer et al. 2015). Several other chemicals, including isoproturon, metribuzin, flumioxazin, dicamba, diuron, and picloram, have also been reported to provide effective control of this weed in non-cropped situations (Fernandez et al. 2014; Odero 2012; Reddy et al. 2007; Shabbir 2014a; Singh et al. 2004). Most of the postemergence herbicides provided effective control of *P. hysterophorus* when applied at the seedling or rosette stages, but their efficacy was reduced when applied to mature plants (Reddy et al. 2007). However, a relatively smaller number of studies have reported successful chemical control of *P. hysterophorus* in crops (Table 3).

Some studies have also highlighted the challenge of effectively controlling *P. hysterophorus* with certain commonly used herbicides. For example, research by Tamado and Milberg (2004) indicated that 2,4-D, a widely used herbicide, showed inconsistent control of *P. hysterophorus* in sorghum crops in Ethiopia. In Sri Lanka, Nishanthan et al. (2018) found that a preemergence application of oxyfluorfen was ineffective in controlling *P. hysterophorus* in capsicum (*Capsicum annuum* L.) crop. Bajwa et al. (2019d) reported that the application of pendimethalin (preemergence) or bispyribac-sodium + bensulfuron-methyl (postemergence) failed to provide good control in a direct-seeded rice crop in Pakistan. Given the widespread infestation of *P. hysterophorus* in various crops globally, this information underscores the need for comprehensive research to identify effective chemical control options for managing this weed across a range of crops.

Table 3. Chemical options that provided an effective control (>90%) of *Parthenium hysterophorus* in different crops when applied either preemergence (PRE) or postemergence (POST) to the crop.

Herbicide and dose (g ai ha ⁻¹)	Application timing	Crop	Country	Reference
Oxadiazon (1,000)	PRE	Rice (<i>Oryza sativa</i> L.)	India	Paradkar et al. (1997)
Oxyfluorfen (370)	PRE			
Butachlor (2,000)	PRE			
Pertilachlor (750)	PRE			
Bromoxynil (240 to 480)	POST	Sorghum (<i>Sorghum bicolor</i> (L.) Moench)	Mexico	Rosales-Robles et al. (2005)
Pendimethalin (407)	PRE	Maize (<i>Zea mays</i> L.)	Pakistan	Rehman et al. (2017)
Atrazine (469)	POST			
S-metolachlor + atrazine (711)	POST			
Bromoxynil + MCPA (445)	POST			
Pendimethalin (750) followed by bispyribac-sodium + bensulfuron-methyl (375)	PRE followed by POST	Rice (<i>Oryza sativa</i> L.)	Pakistan	Bajwa et al. (2019d)

Cultural

In some countries, the manual removal of *P. hysterophorus* is not considered to be a cost-effective approach due to the size of the weed infestations present and the cost of the labor in that country. However, this method of management may affect the health of the workers who are employed to do this job, as *P. hysterophorus* is known to cause contact dermatitis and asthma (Allan et al. 2019). *Parthenium hysterophorus* populations also readily regenerate from the seedbank after manual removal has been applied and will regrow from cut or partly pulled plants that still have a root system. Despite such drawbacks, the hand-pulling strategy is commonly used in developing countries such as India, Pakistan, Bangladesh, and Nepal where labor is cheap, and people are not aware of the associated health risks of pulling up the plant (Khan 2011). Slashing and plowing are only effective for the short term, as these strategies stimulate regrowth and seed germination, respectively (Bhowmik and Sarkar 2005; Haseler 1976).

Physical Control

Physical removal of *P. hysterophorus* is effective but labor-intensive and poses health risks due to the allergenic nature of the weed. *Parthenium hysterophorus* can quickly regrow from slashed or mowed plants, so uprooting plants before they seed set is important (Campbell et al. 2019). The burning of *P. hysterophorus* plants in a rangeland setting can result in the reduction in its numbers but fire can also create an ideal germination bed for surviving *P. hysterophorus* seeds (Vogler et al., 2006). In a field study in northern Australia, Vogler et al. (2006) found that the size of the *P. hysterophorus* seedbank in soil was not affected by the fire. In addition, smoke and heat did not impact *P. hysterophorus* seed germination. However, different responses to fire have been observed (Shabbir 2007). Within a wheat-cropping system in which the wheat residues were burnt after crop harvest, *P. hysterophorus* seedlings emerged rapidly. This emergence was, however, within the residue patches that had escaped the fire and not in the burnt areas.

Biological Control

Biological control involving natural enemies (insect herbivores, plant pathogens, and other organisms) is a widely used approach to manage *P. hysterophorus* in several countries. To date, nine

countries have released one or more biological control agents against this weed, with another four countries having some agents arrive fortuitously or originally released for control of other weed species (Dhileepan 2009; Strathie et al. 2021; Table 4; Figure 7).

Australia is leading the way in using biological control for *P. hysterophorus* management with 11 agents (9 insects and 2 pathogens) so far released since the initiation of the program in 1976 (Table 3). Most of these released agents have become established, with some that are now widespread and abundant and having a significant impact upon weed populations (Dhileepan and MacFadyen 2012; Dhileepan et al. 2018). *Zygogramma bicolorata* (a leaf-feeding beetle), *Listronotus setosipennis* (a stem-boring weevil), *Smicronyx lutulentus* (a seed-feeding weevil), and *Epiblema strenuana* (a stem-galling moth) are some of the widespread and effective insect biocontrol agents (Dhileepan et al. 2018; McFadyen 1992). The most effective agents are now being redistributed to south and southeast Queensland, where *P. hysterophorus* is now spreading from its core infestations in central Queensland (Dhileepan et al. 2018).

Zygogramma bicolorata is the most widely distributed agent, released or arrived fortuitously, in 10 countries (Table 3). Both the larvae and adults of *Z. bicolorata* feed on the leaves of *P. hysterophorus* (Figure 7), and just a few beetles can completely defoliate a plant, especially when present on the early growth stages of the weed (Shabbir et al. 2016). Field occurrences of *Z. bicolorata* are now common in central Queensland, Australia, resulting in a significant reduction in populations of *P. hysterophorus* (Dhileepan et al. 2018).

After its first release in Australia in 1981, the stem-boring weevil *Listronotus setosipennis* has now been released to four other countries, including South Africa, Ethiopia, Uganda, and Pakistan. The larvae of *L. setosipennis* bore through the stem, feed on the pith or epidermis, and can subsequently kill the plant (Wild et al. 1992). *Smicronyx lutulentus* is a seed-feeding weevil, first released in Australia in 1981; since then, it has been released in South Africa and Ethiopia. The adult weevils feed on developing leaf buds and emerged leaves, but they inflict minimal damage. The female lays eggs on the flower buds, and the emerging larvae feed on developing seeds, which causes the seeds to swell greatly, inflicting damage not only to the infested seeds but also to the other seeds in the capitulum that often do not develop (Dhileepan et al. 2018).

Epiblema strenuana is a stem-galling moth first released in Australia in 1982. This agent is also present in China, where it was originally released for the biological control of annual ragweed (*Ambrosia artemisiifolia* L.) (Liu et al. 2013). After its first release in

Table 4. Biological control agents released or present in different countries around the world to aid in the management of *Parthenium hysterophorus*.^a

Agent	Common name	Family	Country of introduction	Mode of introduction	Source country	Established
<i>Zygogramma bicolorata</i>	Leaf-feeding beetle	Coleoptera	Australia	Released	Mexico	Yes
			Bangladesh	Unknown	India	Unknown
			Bhutan	Unknown	India	Yes
			Ethiopia	Released	South Africa	Yes
			India	Released	Mexico	Yes
			Kenya	Released	South Africa	Yes
			Nepal	Unknown	India	Yes
			Pakistan	Unknown	India	Yes
			South Africa	Released	Australia	Yes
			Sri Lanka	Unknown	Unknown	Yes
			Tanzania	Released	South Africa	Yes
			Uganda	Released	South Africa	Yes
			Australia	Released	Mexico	Yes
<i>Epiblema strenuana</i>	Stem-galling moth	Lepidoptera	China	Released ^b	Australia	Yes
			Sri Lanka	Released	Mexico	No
<i>Listronotus setosipennis</i>	Stem-boring weevil	Coleoptera	Australia	Released	Argentina	Yes
			Ethiopia	Released	South Africa	Yes
			Kenya	Released	South Africa	Yes
			Pakistan	Released	South Africa	unknown
			South Africa	Released	Australia	Yes
			Tanzania	Released	South Africa	Yes
			Australia	Released	Mexico	Yes
<i>Smicronyx lutulentus</i>	Seed-feeding weevil	Coleoptera	South Africa	Released	Australia	Yes
<i>Contrachelus albocinereus</i>	Stem-galling weevil	Coleoptera	Australia	Released	Argentina	Yes
<i>Carmenta ithacae</i>	Root-feeding clearwing wasp	Lepidoptera	Australia	Released	Mexico	Yes
<i>Buccalatrix parthenica</i>	leaf-mining moth	Lepidoptera	Australia	Released	Mexico	Yes
<i>Platphalonidia mystica</i>	Stem-boring moth	Lepidoptera	Australia	Released	Argentina	No
<i>Stobaera concinna</i>	Sap-feeding plant hopper	Homoptera	Australia	Released	Mexico	No
<i>Puccinia abrupta</i> var. <i>partheniicola</i>	Winter rust	Uredinales	Australia	Released	Mexico	Yes
			Bhutan	Unknown	Unknown	Yes
			China	Unknown	Unknown	Yes
			India	Unknown	Unknown	Yes
			Nepal	Unknown	Unknown	Yes
			Pakistan	Unknown	Unknown	Yes
			South Africa	Unknown	Unknown	Yes
<i>Puccinia xanthii</i> var. <i>parthenium hysterophorae</i>	Summer rust	Uredinales	Australia	Released	Mexico	Yes
			South Africa	Released	Australia	Yes
			Sri Lanka	Released	Mexico	No

^aAdapted and modified from Dhileepan and McFadyen (2012).^bOriginally released against annual ragweed (*Ambrosia artemisiifolia*).

Australia, *E. strenuana* readily established in most areas where *P. hysterophorus* occurred at that time. The female lays eggs singly on leaves, and the emerging larvae feed on leaf tissue for short periods of time before boring into the stem. The feeding larvae produce stem galls in which developing larvae pupate and emerge out through a hole 4 to 6 wk later (Dhileepan et al. 2018; Figure 7). The stem-galling moth is a widespread and effective agent that can reduce the growth and seed production of *P. hysterophorus* (Dhileepan 2003; Dhileepan and McFadyen 2001). This agent was found to retain its effectiveness to suppress the growth of *P. hysterophorus* under climate change conditions involving an atmosphere of elevated CO₂ (Shabbir et al. 2019b).

Two rust species, *Puccinia abrupta* var. *partheniicola* (winter rust) and *Puccinia xanthii* var. *parthenium hysterophorae* (summer rust) were released in Australia and established in the field, but their prevalence and impact are highly variable and sporadic depending upon the local climatic conditions (Dhileepan et al. 1996). The winter rust is now present in six other countries outside Australia, where its source is unknown (Table 3), with Pakistan being the most recent country where winter rust is reported

(Iqbal et al. 2020; Figure 7). South Africa imported the summer rust from Australia in 2004, and it was subsequently approved for field release after host specificity testing and has now established (Retief et al. 2013; Strathie et al. 2021).

Suppressive plants, also known as competitive plants, can suppress the growth of nearby plants, including invasive plants, through direct physical competition for resources (light, water, space, nutrients) or by releasing allelopathic chemicals. Sowing beneficial suppressive plants in a *P. hysterophorus*-infested areas is an effective strategy to manage this weed (Belgeri et al. 2020; Khan et al. 2015; Shabbir et al. 2019a; van der Laan et al. 2008). Several suppressive pasture plants, both grass and leguminous species, have been reported to suppress the growth of *P. hysterophorus* (Khan et al. 2014b, 2015). This approach has been used to manage *P. hysterophorus* in different parts of the world such as Australia, India, and South Africa (Belgeri et al. 2020; Khan et al. 2019; Knox et al. 2011; Shabbir et al. 2019a; van der Laan et al. 2008). In Australia, more than 30 pasture species (both grasses and legumes) were systematically selected based on their superior growth traits (fast growth rate, higher biomass, tall stature, etc.) and good



Figure 7. Some of the biological control agents released against *Parthenium hysterophorus*. An adult and late instar larvae of *Zygogramma bicolorata* (A), two stem galls produced by *Epiblema strenuana* (B), an adult pair of *Smicronyx lutulentus*, (C), a *Listronotus setosipennis* adult (D), and pustules produced by *Puccinia abrupta* (E).

palatability to suppress the growth of *P. hysterophorus* and at the same time provide fodder for livestock (Bowen et al. 2007; Khan et al. 2014b, 2015; O'Donnell and Adkins 2005). Most of these species suppressed *P. hysterophorus* growth under glasshouse conditions (Khan et al. 2013), while some of them [e.g., Purple pigeon grass, *Setaria incrassata* (Hochst.) Hack.; buffel grass, *Cenchrus ciliaris* L.; *T. triandra*; creeping bluegrass, *Bothriochloa insculpta* (Hochst. ex A. Rich.) A. Camus; Indian bluegrass, *Bothriochloa pertusa* (L.) A. Camus; butterfly pea, *Clitoria ternatea* L.; bull Mitchel grass, *Astrebla squarrosa* C.E. Hubb.] have also proven to be suppressive at different field locations (Khan et al. 2014b, 2015). In a field study in central Queensland, Australia, Shabbir et al. (2019a) tested additional species and found that the introduced pasture grasses [digit grass, *Digitaria milanjiana* (Rendle) Stapf.; *C. ciliaris* (L.) Link] and legumes [round-leaf cassia, *Chamaecrista rotundifolia* (Pers.) Greene; *C. ternatea*], suppressed the biomass of *P. hysterophorus* by 60% to 80%, with *C. ciliaris* and *C. ternatea* producing large amounts of dry fodder biomass (i.e., 0.41 and 0.36 kg m⁻², respectively). Belgeri et al. (2020) studied the suppressive effect of plant mixtures on the growth of *P. hysterophorus* in Australian grasslands. This study found that the mixture composed predominantly of native species [forest bluegrass, *Bothriochloa bladhii* (Retz.) S.T. Blake; Queensland bluegrass, *Dichanthium sericeum* (R. Br.) A. Camus] exhibited greater suppression of *P. hysterophorus* biomass compared with those rich in introduced species. It should be noted that the suppressive legume yellow lucerne (*Medicago falcata* L.) can decrease the root to shoot ratio of *P. hysterophorus*, while alfalfa (*Medicago sativa* L.) increased this ratio, possibly through beneficial nitrogen fixation (Ran et al. 2024).

Integrating suppressive plants with other management strategies, including biological control, can provide enhanced control of *P. hysterophorus* (Shabbir et al. 2013, 2015, 2018, 2020a, 2020b). Some of the biological control agents released in Australia (*E. strenuana*, *Z. colorata*, and *P. abrupta*) have been shown to work synergistically or additively with selected suppressive plants (e.g., *C. ternatea* and *A. squarrosa*) to provide good control of *P. hysterophorus* (Shabbir et al. 2013, 2018). Further, the

complementary effects of suppressive plants with biological control could be retained under an atmosphere of elevated CO₂ in various changing climate scenarios (Shabbir et al. 2019b, 2020b). In summary, sowing suppressive plants in *P. hysterophorus*-infested areas has shown good potential to aid the management of *P. hysterophorus*, and it can be combined with other strategies such as biological control to provide resilient management across diverse landscapes. Exploring new suppressive plants suited to local climates would provide effective management of *P. hysterophorus* and promote environmental sustainability.

General Outlook

Parthenium hysterophorus is a highly invasive plant species of global concern. It impacts agriculture, natural ecosystems, human and animal health, and livelihoods around the world. Already, the weed has invaded more than 50 countries across its introduced range and is expanding even in parts of its native range, particularly in the southwestern United States. Global climatic suitability modeling indicates that this weed has not yet reached its full spread potential, and there are many more areas (e.g., sub-Saharan and western Africa, eastern Europe, southeast Asia) that are highly susceptible to future invasion. The rapid spread of *P. hysterophorus* in densely populated countries like China, India, and Pakistan poses a significant threat to the environment, human health, and the sustainability of resources. The ability of this plant to produce many highly viable seeds and disperse them through various vectors, coupled with intensified global trade and travel, pose a serious threat to all those suitable uninhabited areas. Climate change is also in favor of *P. hysterophorus*, promoting its growth and reproduction under increasing temperature and atmospheric CO₂ concentrations. Current control options are partially effective in most circumstances. Effective biosecurity legislation and investment in border control of this weed are the most cost-effective ways to protect new areas from invasion; however, these would be expensive to implement in most developing and low-income countries. A suite of biological control agents has been released against *P. hysterophorus* in Australia and South Africa with partial

success. However, a combination of approaches built into a sustainable integrated weed management plan is advised. Other countries with a prevailing *P. hysterophorus* problem could learn from these experiences and benefit from this strategy, and at a much lower cost and with rapid delivery. Collaboration among researchers, policy makers, and local communities is key to addressing the *P. hysterophorus* issue, on both local and global scales.

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Parthenium hysterophorus at a glance . . .

Impacts

- Outcompetes native vegetation and reduces biodiversity
- Reduces agricultural production and impacts socioeconomic health in rural communities
- Causes allergies and other health problems in humans and animals

Dispersal

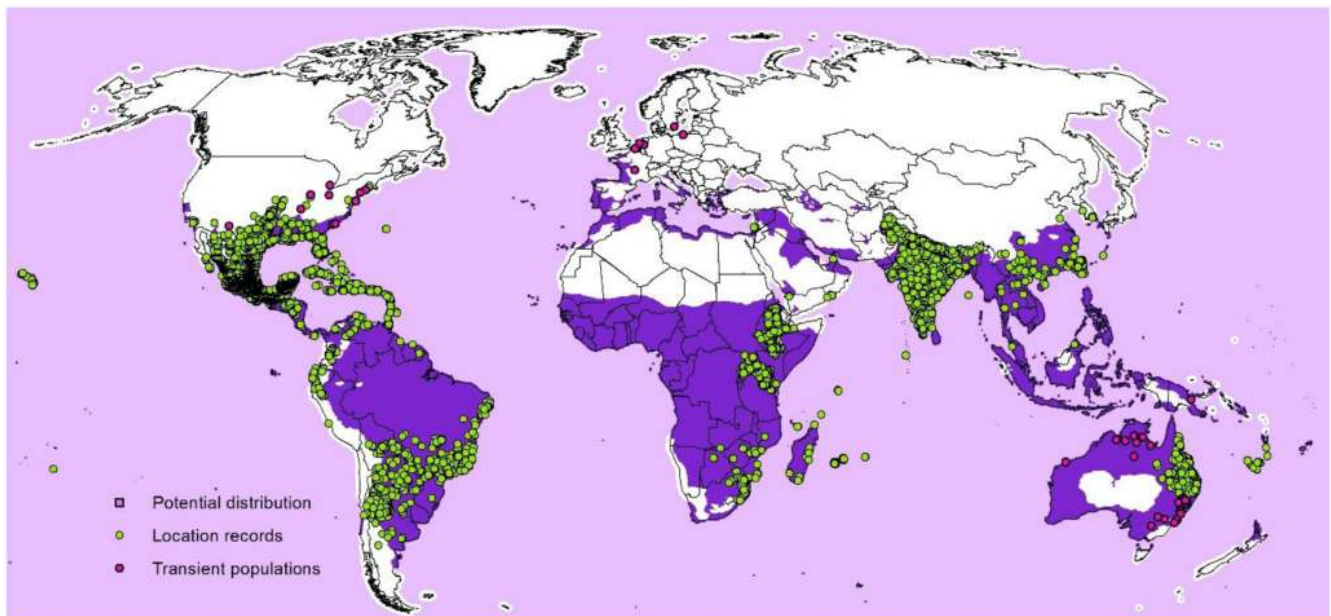
- Seed dispersed by wind and water, via movement of livestock and native and feral animals, and attached to agricultural machinery and vehicles

Management

- Several herbicides provide effective control
- Suite of biocontrol agents available
- Suppressive plants also effective alone and or in combination with biocontrol
- True integrated management lacking

Biosecurity

- One of the world's worst invasive species
- Recognized as a major biosecurity threat and a Weed of National Significance in Australia
- Spread through contaminated seed, feed, and machinery
- Most of sub-Saharan Africa, eastern Europe, and southeast Asia at risk of invasion



Structured Appendix

Methods for Distribution Data and Köppen-Geiger Climates

Plant localities were taken from GBIF (2024), REMIB database (2024) (Ghazanfar 2017; Kawi and Orapa 2010; Shabbir 2017; Sushilkumar 2012; Tominaga 2013), published surveys (Jayasuriya 2005; Kirshanthan et al. 2016; Shabbir et al. 2012), and recent, but unpublished, surveys in Thailand (S Zungsontiporn, personal communication, 2024), Saudi Arabia, Eritrea, and Bermuda to the Caribbean region (A Witt, personal communication, 2024). Locality data were refined by (1) correcting coordinate errors, where possible; (2) removing duplicate records; (3) removing instances with a locational error

or an artificial cultivation of *Parthenium hysterophorus* (e.g., university campuses, botanical gardens); and (4) reevaluating coordinates older than 50 yr and/or with no additional locations near them, deeming them transient, and removing them in Belgium, France, Poland, Sweden, the Netherlands, and parts of the United States.

Climatic data were downloaded from World Maps of Köppen-Geiger Climate Classification (<http://koeppen-geiger.vu-wien.ac.at>). Distribution maps with Köppen-Geiger climates as a background were generated using ArcMap (ESRI, Redlands, CA). We used the CLIMEX model developed by Shabbir et al. (2023) to show the potential distribution of *P. hysterophorus* around the world.

Table A1. Köppen-Geiger climate zone classifications globally that indicate habitat suitability for the survival and growth of *Parthenium hysterophorus*

Köppen-Geiger code	Description
Contains established populations	
Af (native range)	Tropical rainforest
Am	Tropical monsoon
As	Tropical savanna, with dry summer characteristics
Aw (native range)	Tropical savanna, with dry winter characteristics
BSh (native range)	Semiarid (steppe) climate, hot
BSk (native range)	Semiarid (steppe) climate, cold
BWh	Arid, hot desert
BWk	Arid, cold desert
Cfa (native range)	Humid, subtropical
Cfb	Oceanic
Csa	Mediterranean–dry hot summer
Csb	Mediterranean–dry warm/cool summer
Cwa (native range)	Dry winter, humid subtropical summer
Cwb	Dry winter, subtropical highland
Dsb	Dry summer, warm summer continental
Dwa	Hot summer continental

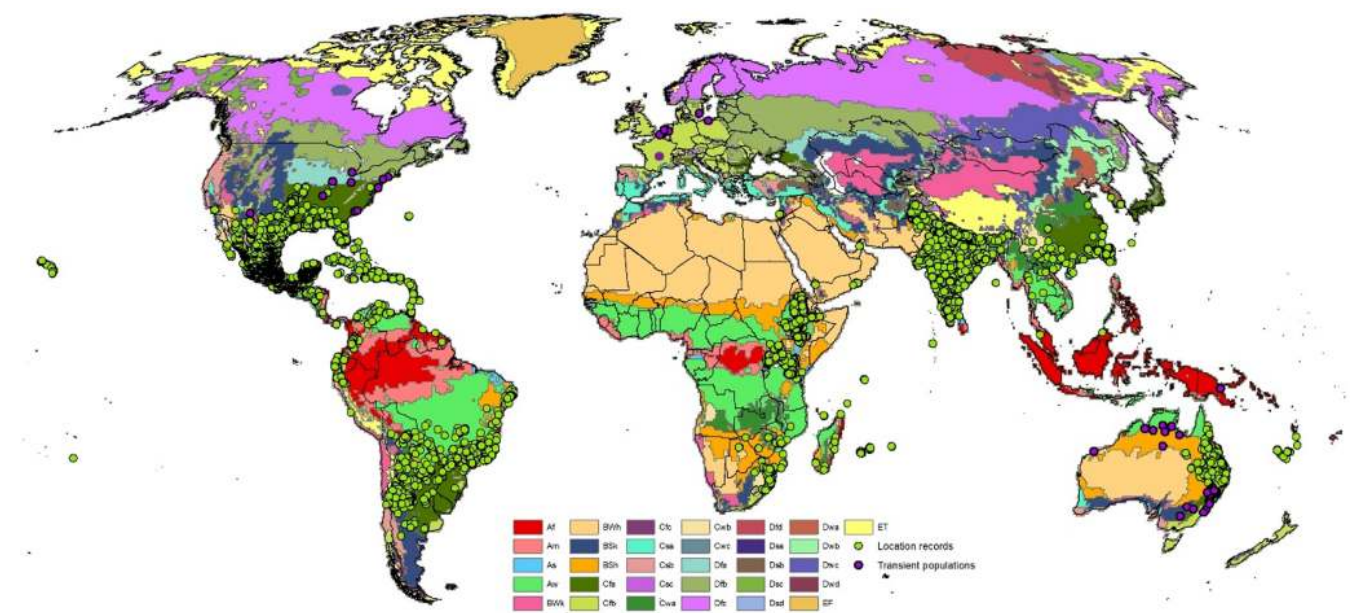


Figure A1. The known occurrence of *Parthenium hysterophorus* populations overlaid on climatic zones based on the Köppen-Geiger classification system. *Parthenium hysterophorus* is mainly found in subtropical and tropical regions of the world. Köppen-Geiger legends are explained in Table A1.