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Biology of Invasive Plants 6. *Iris pseudacorus* L. (Iridaceae)

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Scientific classification

Iris pseudacorus L. (Linnaeus, 1753) (Iridaceae)

Synonyms: *Acorus adulterinus* Ludw., *Iris acoriformis* Boreau, *Iris acoroides* Spach, *Iris bastardii* Boreau, *Iris curtopetala* Redouté, *Iris flava* Tornab., *Iris lutea* Ludw., *Iris pallidior* Hill, *Iris paludosa* Pers., *Iris palustris* Gaterau, *Iris pseudacorus* var. *longifolia* DC., *Iris pseudacorus* subsp. *acoriformis* (Boreau) K. Richt., *Iris pseudacorus* subsp. *bastardii* (Boreau) K. Richt., *Iris sativa* Mill., *Limnirion pseudacorus* (L.) Opiz, *Limniris pseudacorus* (L.) Fuss, *Moraea candolleana* Spreng., *Pseudo-iris palustris* Medik., *Vieusseuxia iridioides* Redouté, *Xiphion acoroides* (Spach) Alef., *Xiphion pseudacorus* (L.) Schrank, *Xyridion acoroideum* (Spach) Klatt, *Xyridion pseudacorus* (L.) Klatt.

Name and taxonomy

Kingdom: Plantae

Phylum: Magnoliophyta

Class: Angiospermae

Order: Asparagales

Family: Iridaceae

Subfamily: Iridoideae

Genus: Iris

Species: *Iris pseudacorus* L. (IRIPS)

Among the plethora of common names used to identify *Iris pseudacorus,* the most common ones are yellow iris, yellow flag, yellow flag iris, pale-yellow iris, water iris and water flag. In other languages, the species is referred to as iris de marais, iris faux-acore, iris jaune (France); giaggiolo acquatico, iris palustre (Italy); lirio amarillio, falso acoro (Spain); gele lis (Netherlands); and sumpf-schwertlilie (Germany).

Iris pseudacorus belongs to the genus *Iris*, within the family Iridaceae (Wilson 2006). This is among the largest families of the order Asparagales, including over 2,000 species divided among 65 to 75 genera (Goldblatt et al. 2008). Virtually worldwide in distribution, the family has a marked diversity (ca. 63% of species) in sub-Saharan Africa, in contrast to Eurasia and North Africa (ca. 19%), the Americas (ca. 16%) and Australasia (ca. 2%) (Goldblatt 2000).

The genus *Iris* is taxonomically difficult. Conflicting classifications based on anatomical and morphological characters do not reflect the evolutionary relationships illuminated in recent molecular studies, highlighting the need for further consideration (Wheeler and Wilson 2014; Boltenkov et al. 2020).

The name of the genus *Iris* (from Ancient Greek Ιρις = rainbow) refers to the wide variety of flower colours found among its species (Manning and Goldblatt 2008). The specific epithet *pseudacorus* (from Ancient Greek ψευδής = false) refers to the similarity of its leaves to those of *Acorus calamus* (Acoraceae), another common wetland plant species.

Iris includes approximately 260 species, widely distributed in temperate regions across the Northern Hemisphere (Wilson 2011). Although some species are found in mesic and even wetland environments, most occur in arid, semi-arid or dry habitats. The genus has long been subdivided into six subgenera based on morphological characters such as underground organs and sepal beards (Wilson 2006). However, recent phylogenetic analyses based on chloroplast data showed the subgeneric classification to be more complex (Wilson 2011). *Iris pseudacorus* is currently positioned within the subgenus *Limniris* (Wilson 2011) which includes a clade of species with an affinity for wetland habitats. Also positioned within the subgenus *Limniris* is *I. foetidissima* L., a close relative of *I. pseudacorus*, which is reported to be invasive in New Zealand (Howell 2008).

Importance

Negative impacts

Iris pseudacorus readily becomes established and colonises new habitats due to its very prolific nature (Alpert et al. 2000; Silvertown 2008) and the presumed absence of specialised natural enemies in its introduced range (Gervazoni et al. 2021; Sandenbergh 2021). After establishment, *I. pseudacorus* becomes aggressively invasive in natural, urban, and agricultural wetland ecosystems (Gervazoni et al. 2020), where its fast-growing and fast-spreading nature allows it to cause substantial impacts on biodiversity and ecosystem functioning at local and landscape scales (Thomas 1980; Stone 2009; USDA 2013; Global Invasive Species Database 2022).

In natural areas, *I. pseudacorus* can invade and dominate a variety of vegetation types, reducing native plant and animal diversity and altering successional trajectories (Tu 2003). For instance, in the United States, *I. pseudacorus* has completely excluded native marsh vegetation such as *Typha* spp. (Poaceae) (Raven and Thomas 1970), and other marsh plants such as *Carex* spp., *Schoenoplectus acutus* (Muhl. ex J.M.Bigelow) Á.Löve and D.Löve (both Cyperaceae) and *Equisetum fluviatile* L. (Equisetaceae) (Stone 2009). This impact also includes threatened native irises, such as *I. brevicaulis* (Raf.), *I. verna* (L.) and *I. hexagona* (Walter) (Weatherbee et al. 1998; USDA 2013; Mopper et al. 2016), as well as *Peltandra virginica* (L.) Schott (Araceae), whose fruits are an important food source for wood ducks (*Aix sponsa* L.) during the nesting season (Cox 1999). Furthermore, the resulting transformation in riparian vegetation structure has been linked to habitat reduction for several important salmon species (King County Noxious Weed Control Program 2020).

In a recent study, *I. pseudacorus* invasion was shown to disrupt the composition and function of native plant communities across brackish estuarine gradients in North America (Gallego-Tévar et al. 2022). At a local scale, this species forms tall, dense, monospecific stands that overshadow smaller native plants. *Iris pseudacorus* was found to greatly reduce plant richness and diversity in California at local and watershed scales, while native populations in Andalusia, Spain, were associated with high plant species richness, evenness and diversity in similar tidal wetlands (Gallego-Tévar et al. 2022). In Japan, the density of *I. pseudacorus* infestations was linked to a significant decrease in the number of native plant species, and a concomitant increase in the number of invasives (Hayasaka et al. 2018). Similarly, invasive *I. pseudacorus* populations in China have been associated with the displacement of indigenous plant assemblages and a decline in native wetland biodiversity (Xiong et al. 2023). Furthermore, the attractiveness of *I. pseudacorus* flowers has been hypothesised as a cause for reduction in pollination frequency of native flowering species, such as the North American orchid *Galearis spectabilis* (L.) Raf. (Dieringer 1982).

Although *I. pseudacorus* invasions reduce the diversity of native vegetation and the associated biota, including invertebrates, fish, and waterfowl (Preece 1964; Thomas 1980; Noxious Weed Control Program 2009; Stone 2009; Hayasaka et al. 2018; Jacobs et al. 2011; USDA 2013; Global Invasive Species Database 2022; Xiong et al. 2023), knowledge of the effect of this weed on invertebrate assemblages and biotic interactions remains largely unknown.

From a landscape perspective, once a founding population has been established in a shoreline, plant rhizomes retain sediment and organic matter, affecting the hydrology, functioning, and structure of large wetland ecosystems. In this sense, *I. pseudacorus* can be considered an ecosystem engineer, like North American beavers (*Castor canadensis* (Castoridae)) in Southern Patagonian wetlands (Henn et al. 2016; Huertas Herrera et al. 2020; Sonntag 2021).

The intricate rhizome mat compacts soil and elevates topography, creating a drier habitat type with increased rates of siltation and sedimentation (Tu 2003). This creates a positive feedback loop, preventing the germination and seedling growth of other native plant species while improving habitat suitability for *I. pseudacorus* (Sutherland 1990; Tu 2003; Thomas 1980; Morgan et al. 2020). In Montana, USA, *I. pseudacorus* was shown to reduce stream width by up to 25 cm annually by trapping sediment and creating new streambanks dominated by iris seedlings (King County Noxious Weed Control Program 2020). Other observations show that, by preventing the germination and seedling recruitment of characteristic plant species such as willows (*Salix* spp. (Salicaeae)), and providing a raised substrate for the seed bed, *I. pseudacorus* contributes to the conversion of riparian marshes into swamps and mesic forests dominated by *Fraxinus* spp. (Oleaceae) (Thomas 1980; Tu 2003).

Dense *I. pseudacorus* infestations are known to clog small streams, irrigation systems, and flood control structures, often leading to increased flooding (Preece 1964; Stone 2009; USDA 2013; Van Slooten 2016; King County Noxious Weed Control Program 2020). Ecosystem processes and services provided by native aquatic and riparian vegetation can also be detrimentally altered by invasion (USDA 2013). By decreasing stream width, promoting sedimentation, and preventing access to water, *I. pseudacorus* infestations can restrict agricultural, recreational, and fishing activities, having adverse effects on the tourism industry (Wildland Consultants 2011).

Iris pseudacorus has been considered poisonous due to glycoside concentrations found within its tissues (Forsyth 1976), and has been reported as unpalatable or even poisonous to livestock (Bossuyt et al. 2005; Stone 2009). The glycoside concentrations found within *I. pseudacorus* tissue can act as a skin irritant, causing severe dermatitis (Crocker 1906; Fuller and McClintock 1986; Williams and Champion 2008), with effects varying between plant populations. In the UK, gastroenteritis occurred after livestock consumed *I. pseudacorus* leaves, and acute diarrhoea occurred in domestic cattle after rhizome consumption (Sutherland 1990 and references therein). Conversely, extensive grazing of *I. pseudacorus* by wild horses, cattle, sheep, and goats has been documented during field research in Spain and France (Grewell et al. 2023) and deer herbivory has recently been observed in California. However, careful consideration should be given before using cattle grazing as a control method due to the plant’s toxicity.

In natural wetlands of the introduced range, protected areas are of major concern as they contribute to biodiversity conservation, especially in Afrotropical and Neotropical ecozones, which support substantial areas of macrophyte diversity and endemism around the world (Chambers et al. 2008; Murphy et al. 2019, 2020). A recent study in Argentinian wetlands shows that 15 protected areas are invaded by *I. pseudacorus*, of which four have international conservation status (Gervazoni et al. 2020). The invasion of this species in Argentina also represents a threat to the artificial rice wetlands that cover large areas of land in the north-eastern region of the country. This is especially relevant considering that *I. pseudacorus* has previously been reported as a weed of this crop in other countries (Rahimi et al. 2011). Despite the impact of *I. pseudacorus* invasion being evident at both local and landscape scales, studies that investigate the socio-economic costs of *I. pseudacorus* invasions in natural and human-modified wetland ecosystems are scarce (Zilio et al., 2023).

Positive attributes

Iris pseudacorus has showy flowers and is easy to grow, making it a popular ornamental plant for ponds and water bodies in its native and introduced ranges (Hayasaka et al. 2018). Aside from its primary horticultural value, *I. pseudacorus* is also considered a potential candidate for phytoremediation in constructed wetlands, eutrophic water systems, and urban wastewaters (Ansola and De Luis 1994; Zhang et al. 2007; Larue et al. 2010; Zhou et al. 2010; Yousefi and Mohseni-Bandpei 2010; Zhao et al. 2015; Wu et al. 2013), although risk of escape from treatment wetlands is a concern. This species is reported to reduce the concentrations of heavy metals (Branković et al. 2015), organic chemicals (Larue et al. 2010), insecticides (Wang et al. 2013), and bacterial loads (Sutherland 1990; Jacobs et al. 2011) in these systems. It is also a suitable plant for use in erosion control, and for phyto-stabilisation of contaminated soils in its native range (Tu 2003; Pérez-Sirvent et al. 2017). In the introduced range, the use of *I. pseudacorus* for phytoremediation should be avoided as other weeds take advantage of nutrient-rich conditions, making them difficult to control biologically, as has been the case with water hyacinth (Coetzee and Hill 2012).

Several aquatic plants are used in attempts to prevent recurrence of diseases, with extraction of natural products used as alternative medicine and/or drug precursors for the pharmaceutical industry (Mandal and Mondal 2011; Bharthi et al. 2015; Tulika and Mala 2015). *Iris pseudacorus* is not an exception, and its rhizomes are used in India as a part of Ayurveda, a system of traditional medicine, due to the diuretic properties and the effect of preventing the recurrence of urinary calculi (Ahmed et al. 2017; Sharma et al. 2022). In the past, there have been several recreational and/or medicinal uses for *I. pseudacorus*. Sutherland (1990) reports the plant being smoked during World War II. In Turkey, rhizomes are used as a diuretic, to prevent gas, and to treat eczema, whilst roasted seeds are used as a substitute for coffee (Stone 2009), and minced rhizomes are mixed with couscous in a popular dish in northern Africa (IUCN 2012). However, adverse effects on human health have also been reported, including gastric distress after ingestion and irritation when sap is contacted with the skin (Noxious Weed Control Program 2009).

Description, identification, and diagnostic characteristics

Iris pseudacorus is an emergent aquatic macrophyte, ~ 0.5–2.17 m in height (Chambers et al. 2008). Although *I. pseudacorus* is a perennial species, under unfavourable growing conditions, plants may retain leaves in addition to retaining their roots and rhizome material (Campbell et al. 2010; Lui et al. 2010). When in bloom, *I. pseudacorus* is easy to distinguish by the shape and colour of the flowers (Goodridge et al. 2011). The flowers flutter like flags in the breeze, explaining the common name. Flowers are yellow, radially symmetrical, with a perianth with two different looking whorls, the external broadly ovate tepals and internal spatulate ones. The style has three yellow petaloid stylar blades, arched over the external tepals (Figure 1A-D).

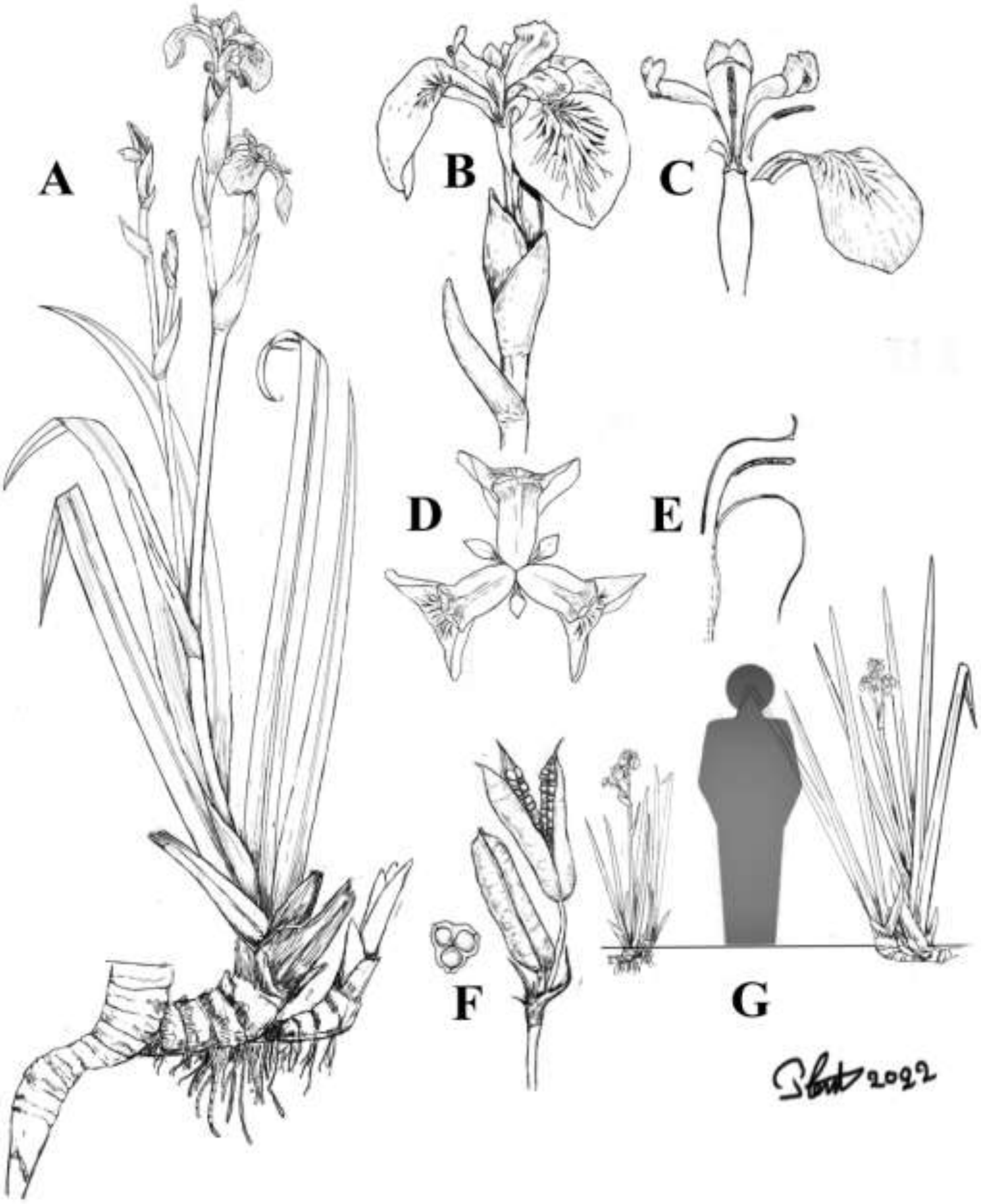

Figure 1: Morphology of *Iris pseudacorus* L. (Iridaceae) and its reproductive structures. A: *Iris pseudacorus* general structure, B-E: details of the flowers, F: detail of the fruit, G: plant size

When not in bloom, it can be difficult to distinguish *I. pseudacorus* from other similar iris species or cultivars (Lui et al. 2010; Sarver et al. 2008). *Iris pseudacorus* has a rhizome rather than a bulb or root tuber characteristic of some irises, it lacks beard or crest ornamentation on its sepals like many irises, it does not have arial outgrowths covering its seeds, and it has a thick, pronounced midrib. The fruits and the numerous thick, fleshy pink rhizomes are also important for differentiation and identification (Noxious Weed Control Program 2009; Campbell et al. 2010).

Distribution

The native range of *I. pseudacorus* extends from northern Africa throughout Europe, western Asia, and parts of the Middle East (Sutherland 1990; Figure 2). While the threat status of native European *I. pseudacorus* is currently Least Concern on the International Union for Conservation of Nature (IUCN) Red List of threatened species (Flora Europaea 2022), the species is a protected endangered species in Finland’s Oulu and Lapland provinces (Nature Conservation Decree 1997).

Due to its ornamental attributes, the plant has been introduced to every continent except Antarctica, and is now considered naturalised or invasive in parts of Canada, the United States, Argentina, Chile, Uruguay, South Africa, Australia, New Zealand, China, Japan, and the Korean peninsula (USDA 2013; POWO 2022), and it is also present in Mexico and Zimbabwe (Naturalista 2022; Hyde et al. 2022). While the recorded distribution of *I. pseudacorus* is expansive, due to limited data and mapping capacities, the true distribution of the species is likely far greater.

Iris pseudacorus is reported as present across much of the United States (Stoneburner et al. 2021), though invasions are most prevalent in east and west coast states, and the Great Lakes region (GBIF 2022). The plant is also recorded in eight Canadian provinces, noticeably along the border with the USA (USDA 2013; Figure 2A), and a single verified record of *I. pseudacorus* was found in Mexico (Naturalista 2022). The species has been observed in eight provinces in Argentina, with the majority of records concentrated in the Buenos Aires and Córdoba provinces (Gervazoni et al. 2020; Figure 2B). *Iris pseudacorus* is also present in the coastal region of Uruguay (Masciadri et al. 2010) and is listed among the alien flora of Chile (Ugarte et al. 2011) (Figure 2B).

Iris pseudacorus is listed as a cultivated plant in Zimbabwe, with records of infestations in public parks (Hyde et al. 2022). In South Africa, *I. pseudacorus* is present in eight of the country’s nine provinces, with the majority of infestation reports coming from Johannesburg and Cape Town, two of the country’s major cities (Jaca 2013; NEMBA 2014; Jaca and Mkhize 2015; Sandenbergh et al. 2024; Figure 2C). Australian *I. pseudacorus* infestations are confined to Tasmania and the south-east region of the country (AVH 2022;

Figure 2D). In New Zealand, *I. pseudacorus* has been recorded as an environmental weed in numerous wetlands across the country (Howell 2008) (Figure 2D). The species has been recorded in the Korean Peninsula (Chang et al. 2014), in Japan (Kadono 2004), and in China, where it has successfully established across 26 provinces, autonomous regions, and municipalities (Xiong et al. 2023) (Figure 2E).

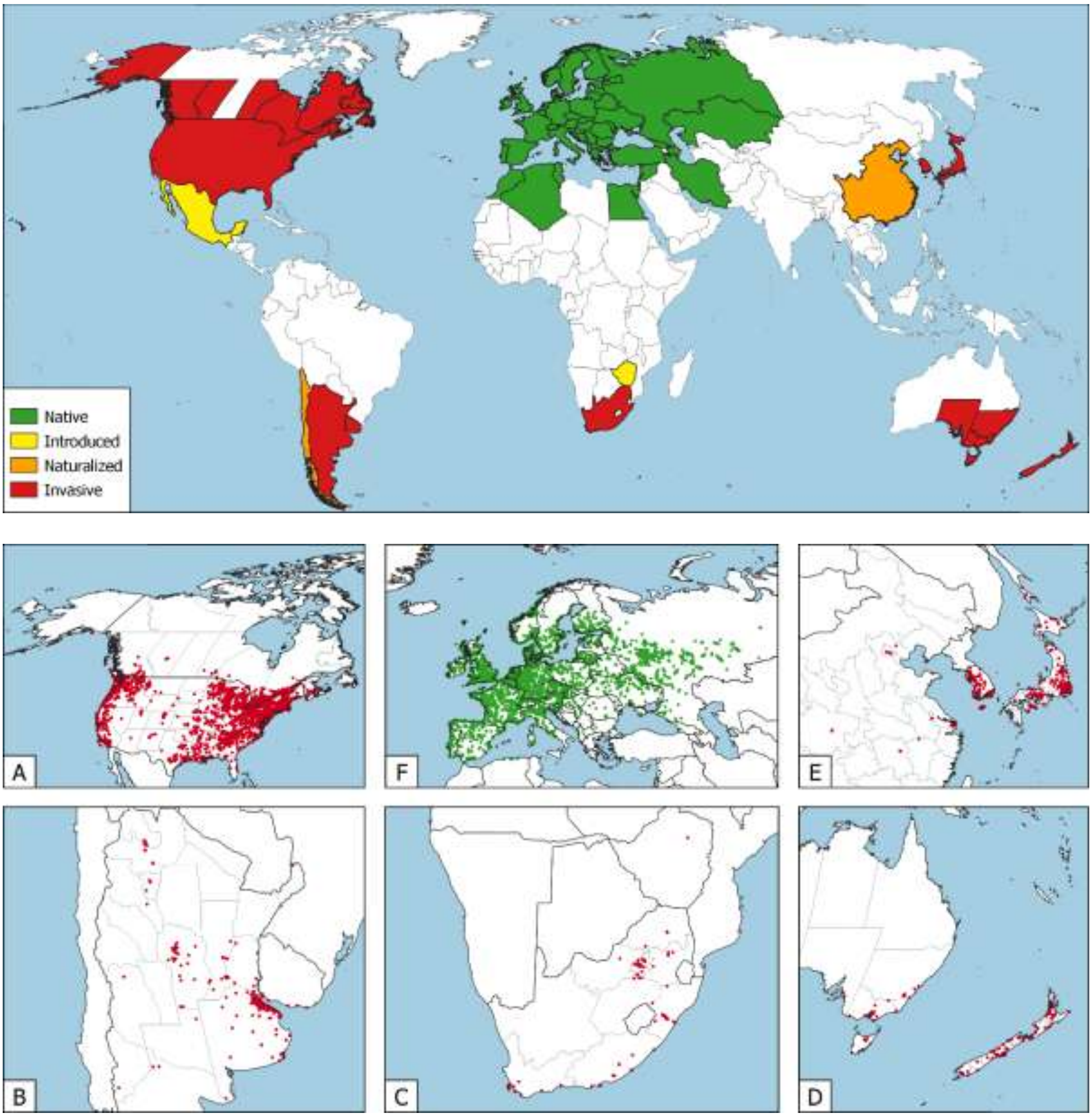

Figure 2: Worldwide distribution of *Iris pseudacorus.* Top: political map of regions where *I. pseudacorus* is reported to occur (invasion status inferred from literature, see text for details). Bottom: Introduced (A-E, red) and native (F, green) range records for *I. pseudacorus* downloaded from GBIF (GBIF 2022).

Invasion risk

A potential distribution model of *I. pseudacorus* was developed in order to identify areas with climatic suitability for this species and to prioritise areas at risk of invasion. The model was developed with the software Maxent 3.4.1 (Phillips et al. 2017) (see methods detailed in Appendix), which has been shown to be efficient in handling presence-only data (Elith et al. 2010; Elith et al. 2011).

The model showed areas at high risk of invasion by *I. pseudacorus* across different continents, both in the northern and southern hemispheres (Figure 3). In the northern hemisphere, in addition to the climatic suitability across Europe (native range), Asia, the eastern regions of China and Japan also show a high probability of the plant thriving. In North America, areas in the northeastern United States, mainly around the Great Lakes and parts of the southeast such as Georgia and South Carolina, show high suitability as well. On the other hand, areas with moderate suitability are predicted on the west coast of the United States, particularly in California. Regarding the southern hemisphere, in South America, some areas in southern Brazil and northeastern Argentina have moderate to highly suitable conditions for the establishment of the species. Moderate to highly suitable regions are also observed in South Africa, New Zealand and southeast of Australia (Figure 3).

The invasion risk of *I. pseudacorus* has been studied previously not only by determining its current climatic suitability and potential distribution (Minuti et al. 2022), but also by studying its future distribution (2040 - 2060), taking into account several climate change scenarios (Minuti et al. 2023). According to that study, in North America and eastern Asia, the potential distribution of the plant is expected to increase and shift northwards, but in the southern hemisphere on the other hand (South America, southern Africa, and Australasia), the future distribution is predicted to reduce in response to climate change (Minuti et al. 2023).

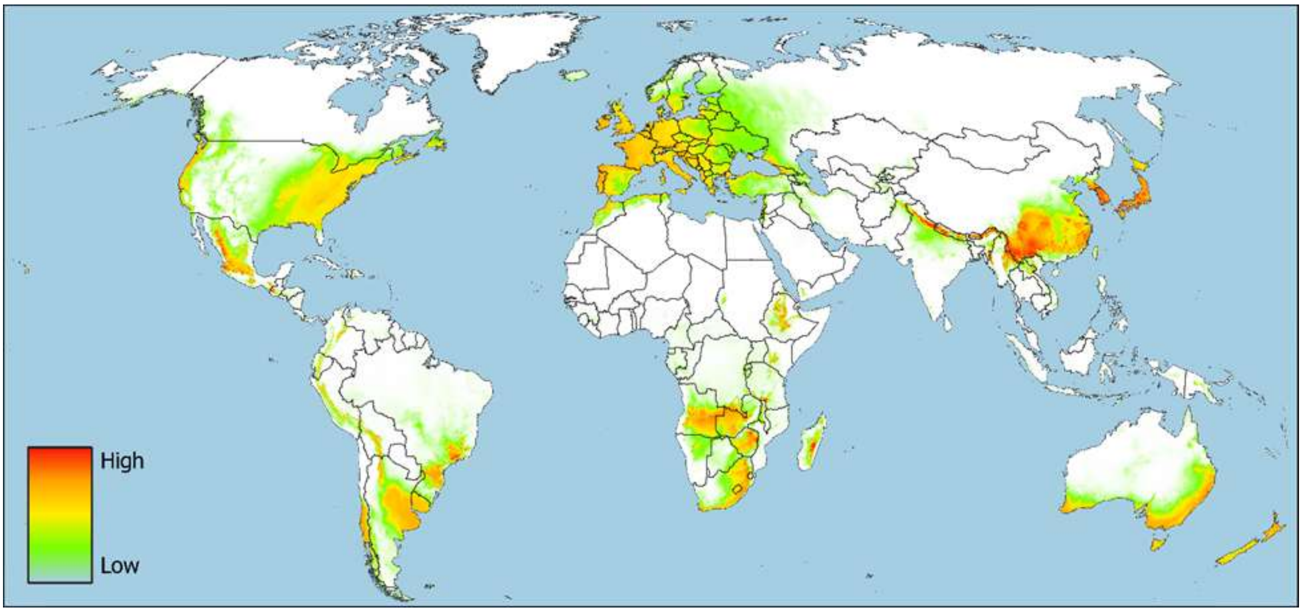

Figure 3: Global climatic suitability for *Iris pseudacorus* computed in MaxEnt (see methods in the Appendix)

Invasion pathways

Yellow-flag iris is an aesthetically pleasing plant given its beautiful yellow flowers and has been widely planted as a garden plant. This high ornamental value of *I. pseudacorus* is, unfortunately, one of the primary invasion pathways allowing this plant to spread anthropically across continents and large regions and scaping cultivation (Cody 1961; Jaca & Mkhize 2015; USDA-APHIS 2013). Likewise, the use of this plant for its phytoremedial properties constitutes another anthropic factor that induces the introduction of this plant to new sites (Edivianі et al. 2018; Mohsinet al. 2023).

The exchange of specimens for gardens together with their use for water purification allowed *I. pseudacorus* to have an extensive human-mediated distribution. For instance, in Argentina, a citizen science study demonstrated its association with urban centres, where the trade and sale of specimens and seeds in nurseries, and even on online platforms, significantly increase their populations (Gervazoni et al. 2021).

Natural means of dispersal of this species include the production and release of propagules (seeds and rhizomes fragments) to water currents. The buoyant seeds of *I. pseudacorus* can remain viable over a long period (even up to two years), floating in the water and consequently arriving at new distant sites, promoting new invasions (Coops and Van Der Velde 1995, Gaskin et al. 2016), which allow the species to spread over long distances, particularly when associated with flowing lotic water bodies (Ramey and Peichel

2001). Additionally, human modifications of freshwater ecosystems through hydraulic structures (such as embankments, dams, dikes, and causeways) can facilitate the spread of aquatic invasive species like *I. pseudacorus* (Thomson et al. 2021).

Habitat

Climate

Iris pseudacorus occurs across a wide variety of climatic and environmental conditions (Figure 4). In its native range, according to the Köppen-Geiger climate types (Beck et al. 2018), it occupies mostly humid temperate (Cfa), oceanic (Cfb) and continental (Dfa, Dfb) climates, but it is also present, albeit less common, in semi-arid (BSk) and Mediterranean (Csa, Csb) areas. The species is absent from the Alps and the Pyrenees, but in its northernmost distribution, it is observed within boreal climates (Dfc). The climates occupied by the species outside of its native range vary depending on the region of introduction. In North America, *I. pseudacorus* is most abundant across the continental (Dfa, Dfb) and humid temperate (Cfa) climates of the east coast, but is also observed within the semi-arid (BSk) and Mediterranean (Csa, Csb) climates of western United States (Figure 4A). In South America, most invaded are the humid subtropical (Cwa, Cwb, Cfa) and oceanic (Cfb) climates of the Argentinian pampa and coastal Uruguay (Figure 4B). A similar scenario is observed in South Africa, where a high representation of humid subtropical and subtropical highland (Cfa, Cwa, Cwb) and Mediterranean (Csb) climates occur. Additionally, the temperate oceanic (Cfb) climate zone is well represented in the invaded South African range (Figure 4C). In Australasia, *I. pseudacorus* has invaded the oceanic climates (Cfb) of New Zealand and south eastern Australia, with a slight expansion towards semi-arid (BSk) and Mediterranean (Csa, Csb) regions (Figure 4D). Finally, in eastern Asia the plant is found mostly across the humid temperate (Cfa) climates of eastern China and southern Japan and the continental climates (Dfa, Dfb, Dwa) of northern Japan and the Korean peninsula (Figure 4E). This species is most common from sea level up to 300 m altitude above sea level (ASL), but has been recorded at elevations over 1000 m ASL (Sutherland 1990). In its invaded South African range, it occurs in the elevated interior, well above 1200 m ASL.

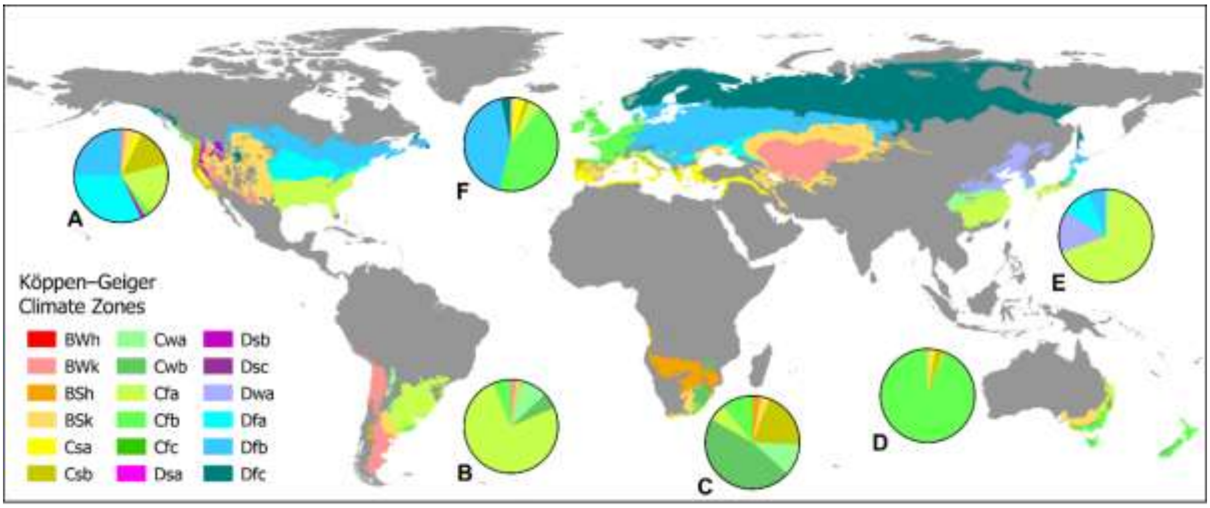

Figure 4: Köppen-Geiger climate zones occupied by *Iris pseudacorus* worldwide. The map was created based on *I. pseudacorus* distribution and the climate classification provided by Beck et al. (2018). Pie charts represent the relative density of occurrence points within each range (A: North America; B: South America; C: South Africa; D: Australasia; E: Eastern Asia; F: Europe).

Land use associations

Iris pseudacorus occurs in habitats associated with water. It is found on the banks of lakes, rivers, in wetlands like ponds, streams, swamps and marshes, but also in woodlands, open woods and forest edges where the soil is moist or regularly flooded (Sutherland 1990; Stone 2009). Being disturbance-adapted and commonly planted as an ornamental, it often occurs in human-modified habitats such as meadows, wet pastures, roadside ditches, irrigation channels, artificial wetlands, and gardens (Stone 2009).

Soil types

Iris pseudacorus usually grows in sites with high soil-water content, although it does not require constant submersion and can tolerate extended periods of drought (Sutherland 1990; Jacobs et al. 2010a). This species is commonly found on water-deposited substrates such as silt, sand, gravel, and cobbles, and is associated with calcareous, sandy loams, clay loams and other soils derived from sandstone and schist (Sutherland 1990; Mulqueen and Gleeson 1988; Stone 2009). *Iris pseudacorus* occurs in fens and fen woodland, but is less frequent in areas of chalk (Sutherland 1990). It can colonise a variety of soil types ranging from shingle, peat soils, permanently submerged organic and inorganic matter on gravel or sand, to orthodox gleys and shell hash (Sutherland 1990; Gerwing et al. 2021). It persists in the higher zones of saltmarshes and can tolerate soil acidity (at 0-30 mm depth) from pH 3.6 to 7.7 (Sutherland

1990). Being a nitrophile, it prefers high nutrient soils and grows well in eutrophic conditions (Sutherland 1990; Tu 2003; Stone 2009).

Invasion history

Early occurrence records (17th – 19th century) of *I. pseudacorus* are scant, and are mainly limited to herbaria records from Great Britain and France (GBIF 2021). The species has been introduced from the Palearctic ecozone into many areas worldwide, including the Neotropics, Afrotropics, Nearctic, Indomalaya, and Australasia regions. Its distribution area in the introduced range has been increasing over time and now comprises at least 13 countries (Howell 2008; Masciadri et al. 2010; USDA-APHIS 2013; GBIF 2021) (Figure 5).

Northern hemisphere

Available records indicate that *I. pseudacorus* was documented outside its native range for the first time in the Nearctic ecozone. These introductions, prior to 1800, were intentional introductions as an ornamental pond plant to the United States (Wells and Brown 2000; Champion et al. 2022; Natural History Museum (London) 2014). While gardens are believed to be the most frequent source of introductions, *I. pseudacorus* was included on a list of ballast water plants documented in New York and Philadelphia harbours (Torrey Botanical Club 1888), suggesting ship ballast water is a likely introduction source elsewhere.

The oldest report in this region corresponds to 1771, being cultivated in Virginia, United States (Wells and Brown 2000). By 1800 it was noted in records of vascular plants introduced in low forest habitat along the upper Potomac tidal river at Mount Vernon Virginia (Wells and Brown 2000). By the 1860s, *I. pseudacorus* had escaped cultivation and had established along the Potomac, Delaware, and the Hudson River Valley in New York. It was naturalised at Lake Ontario in the Great Lakes Region in 1886, and by 1900, herbaria records place it in the Chesapeake Bay Estuary. A voucher specimen collected in 1911 was reported as having escaped from household gardens in Newfoundland, Canada, and subsequently spread rapidly to swamps and other moist habitats, forming extensive stands (Fernald 1950; Cody 1961). The species was well naturalised in southern Nova Scotia by at least 1915 (Fernald 1921; Roland 1945).

Written records and herbarium specimens suggest the North American invasion of *I. pseudacorus* was a result of multiple independent introductions. It was established in far western Canadian wetlands in British Columbia in 1931 prior to the earliest documented occurrences in eastern and central Canada at Prince Edward Island (1939), Ontario (1940), Quebec (1943), and Manitoba (1953), but invasive spread was most rapid in Ontario (Cody 1961). Invasions were also underway in the Pacific Northwest and California by 1948, and it was well established in the Merced River watershed and the San Francisco Bay region (California Academy of Sciences and California Department of Food and Agriculture herbaria databases), but the first naturalised records in Montana were from the late 1950s (Preece 1964). By the 1960s, *I. pseudacorus* was abundant in Canadian wetlands and in many regions of the United States (Hitchcock 1969; Raven and Thomas 1970), and it has now invaded eight Canadian provinces and 48 of 50 states in the United States (Stoneburner et al. 2021). In 1890, *I. pseudacorus* was first reported as introduced in a new Palearctic area, Japan, where it was introduced and cultivated intentionally for ornamental purposes (Kadono 2004).

Southern hemisphere

In the Australasian ecozone, *I. pseudacorus* was reported growing wild in New Zealand for the first time in Lower Hutt in 1938 (Te Waihora Co-Governance 2019), and in Australia by 1945, according to herbarium specimens (AVH 2022). In New Zealand, it has since spread to many other parts of the country with dense, severe infestations occurring on the lower Avon River in Christchurch and in particular the lower Waikato River catchment (Maw 2010; Wildland Consultants 2011). *Iris pseudacorus* was first recorded in the Waikato region in January 1990 at Lake Hakanoa, Huntly, and this is believed to be the source population of the current infestation along the lower Waikato River catchment (Champion et al. 1993). Aerial surveys conducted along the Waikato River showed that up to 50 km of riverbank and river island shoreline contained *I. pseudacorus* (Wildland Consultants 2011). High seed production levels and nitrogen runoff from pastures into the Waikato River are suggested to have exacerbated the spread of *I. pseudacorus* within the Waikato region (Wildland Consultants 2011; McGrannachan and Barton 2019). Because of its threat to native biodiversity and natural ecosystems, *I. pseudacorus* has been classified as an unwanted organism in New Zealand under the Biosecurity Act (1993). It is also prohibited from being sold and distributed in New Zealand due to its listing as a National Plant Pest Accord Species (McGrannachan and Barton 2019).

The first record of *I. pseudacorus* in the Neotropics was made in 1931, when it was documented in Buenos Aires, Argentina (Gervazoni et al. 2020; Global Invasive Species Database 2022). Distribution studies have shown that after its introduction, the number of invaded localities increased significantly over the years (Gervazoni et al. 2020). However, the general status of the invasion in the country was unknown until recent years (Gervazoni et al. 2020). After the first report in Buenos Aires, *I. pseudacorus* was reported in 1964 in the northwest of Argentina, in Jujuy province. Currently, *I. pseudacorus* is present across at least eight provinces, throughout a diversity of habitats, ecoregions, water condition and latitudes (Gervazoni et al. 2020). In Argentina, it is catalogued as an alien invasive species (Kalesnik and Malvárez 2004) and is currently a Restricted Species with mandatory control, under the Conservation of Biodiversity Program (Ministry of Environment and Sustainable Development of Argentina 2022). The species is also reported on the coastal region of Uruguay, in the cities of Montevideo, Maldonado, Rocha, and San José where it is considered invasive (InBUy 2011).

The first naturalised population of this plant in the Afrotropics was reported in 2004 in South Africa, where it was growing along the Vaal River in the Gauteng Province (Jaca and Mkhize 2015; Sandenbergh et al. 2024). While the weed’s invasion in South Africa is still in the “lag” phase (Blackburn et al. 2011), the number of *I. pseudacorus* infestation records has increased substantially since it was first recorded. About a decade after the first report, Jaca and Mkhize (2015) reported 23 new infestations in South Africa. The number of records of *I. pseudacorus* in South Africa continues to increase rapidly, with a recent study reporting more than 110 confirmed localities in all provinces except the arid Northern Cape (Sandenbergh et al. 2024). *Iris pseudacorus* has been categorised as a 1A invader under the National Environmental Management: Biodiversity Act, listing it as an eradication target (Jaca and Mkhize 2015).

The wide dispersion of *I. pseudacorus* over the introduced range shows a great adaptability in this species to invade under a wide range of environmental conditions, which is alarming due to the profound modification it produces in invaded ecosystems and the economic damage it causes. Due to the scarcity of ecological studies of *I. pseudacorus* in the Southern Hemisphere, a global south collaboration alliance was initiated to study its distribution and ecology, and to develop appropriate management strategies (Gervazoni et al. 2020).

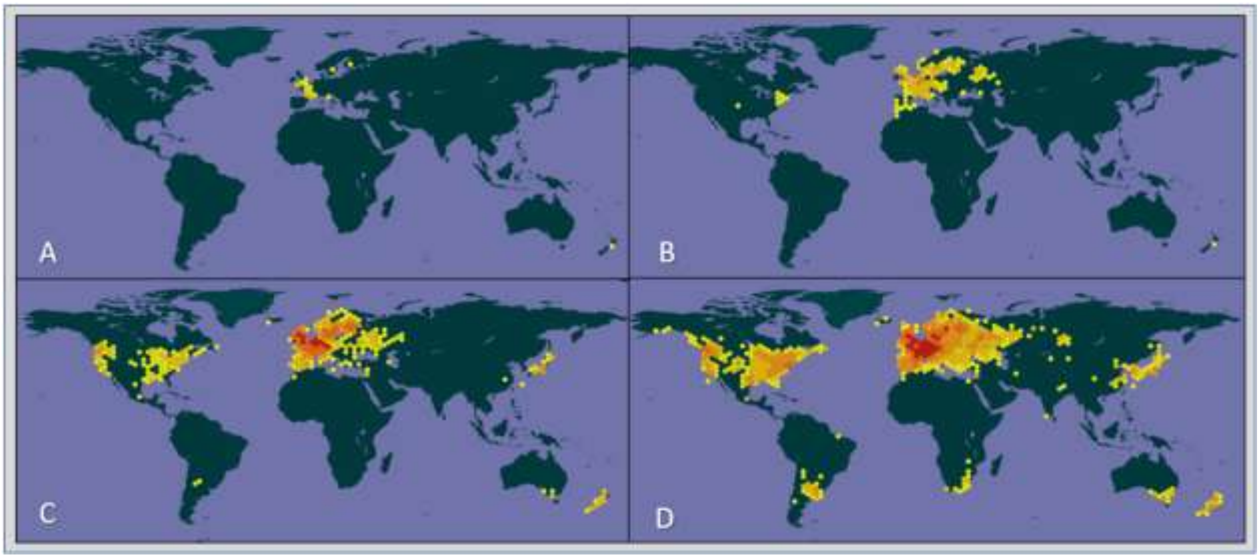

Figure 5: Records of occurrence of *Iris pseudacorus* in the Global Biodiversity Information Facility (GBIF) platform. Although this open database does not provide all existing records of *Iris pseudacorus*, it allows for the visualisation of the increase over time in its geographic distribution (GBIF 2022). A: 1600 – 1800, B: 1900, C: 2000, D: 2022. The shading of the dots represents the number of occurrence records, with darker (red) shading indicating many records and lighter (yellow) shading indicating fewer records.

Life-form and life history

Iris pseudacorus is categorised as a telmatophyte or helophyte according to the Raunkiaer system (Raunkiaer 1934) as it is a perennial plant that almost always has its rhizomes and resting buds under the waterline. Nonetheless, the plant can remain in dry soil for long periods (Sutherland 1990; Jacobs et al. 2010a). Leaves have aerenchyma and they are always above the waterline. *Iris pseudacorus* typically occurs on high grounds on the shore and wetlands because seeds and seedlings require exposed soil conditions (Coops and Van der Velde 1995).

Iris pseudacorus individuals take two (Authors unpublished data) to three years (Tyron 2006) to mature before flowering, but this can vary as a result of different growing conditions. Flowers typically bloom from April to July in the Northern Hemisphere (Good 1986; Lui et al. 2010; Sutherland 1990) though the timing varies among climate zones and hydrological settings. Bloom time is from September to December in the Southern Hemisphere (Sandenbergh 2022; Gervazoni 2024).

After the reproductive period, depending on climatic and environmental conditions, the plant may remain green over winter (Noxious Weed Control Program 2009). Above and below-ground biomass increases seasonally, with the highest values of above ground biomass in summer and negligible in winter (Larue et al. 2010). The seasonal accumulation of storage materials in the below-ground organs of the plant result in the rhizomes forming a series of annual segments or ‘bulges’, providing a record of the plant’s growth history (Sutherland 1990; Rakhimov et al. 2006). The plant biomass of *I. pseudacorus* in the native range was estimated at 7-8 tonnes ha^{-1} (Falińska 1986; Sutherland 1990), which is lower than the biomass produced by other coexisting emergent aquatic macrophytes (Neiff 1990).

Dispersal and establishment

Propagules of *I. pseudacorus* are produced both sexually and asexually, through the fragmentation of rhizomes and the production of seeds (Sutherland 1990; Lamote et al. 2002; Gaskin et al. 2016). Clonal reproduction by rhizome was initially considered the primary mode of spread for *I. pseudacorus* (Barrett 2015). Rhizome fragments are adapted for hydrochory, and are often spread downstream after flooding events (Sutherland 1990), and it was observed that rhizome fragments of 2 cm can develop into a new plant (Jaca 2013). However, when reproducing sexually, *I. pseudacorus* populations produce a vast number of highly buoyant seeds, adapted to dispersal by water (Coops and Van der Velde 1995; van den Broek et al. 2005), and studies carried out both in the native and introduced range compared populations of *I. pseudacorus*, found genetic divergence between them, indicating that the propagation and spread of this species are predominantly a result of sexual reproduction (Lamote et al. 2002; Gaskin et al. 2016; Gallego-Tévar et al. 2024; Sandenbergh 2021).

The relative employment of each reproductive strategy appears to be context-specific, and the data so far suggest that introduced *I. pseudacorus* populations employ sexual reproductive strategies to a greater degree than native *I. pseudacorus* populations (Lamote et al. 2002; Gaskin et al. 2016). However, Gallego-Tévar et al. (2024) found higher genetic diversity in the native (Spain) range than was the case for the invaded (California) range.

In tidal wetlands, floating wrack mats comprised of senescent plant debris and live plant propagules are significant vectors of macrophyte seed dispersal into wetlands (Huiskes et al. 1995). Tide-transported wrack mats are often deposited at high elevation tide strandlines where *I. pseudacorus* regularly occurs, and seed burial by wrack mats can limit seedling recruitment of macrophytes. Castillo et al. (2023) found *I. pseudacorus* seedling recruitment can be limited by up to 8 cm depth of seed burial by wrack, but quiescent seeds persist in the seed bank which can germinate and emerge in disturbance-generated gaps, or as wrack decomposes.

Due to its high ornamental value, anthropogenic dispersal also plays an important role in facilitating the spread of *I. pseudacorus*. Propagules are often exchanged by horticulturalists and sold in nurseries and online, allowing for long-distance dispersal of propagules into novel environments, aggravating the risk of new establishments and subsequent invasions (Raghu and Morin 2017; Mercado Libre 2022). In South Africa, for example, the species was promoted for use in the trout farm industry, as well as for phytoremediation and the prevention of soil erosion, further promoting its dispersal and establishment (Sandenbergh et al. 2024; Authors pers. obs.). ‘Escaping’ cultivation has been reported as a main pathway of the establishment and subsequent invasion of *I. pseudacorus* (Morgan et al. 2020; Minuti et al. 2021; Sandenbergh et al. 2024).

Once dispersed, *I. pseudacorus* propagules, being disturbance-adapted, can take advantage of undesirable conditions in novel environments. Disturbance favours *I. pseudacorus* establishment, with fire and flooding events aiding their dispersal and establishment (Stone 2009). Anthropogenic disturbances such as eutrophication, habitat modification, and management activities can further promote the establishment of *I. pseudacorus* (Sutherland 1990; Stone 2009). Such events and the subsequent knock-on effects (i.e., indirect consequences) they have on plant communities can decrease the biotic resistance of the community while increasing resource availability, creating favourable conditions for *I. pseudacorus* establishment (Tu 2003; Stone 2009). Contrarily, soil drainage and pasture improvement have been observed to hinder the spread of the invasion (Sutherland 1990).

Growth and development

Morphology

There are several diagnostic characteristics which describe the morphology of *I. pseudacorus*. In North America, identification can be confirmed in the reproductive stage, as *I. pseudacorus* is the only iris with completely yellow flowers naturalised in wet environments away from gardens (Henderson 2002; Goodridge et al. 2011). Taxonomic descriptions from published floras vary slightly in size ranges of specific characters based on specimens from local regions, but descriptions for this species, particularly for floral and other reproductive traits, are comparable for identification in the native and invaded range (Tutin et al. 1980; Sutherland 1990; Henderson 2002; Stone 2009; Klinkenberg 2010; Lui et al. 2010; Flora Europea 2022; NatureGate 2022; World Flora Organization 2022). Descriptions that follow reflect cross-reference among published descriptions.

Iris pseudacorus is an emergent aquatic angiosperm from the rhizomatous, beardless subgenera *Limniris* sect. *Limniris* (Wilson 2006). Above ground, the plant typically ranges in height from 0.5 – 1.5 m tall (Figure 1G). However, overall height of *I. pseudacorus* can vary considerably across environmental gradients, including in the native range, and has been observed to reach up to 2.17 m when growing in light-limited conditions inside forests (Gervazoni 2024). It produces a simple erect stem that is solid, and often has one branch. The erect flattened green leaves, up to 10 per ramet, with a dominant raised midrib and parallel veins are primarily basal, linear to lanceolate; they emerge from the soil surface in a fan-shape arrangement, are typically 2-4 cm wide and 40 cm – 1.5 m long and sword-shaped with pointed tips and may be downward-curved near the top (Sutherland 1990; Negrut et al. 2018).

The plant has bisexual pale to bright yellow flowers (8-10 cm diameter; flowers larger than 10 cm across are reported in Finland) (NatureGate 2022). They are radially symmetrical, actinomorphic, and grouped as an inflorescence. The cyme-like inflorescences may each include 4-12 (often 5-10) flowers partially enclosed by inner and outer green spathes (bracts) with brown margins, the outer being strongly keeled and the inner is unkeeled. There are 4–12 flowers per inflorescence which are arranged on round erect 2-5 cm long peduncles (stalks) that are often branched (Figure 1 A-D). The flowers have six clawed, yellow perianth segments that include two different whorls, including three large lanceolate to ovate or suborbiculate downward-spreading sepals (petal-looking) and three smaller erect upward petals that are narrowed in their midsection. External tepals are 40-80 by 20-45 mm, with a broadly ovate blade, sharply attenuated at the base and recurved, bright yellow in colour, and short radiating brownish lines. Internal tepals are 10-30 by 3-8 mm, erect, yellow, spatulate to oblanceolate, obtuse, and shorter than stigmatic blades (Lui et al. 2010). The showiest parts of the flower are the external tepals and the petaloid styles (Figure 1B).

The inferior ovary is 12-20 mm long, triangular in cross-section with concave sides; pedicel is 3-5 cm long. There are 3 keeled styles and 3 stigmas per flower. The style is filiform ending in 3 petal-like yellow branches arched over the external tepals, and a small rounded stigma with a prominent tongue on the underside (Figure 1E). The 3 stamens are hidden under the 3 style branches (Figure 1C). Floral tubes are 6-8 cm long with no constriction to the ovary. Each large yellow sepal has a darker yellow basal signal patch and short brown to purple lines or flecks that serve as pollinator nectar guides. Fruit type is a capsule (seed pod), prismatic to oblong-ovoid, 2.5–8.5 cm long with a 5 mm beak, and most often described as 3-angled with obvious groove at each angle (but see WFO and Gleason and Cronquist 1991 for reports of 6-angled). Developing capsules are yellow-green to green in colour, and can be dull to glossy in appearance, becoming dark brown and dehiscent when mature and the capsule splits to release seeds (Figure 1F). Each locule of the capsule contains rows of smooth flattened, disk-shaped (6-7 mm), lustrous corky seeds. When mature, the capsule splits and releases seeds which disperse directly into or near shallow water. Seeds have a hard seed coat enclosing a gas space, enhancing their buoyancy in water and dispersal by hydrochory. Chromosome numbers reported are 2n=24, 30, 32, 34 (Dyer et al. 1976; Choi et al. 2020; Henderson 2002).

Below the surface, *I. pseudacorus* can produce a woody crown below the leaf base, from which dense, freely branching pink rhizomes (1-5 cm in diameter) form extensive clumps that can protrude at the surface and are often exposed by erosion. White adventitious roots can form above the soil at the base of the leaves (Sutherland 1990; Jacobs et al. 2010a; Yu et al. 2022). Fleshy roots (10-30 cm long) extend into the soil (Sutherland 1990) (Figure 1A). Belowground biomass, comprising rhizomes and roots, may represent over 99% of the total biomass, which is evidence for the resilience and the ability of this weed to compete for space and resources (Sutherland 1990; Mopper et al. 2016; Minuti et al. 2021). Rhizomes make up most of the belowground biomass, with roots representing just over 39% (Larue et al. 2010).

Stress tolerance

Iris pseudacorus is an obligate wetland species that is often observed at the water's edge of inland lakes, rivers, canals, dry wetland soil suggesting a degree of tolerance to the water level fluctuation. The species can tolerate water with low levels of oxygen and can survive under anoxic conditions for extended periods of time (up to and exceeding eight weeks) (Hetherington et al. 1982; Mulqueen and Gleeson 1988; Sutherland 1990; Hunter et al. 2001). Anoxia in plants like *Iris pseudacorus* typically occurs due to environmental conditions such as prolonged waterlogging, total submergence, or ice-encasement. However, *Iris pseudacorus* stores its carbohydrate reserves in the form of fructans, primarily within its rhizomes (Schlüter and Crawford 2001), and rhizomes and roots exposed to inundation have aerenchymous tissue that provides an adaptation to low oxygen conditions in flooded environments (Yu et al. 2022). Reserves in below ground tissues may also allow the plants to survive extended drought (Fitter and Hay 2012). Greater allocation of biomass to below ground structures than shoots could also provide some degree of protection to prevent juvenile plants from being washed away in high flows (Whitehead 1971; Sutherland 1990).

Deep water can prevent seed germination (Lenssen et al 1998) and limit growth of seedlings (Coops and van der Velde 1995) which explains its common occurrence in shallow water or wet soils. However, in New Zealand, the plant has occupied water depths from 0 to 0.8 m (Tanner et al. 1990), and in Montana, it was found in water depths up to 1 m (Preece 1964).

Iris pseudacorus tolerates coastal habitats, including tidal freshwater, brackish (Dutton and Thomas 1991; Strong and Kelloff 1994, Grewell et al. 2021) and salt marshes (reviews by Sutherland 1990; Tu 2003). Sutherland and Walton (1990) observed that *I. pseudacorus* in high elevation Irish tidal wetlands had more and longer leaves and high rhizome terminal bud survival compared to plants in low elevation sites where frequency and depth of tidal inundation were higher.

Global warming and associated sea level rise have raised questions about the physiological tolerances of invasive *I. pseudacorus* in estuarine wetlands in the naturalised range (Gerwing et al. 2021; Grewell et al. 2021). Grewell et al. (2021) conducted greenhouse experiments to evaluate the response of pre-reproductive *I. pseudacorus* populations (the colonising life stage) from the San Francisco Bay Delta Estuary to increasing salinity, inundation and their interaction. Growth, biomass allocation, and morphological, physiological and biochemical traits were evaluated in response to freshwater to marine salinity levels. Results indicated that *I. pseudacorus* populations at the colonising life stage were highly vulnerable to increasing salinity, even at 17 ppt brackish concentration. While the species showed tolerance to inundation, increasing salinity limited its capacity to acclimate to greater inundation. Experimental results from the greenhouse study with California populations inform risk assessments in light of climate change and suggest efforts to control invasive estuarine populations should prioritise freshwater tidal habitat since successful growth and spread is best supported in these areas (Grewell et al. 2021). However, dense populations of *I. pseudacorus* have been observed in marine wetlands of the Punta Lara Reserve in Argentina (Authors pers. obs.) suggesting possible genotypic variation in salinity tolerance among invaded ranges.

Phenology and reproduction

The timing of phenological development and life stage transitions of *I. pseudacorus* can be expected to vary widely given climate and other environmental conditions across the broad extant range from 68 °N – 28 °S latitude, and with differences in altitude (sea level to 1315 m: Welsh et al. 1987), climate, and hydrological regimes that all play a role. Even so, there are many common aspects regarding the life history of the species.

The perennial life cycle of a newly establishing *I. pseudacorus* plant begins with the germination of a seed or the sprouting of an established rhizome fragment. Riverine and other wetland types occupied by *I. pseudacorus* are subjected to regular disturbance regimes (e.g., flooding, bank erosion, etc) that create gaps which promote the rapid colonisation of systems by *I. pseudacorus* (Pyšek and Prach 1993; Barrat-Segretain and Bornette 2000; Grewell et al. 2019).

Water-dispersed seeds are often deposited along high-water lines where they are most likely to germinate and establish as seedlings (Tu 2003). During the seedling stage, inundation reduces *I. pseudacorus* seedling growth, but seedlings recover soon after (Coops and van der Velde 1995; Lenssen et al. 1999). Thomas (1980) found that *I. pseudacorus* plants experiencing short inundation had higher growth than plants with long inundation on the Potomac River near Washington DC, while in Montana, Preece (1964) observed more vigorous growth in *I. pseudacorus* growing in 1 m deep water than plants that were not inundated.

For established perennial stands, new seasonal growth of *I. pseudacorus* commences with resprouting from rhizome bud banks or new emergence from seedbank during the early spring season (Jacobs et al. 2010b; Fitter and Hay 2012). Annual rhizome growth continues through each growing season typically until branching begins after flowering (Jacobs et al. 2010b). Sutherland (1990) studied the species in Ireland, and reports that when rhizomes reach about 10 years in age, they fragment and disperse via hydrochory to form new clones. However, in the native range, many stands are observed to persist and flower for 30-40 years with continued incremental growth (Whitehead 1971), and some extant naturalised population patches in the invasive California range have been present for at least 50 years (Authors pers. obs.; Consortium of California Herbaria 2022). While genetic studies reveal the primary dispersal and colonisation is from seeds (Gaskin et al. 2016), local spread by radially spreading clones produces dense stands that displace resident vegetation (Preece 1964; Thomas 1980; Falińska 1986).

During pre-reproductive growth, the plants also store carbohydrates in roots, leaf bases, and pre-flowering shoot tissues (Sutherland 1990; Grewell et al. 2021). Seasonal leaf growth proceeds from the leaf base-rhizome interface. However, in most temperate and colder areas, leaves die back seasonally. *Iris pseudacorus* plants remain in a pre-reproductive life stage through their early years of colonisation while there is significant investment of resources towards below ground growth and carbon reserves (Sutherland 1990; Jacobs et al. 2010a).

Following emergence of fan-shaped leaf clusters, mature plants begin to flower. Like all other life stage transitions, timing of flowering each year is dependent on local climate and hydrologic conditions. In areas with mild winter climates, leaf growth from rhizomes can occur all year (Jacobs et al. 2011). Pollination begins during flowering, with capsules expanding and filling with seeds. The seeds then mature and disperse, completing the plants' seasonal life cycle.

Floral biology

Sexual reproduction in *I. pseudacorus* occurs by obligate outcrossing (Fryxell 1957) and, like many other species in the same genus, flowers are adapted for large pollinators. The nectar produced by the flower is situated outside the whorl of stamens (Sutherland 1990). When insects visit the flowers, they pass between the stamens and outer tepals, making contact with petaloid stigmas and stamens depending on the insect size and the flower morph: bombophila and syrphophyla (Sutherland 1990). In the bombophila flower, the petaloid stylar branches are situated 6-10 mm above the corresponding outer perianth segment and are pollinated by bumble bees large enough to enter in contact with stamens and stigma (Figure 1 A, B). In the syrphophyla morph, the petaloid stylar branches are situated close to the outer perianth segment, thus much smaller insects, such as syrphid flies, act as effective pollinators (Good 1986).

Among the floral visitors of this species, bees (Hymenoptera) and long-tongued flies (Diptera), are the most frequently mentioned (Sutherland 1990; McGrannachan and Barton 2019). Observations made in the native range included mainly bumblebees of the genus *Bombus*, as well as *Apis mellifera* L. (Apidae) and *Osmia rufa* L. (Megachilidae) bees. Syrphid flies including *Rhingia campestris*, *Episyrphus balteatus* and *Eristalis sp*. were also included, as were the scathophagids *Scatophaga stercoraria*, the Hepialidae moth *Hepialus humuli* and the Noctuidae moths *Apamea monoglypha*, N*octua pronuba*, *Ochropleura plecta*, and *Apamea crenata* (Good 1986). In the introduced range, the pollinators associated with *I. pseudacorus* include *Bombus* bumblebees, *A. mellifera* bees, the soldier flies *Hedriodiscus pulchur* Wiedemann (Stratyomidae), and some coleopteran species, including the coccinellid predator *Eriopis connexa* Germar (Stone 2009).

Seed production

In the native range, an average of five capsules per plant has been documented by Sutherland (1990), along with a mean seed production per capsule that varied between 32 and 46 at different sites. Additionally, Coops and Van Der Velde (1995) reported a mean of 47 seeds per reproductive stem. In the Afrotropics (South Africa), a mean of 7.9 flowers and 2 seed capsules were produced per reproductive stem, with 42.5 (± 1.9) seeds produced per seed capsule, resulting in 773.5 seeds produced per m^2 (Sandenbergh et al. 2024). In the neotropical invaded range (Argentina), preliminary results show an average of 3.44 flowers and 4.32 capsules per stem, and a seed production of 65.54 (± 32.71) seeds produced per capsule (Gervazoni et al. unpublished).

These results show an increased production of flowers, capsules, and seeds per capsule for *I. pseudacorus* in the introduced range. Enhanced reproductive potential for this species in Argentina and South Africa could be explained by different hypotheses, including the more effective use of resources by invasive species in the introduced range as a result of 'escaping' predation by the natural enemies with which they have coevolved (Keane and Crawley 2002; Liu et al. 2006; Puliafico et al. 2008).

Seed banks

Iris pseudacorus forms soil seed banks, but longevity of these below ground banks is uncertain, likely varies with environmental conditions, and may be impacted by global environmental changes. Sutherland (1990) did not observe seedlings in most native habitats visited, but it is possible that conditions during the short period of observation were not sufficient for seeds to break dormancy and emerge. In France, *I. pseudacorus* was abundant in a wet meadow, but was absent from the soil seed bank (Vecrin et al. 2007), while in the Netherlands, *I. pseudacorus* emerged from 25% of soil seed bank studies in an emergence assay, though the species was present in standing vegetation at 84% of sampled fens (van der Valk and Verhoeven 1988). In the invaded range, Leck et al. (2005) recorded seed bank emergence in freshwater tidal wetlands in Delaware, USA. Along Vancouver Island's Courtenay River in British Columbia, Canada, *I. pseudacorus* has formed "considerable viable seed banks" that continuously recruit thousands of emergent seedlings which have been targeted for removal by weed managers (Evergreen 2007).

Seed viability and germination

Iris pseudacorus allocates significant resources to seed production. Seed germination is a critical life stage that is often overlooked, but can be key to the spread of invasive plants (Gioria and Pyšek 2017). Contradictory accounts in the literature, typically reported in reviews or anecdotal accounts, have often not been supported with methodological details (see Gillard et al. 2022). For example, Baskin and Baskin (2014) claim the species has morphophysiological dormancy that requires cold stratification without scarification. However, Guppy (1912) reported that *I. pseudacorus* seeds from England did not present dormancy and germinate rapidly, though Suzuki and Yamagata (1980) achieved germination only after removing the seed cap or damaging the seed coat. Crocker (1906) documented 97% germination of seeds with caps removed within one month. A review by Sutherland (1990) suggests seeds from the Netherlands achieved 25% germination during 6 weeks in drained soil, while 40 – 48% germination was recorded for non-scarified seeds from Great Britain. Germination of *I. pseudacorus* is hypogeal and cryptocotylar (Authors unpublished). Vivipary has been observed in the field in California (Gillard et al. 2021), Argentina, and South Africa (Sandenbergh 2021; Gervazoni 2024), (Figure 6), whereby seeds have germinated inside of recently dehisced seed capsules, providing evidence that dormancy may not be required. Accordingly, in Argentina, a germination experiment showed that seeds with a cold pre-treatment for dormancy breaking, had a lower germination percentage than the control (Gervazoni et al. 2023; Gervazoni 2024).

The germinability of *I. pseudacorus* seeds has been tested by different authors in different regions under varying conditions. In the native range (Netherlands), germination of *I. pseudacorus* was assessed by Coops and van der Velde (1995) at 20-25 °C, with a photoperiod of 12L:12D and was reported as relatively low, with only around 25% of the tested seeds germinating. A more recent study conducted in Germany showed a germination percentage of 100% under alternating temperature conditions of 22/14 °C and 14 hours of light, although this percentage decreased to 19% under constant temperature conditions (22 °C) (Rosbakh et al. 2020).

In the invaded range, greenhouse experiments performed in California, USA, with an average temperature of 21.4 ± 5.1 °C, showed that, under freshwater conditions, approximately 96% of seed could germinate – a proportion which decreased with increased aqueous salinity (Gillard et al. 2021). Additional tests performed in the same region determined 28.2 ± 0.5 °C as optimal and 41.0 ± 1.7 °C as the maximum temperature at which germination could occur. The study showed that although fluctuating temperatures and light are a key factor to achieve high germination rates, seeds can also germinate in conditions of constant temperature, as well as in the dark (Gillard et al. 2022). Regarding other regions of the invaded range, Sandenbergh et al. (2024) also reported high germination rates (approximately 83% of germination with a cold pre-treatment) for seeds collected at different sites across South Africa. In Argentina, 60.56% of germination was obtained for seeds with the cold pre-treatment and 84.17% for the control group. Seed viability was assessed by Gaskin et al. (2016), who reported 99.1% seed viability of seeds from Montana, USA.

These results demonstrate that *I. pseudacorus* is a plant with a broad capacity for germination, being able to produce seedlings under different environmental conditions. Additional germination experiments are being conducted in the introduced (Argentina) and native (Belgium) range in order to achieve a more comprehensive dataset for the germination potential of *I. pseudacorus* (Authors unpublished).

Sexual reproduction can be expected to be increasingly more important as climate change drives changes in water levels that promote increased seed bank emergence from greater exposure of moist soil in wetlands. *Iris pseudacorus* seeds germinate best in moist soil, rather than water-logged soils (Thomas 1980; Coops and van der Velde 1995; Lenssen et al. 1998). Climate warming is altering cues that drive germination, prompting the need for a better understanding of how *I. pseudacorus* will respond to continuing environmental changes. Gillard et al. (2022) experimentally evaluated the effects of stratification, light, seed coat presence or absence, and constant vs. alternating temperatures on the germination of *I. pseudacorus* seeds from California, and used the results in a thermal time model. Prior exposure to cold or warmth was not a prerequisite for germination, seeds could germinate with or without their seed coat, and in light or dark conditions. The highest germination rates were achieved with exposure to diurnally fluctuating temperatures (Gillard et al. 2022). At high temperatures (36 °C), seeds from multiple study populations proved viable and germinated. Collectively, results reveal a broad capacity of *I. pseudacorus* for germination that will likely support continued invasiveness where environmental conditions are changing, including under higher temperatures predicted with global warming (Gillard et al. 2022).

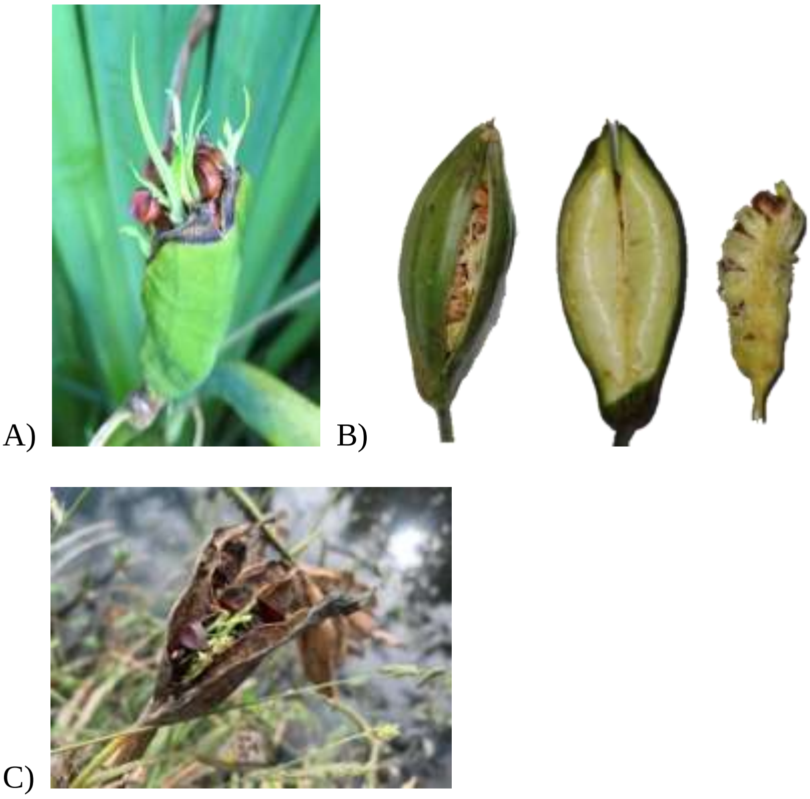

Figure 6: Vivipary in A: South African, B: Argentinian, and C: Californian *Iris pseudacorus* seed capsules (Photos: Emma Sandenbergh, Johannesburg, 2020; Paula Gervazoni, Misiones, 2023; Joy Futrell, Brannon Island, 2018).

Vegetative reproduction

Vegetative reproduction by *I. pseudacorus* occurs through the fragmentation of rhizomes, as detailed in ‘Dispersal and establishment’ and ‘Phenology and reproduction’.

Population dynamics

Population genetics

At present, the genetic and geographical origins of invasive *I. pseudacorus* populations are not known (Minuti et al. 2021), but a few studies regarding the population genetics of *I. pseudacorus* are available (Lamote et al. 2002; Gaskin et al. 2016; Gallego-Tévar et al. 2024). As an invasive aquatic plant, *I. pseudacorus* is expected to demonstrate low levels of genetic variation, as many aquatic invasive angiosperms primarily reproduce asexually. However, Lamote et al. (2002), Gaskin et al. (2016) and Gallego-Tévar et al. (2024) found populations of *I. pseudacorus* to be more genotypically diverse than previously anticipated, suggesting the species may employ sexual modes of reproduction to a much higher degree than was thought to be the case. While Lamote et al. (2002) observed distinct grouping patterns in Bulgarian *I. pseudacorus* populations as a result of geographic barriers, their results suggest that both sexual and asexual reproduction is occurring in each of the separate populations. Gaskin et al. (2016) report that *I. pseudacorus* populations in the northwest USA reproduce almost solely by seed, with 98% unique genotypes observed throughout the invasion, and Gallego-Tévar et al. (2024) report high rates of intra-population genetic variance within both native (Spain) and introduced (California) *I. pseudacorus* populations, with the former demonstrating higher levels of genetic diversity than the latter.

Similar results were found for South African *I. pseudacorus* populations, with ~ 98% unique genotypes observed and a high level of genetic diversity present between and within populations (Sandenbergh 2021). Population genetics studies are being conducted on *I. pseudacorus* populations in Argentina and New Zealand to elucidate aspects of the genetic composition and diversity of populations in other regions of the introduced range (Sandenbergh 2021). The results thus far are in agreement and suggest that *I. pseudacorus* spreads primarily through the production and dispersal of sexually produced seeds. As *I. pseudacorus* was formerly thought to reproduce predominantly by clonal rhizome fragmentation, these results provide important information for management and control organisations, whose efforts should be focused on preventing or reducing seed production in the field.

Patch composition and competition

Depending on the stage of invasion, in the introduced range, *I. pseudacorus* populations can occur as solitary plants, small patches, and large, monospecific stands. In the eastern USA with a long history of invasion, *I. pseudacorus* occurs in *Acer rubrum - Betula nigra - Fraxinus pennsylvanica* swamp forest associations; shrub-swamp communities with *Myrica gale*, *Rosa palustris,* and *Alnus serrulate*; association, natural and constructed freshwater marshes with *Leersia oryzoides*, *Pontederia cordata*, and *Typha* spp.; marshes and swamps with emergent macrophytes such as *Sagittaria australis* and *Carex* spp. and with trees typical in swamp forests (see review, Stone 2009). In West Virginia, southern U.S.A. it occurs in diverse fringed sedge table wetlands with mostly native *Carex* spp., *Scirpus* spp., and *Juncus* spp.; in regularly inundated floodplain and riparian sycamore-birch forests; and riverine wetlands with *Vallisneria americana-Potamogeton* spp. associations (Suiter and Evans 1999). In central and northern plains states, *I. pseudacorus* is reported to occur in monocultures or intermixed with *Salix interior - Typha latifolia* communities (Preece 1964 in Stone 2009). *I. pseudacorus* invasions in freshwater wetlands of California and Oregon impact native emergent *Typha latifolia*, *Sagittaria latifolia*, *Schoenoplectus* spp. communities. In tidal wetlands of North American Pacific estuaries, *I. pseudacorus* occurs with *Juncus balticus*, *Schoenoplectus acutus*, *Typha angustifolia*, *Oenanthe sarmentosa* and associates (Gallego-Tévar et al. 2022). Given the shorter history of invasion, there is very little information available regarding plant communities associated with *I. pseudacorus* in the Southern Hemisphere. However, it is known that *I. pseudacorus* often co-occurs with Typhaceae species, including *Typha latifolia* L. (in South Africa and Argentina), *Typha capensis* Rohrb. (in South Africa) and *Typha orientalis* Presl. (in New Zealand), as well as with species from the Cyperaceae and Pontederiaceae families, amongst others (McGrannachan and Barton 2019; Gervazoni 2024; authors pers. obs.).

Due to its ability to form dense rhizomatic mats which exclude co-occurring species, *I. pseudacorus* has been described as an aggressive competitor, capable of engineering ecosystems and drastically reducing native plant diversity (Thomas 1980; Lamote et al. 2002). Hayasaka et al. (2018) recorded richness of vascular plants in the presence of *I. pseudacorus* in Japan, finding a negative relationship between the cover of *I. pseudacorus* and species richness. The results showed a significantly lower number of other species when the coverage of *I. pseudacorus* was more than 50%. Displacement of native populations was also observed in New Zealand with *Typha orientalis* and *Carex sp.* (Authors pers. obs.), and in South Africa with *T. capensis* and *Pontederia cordata* (Sandenbergh 2021). In Argentina, sites with advanced stages of invasion have been reported, where the cover of *I. pseudacorus* can be observed up to the horizon, with pre-existing native vegetation having been displaced (Figure 7; Gervazoni et al. 2020; authors pers. obs.).

Figure 7: *Iris pseudacorus* invasion in Buenos Aires province, Argentina (Photo: Ana Faltlhauser)

Management options

Mechanical/physical control

Iris pseudacorus is often problematic to control by mechanical or manual means as the process is time intensive and laborious, and the plant's capacity for vegetative reproduction allows swift recovery (Tu 2003). This is particularly concerning in riparian habitats, as small fragments of rhizome can be dislodged and carried by moving water to establish new populations downstream (USDA-APHIS 2013). However, mechanical or manual methods are only effective for small infestations (Ramey 2001). Methods such as clipping or mowing the flower heads prior to seed production may help to reduce viable seed capacity and prevent cross-pollination, but do not kill the plant (Tu 2003; DiTomaso and Kyser 2016). Annual management of an invaded site by hand pulling, digging, and cutting can weaken and eventually kill targeted plants, but this process is both time- and labour-intensive, and requires repeated efforts over several years (Tu 2003). Benthic barriers such as rubber matting have proven effective against part-submerged populations, with rhizomes killed within 70 days and no detection of regrowth after 200 days (Tarasoff et al. 2016). Likewise, Tarasoff and Gillies (in review) found that cutting stems to the base of the plant and submerging them in 5 cm of water is sufficient to kill yellow flag iris rhizomes. This is consistent with Stoneburner (2021), who found that cattle trampling combined with inundation was an effective treatment to reduce the height and density of *I. pseudacorus.*

Chemical control

Chemical control methods are often used to manage invasive *I. pseudacorus* populations, and the herbicides glyphosate, imazapyr and metsulfuron have shown certain levels of effectiveness (Wildland Consultants 2011; DiTomaso and Kyser 2016; Global Invasive Species Database 2022). Glyphosate is commonly used in a 5 to 8 percent solution with a surfactant during late spring or early summer, to prevent seed development. During fall, a 2 to 8 percent solution has also been shown to be effective according to weed managers (Jacobs et al. 2011). DiTomaso and Kyser (2016) found that drizzle application of imazapyr gave significantly better control (99.2%) compared to glyphosate (86.6%) and was as effective as boom-sprayer treatments with both herbicides. However, non-target effects after herbicide applications are difficult to avoid, particularly in aquatic systems (DiTomaso and Kyser 2016), and as there is no species-specific herbicide registered against *I. pseudacorus*, it is likely that the herbicides used will also affect co-occurring indigenous plant species. These effects will depend on the herbicide used, rate of application, and the life form of the co-occurring indigenous plant species.

The financial costs associated with chemical control of *I. pseudacorus* can be substantial, with labour, time, equipment, and chemical costs all contributing to high expenditures. In New Zealand, chemical control costs (including labour and herbicide) of *I. pseudacorus* were estimated to be NZD$100 to $340 (± USD$60 to $210) per hectare for isolated patches, and more than NZD$1350 (± USD$830) when *I. pseudacorus* cover exceeds 40% (Wildland Consultants 2011).

Biological control

Iris pseudacorus has a wide distribution (GBIF 2022) with a broad ecological tolerance and a high competitive ability. Coupled with its ability to reproduce rapidly by both rhizome fragmentation and seed dispersal, these attributes make *I. pseudacorus* a challenging species to control mechanically and chemically. As such, biological control may be the most feasible option to manage and control *I. pseudacorus* infestations both effectively and sustainably. However, cooccurrence of a wide range of native and horticulturally valuable iris species may pose challenges to the adoption of a biological control programme.

The aim of any biological control programme is to identify and select potential agents based on the exploration of the weed's natural enemies in the native range, as well as to test the specificity of the enemy to its host, thus reducing environmental risks and associated economical costs (Briese 2004; van Klinken and Raghu 2006). The invertebrate fauna associated with *I. pseudacorus* in the native range was surveyed in several countries including Britain, Belgium, and Italy (Sutherland 1990; Minuti et al. 2021). Approximately 65% of the herbivore assemblages in the native range are represented by Coleoptera, whereas the remaining were species in the Hemiptera, Orthoptera, Lepidoptera, and Hymenoptera (Minuti et al. 2021). Almost all of these herbivore species are leaf miners and defoliators, while some are associated with flowers, fruits, and rhizomes (Sutherland 1990; Minuti et al. 2021).

The assessment of the prioritisation process considering geographic distribution of the insects, impact of the plant damage, and inferred host specificity, evidenced that most of the herbivorous insects of the assemblages were incidental visitors and polyphagous feeders, and hence considered unsuitable as potential biocontrol agents. Three herbivorous species, the flea beetle *Aphthona nonstriata* Goeze (Coleoptera: Chrysomelidae) (Figure 8A), the seed weevil *Mononychus punctumalbum* Herbst (Coleoptera: Curculionidae) (Figure 8B), and the the sawfly *Rhadinoceraea micans* Klug (Hymenoptera: Tenthredinidae) (Figure 8C), are being evaluated as potential biocontrol agents due to their unique association with species in the genus *Iris*, and their potential to cause relevant plant damage to *I. pseudacorus* (Minuti et al. 2021).

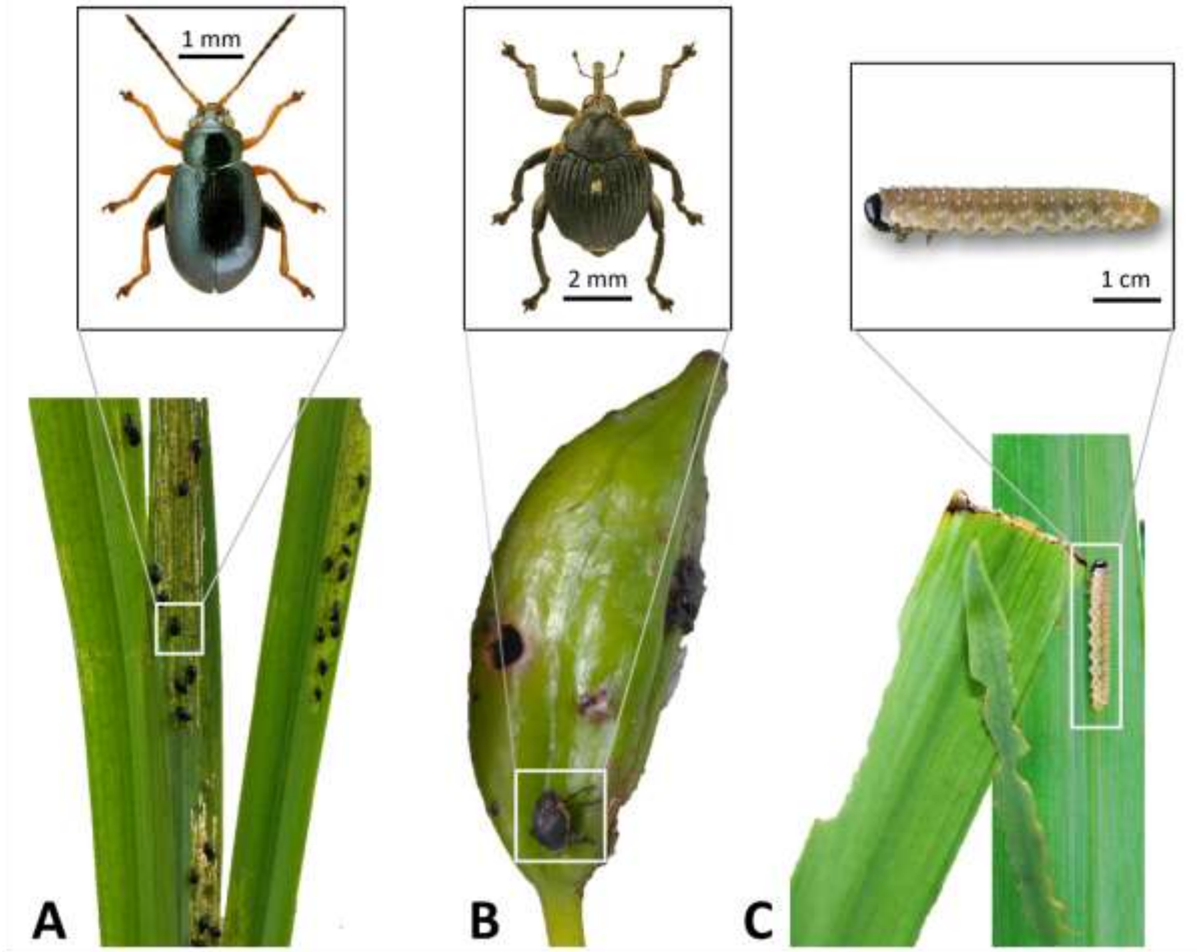

Figure 8: Representation of damage caused to *Iris pseudacorus* by three potential biological control agents. A: *Aphthona nonstriata* (Coleoptera: Chrysomelidae); B: *Mononychus punctumalbum* (Coleoptera: Curculionidae), and C: *Rhadinoceraea micans* larvae (Hymenoptera: Tenthredinidae).

Larvae of the sawfly *R. micans* are highly damaging and can completely defoliate their host. This species is considered an interesting option for release in big wetland areas of Argentina invaded by *I. pseudacorus* (Minuti et al. 2021) due to its highly specific oviposition preference on the host plant. Their larvae are believed to sequester and store secondary plant metabolites which could be an effective defence against generalist predators, as well as the strongly hydrophobic cuticle which allows them to move on the water's surface to reach new plants (Voigt et al. 2011; Boevé et al. 2013). The occurrence of this species is associated with temperate and cold areas (GBIF 2021a), which could limit its establishment in subtropical wetland areas of the introduced range where *I. pseudacorus* has a considerable level of invasion (Gervazoni et al. 2020).

The weevil *M. punctumalbum* is an interesting candidate due to intensive feeding by the adults on flowers and fruit, and because the larvae bore the seeds pupating within the mature fruit (Minuti et al. 2021; Sutherland 1990). Because *I. pseudacorus* has high seed production, viability, and dispersion rates, this candidate could be effective in limiting the spread and colonisation of new habitats. However, considering its current distribution in the native range (GBIF 2022), its establishment could be limited mainly to temperate and cold habitats (GBIF 2021b).

The flea beetle, *A. nonstriata*, is a common and abundant insect species in its native range (Minuti et al. 2021), and its occurrence is linked to a range of climates and habitats (GBIF 2021c). Adults feed on leaves and overwinter among leaf litter, whereas larvae are stem borers which feed on the rhizome. Currently, a quarantine population of *A. nonstriata* is under evaluation in South Africa and preliminary results indicate that rearing is feasible to be conducted under controlled conditions, and that larvae cause significant damage to rhizomes and roots (Minuti et al. 2021). A recent study predicts the highest climatic suitability for *A. nonstriata* across north-east Argentina, Uruguay, southern Brazil, southern South Africa, south-east Australia, and New Zealand. Therefore, these wetland areas should be prioritised when releasing *A. nonstriata* to allow for the establishment of the flea beetle, and to allow for the agent to perform optimally (Minuti et al. 2022).

Preliminary surveys of the insect fauna associated with *I. pseudacorus* in Argentina and South Africa show that invertebrate assemblages include insects belonging to a range of orders, including the Hemiptera, Coleoptera, Diptera, Dermaptera, Hymenoptera, Orthoptera, Lepidoptera, Blattodea, Psocoptera, Thysanoptera and Ephemeroptera (Gervazoni et al. 2021; Gervazoni 2024). Currently, the candidate agents from the native range have not been found in field surveys in Argentina, South Africa and New Zealand, and the presence of native analogue species is under evaluation (Gervazoni et al. 2021; Gervazoni et al. 2022; Gervazoni 2024). Preliminary assessment of herbivory in Argentinian wetlands shows that, occasionally, flowers have feeding spots on tepals that could be attributed to weevils. Generalist ants may occasionally damage margins of the tepals and other flower structures. No significant damage has been recorded in the rhizome and roots in the introduced range (Authors unpublished). Fruits and seeds present consistent damage by borer insects, but taxonomical identification and their inferred host range are under evaluation (Gervazoni et al. 2022; Gervazoni 2024). Damage to leaves could be frequent in populations of some wetland areas of Argentina, but the percentage damage is low with no significant impact to the foliage (Franceschini et al. unpublished).

It is important to understand the full implications of current management options for *I. pseudacorus* on the aquatic ecosystems it invades, and what that means for the sustainability and provision of freshwater ecosystem services. The aim of biocontrol against invasive macrophytes is to diminish invasive populations and restore access to clear freshwater dominated by native biodiversity, but in the absence of addressing the drivers of these invasions, aquatic systems are highly susceptible to secondary invasion by submerged and emergent exotic aquatic plant species.

General outlook

Iris pseudacorus is an invasive macrophyte that is difficult to manage in affected ecosystems. The risk of introductions to new areas is high given its horticultural value particularly in the wetland/aquatic landscaping field, e.g., golf courses and trout farms. To minimise the impacts of new *I. pseudacorus* invasions, prevention of continued introduction and early warning will be the most effective strategy through public awareness campaigns in vulnerable regions. As invasions continue to spread, research must focus on understanding the mechanisms facilitating new invasions, and on devising successful integrated management strategies that address those mechanisms. Recent studies highlighting the efficacy of the potential biocontrol agent, *A. nonstriata*, reducing seedling establishment are promising because the main pathway of spread is through seed dispersal and seedling establishment (Minuti, unpublished data). Further suppression of seed production could be realised through the release of the seed feeding weevil, *M. punctumalbum*, but the potential non-target effects on *Iris* species in the horticultural industry will have to be weighed carefully as this weevil is an *Iris* specialist. Such strategies must also address ecosystem-level responses to control, to improve the chances of long-term success. Traditionally, intervention has been aimed at restoring invaded ecosystems by removing the invader and relying on natural restoration processes. However, when restoration is considered in the context of regime shifts between degraded stable states, there is a clear need to adopt an all-inclusive approach focused on active restoration. It is important, therefore, to consider the effects that invasive species such as *I. pseudacorus* have upon the multitrophic interactions that define ecosystem structure and functioning, which could elucidate the drivers that determine levels of success and failure in the establishment of this species.

Finally, an effective weed management plan for *I. pseudacorus* should include the collaboration of all social actors, the scientific community, citizens, and governments, considering activities of environmental education, training for the economic sector related to gardening, landscaping, and nursery as well the generation of law and regulations that aim to prohibit its commercialization and avoid new areas of invasion.

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Competing interests

The authors declare no competing interests in undertaking this work.

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***Iris pseudacorus* at a glance…**

Impacts:

- Rhizomes form impenetrable mats
- Displaces native vegetation
- Changes to hydrology

Dispersal:

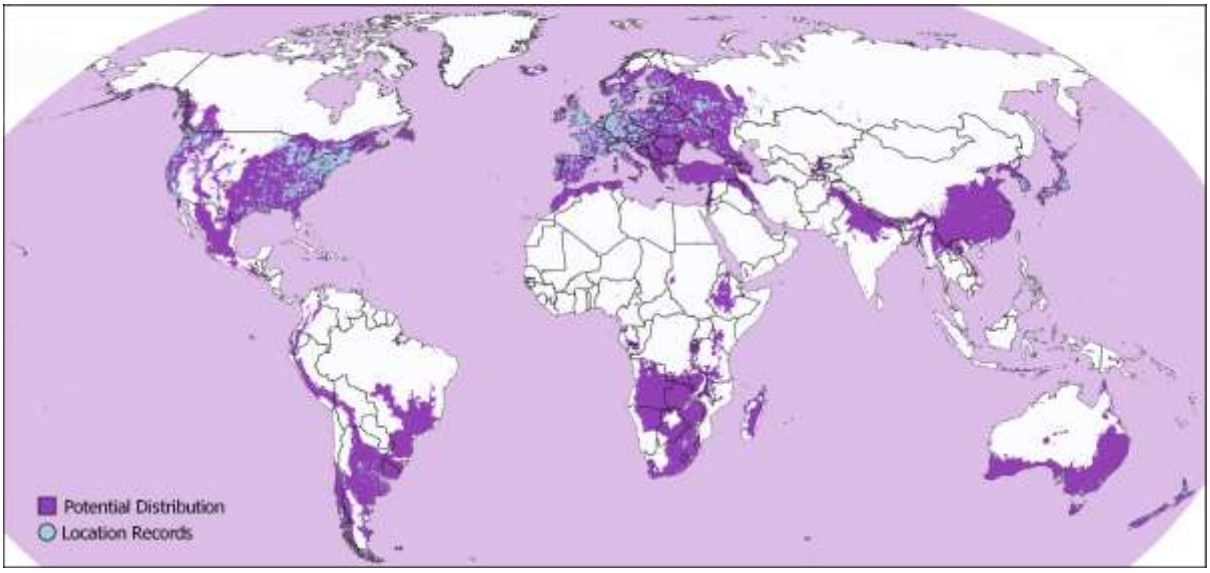
- Seeds and rhizomes adapted to hydrochory
- Spread by humans for ornamental purposes and for phytoremediation

Management:

- Clipping sexual reproductive structures prior to seed production and manually removing rhizomes
- Herbicide application
- Existing methods often unsafe and unsustainable at the ecosystem level
- Biological control programme underway with candidate biocontrol agents *Aphthona nonstriata*, *Mononychus punctumalbum*, and *Rhadinoceraea micans* identified through native range surveys

Biosecurity:

- Introductions largely intentional for ornamental and phytoremediation purposes
- Introduced to every continent except Antarctica
- Propagation illegal in many countries

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Appendix

Species distribution model

Occurrence records for *I. pseudacorus* were sourced from the Global Biodiversity Information Facility portal (GBIF, 2022). These were then cleaned by removing duplicate records, correcting erroneous or imprecise coordinates, and omitting records assigned to political centroids and biodiversity institutions. The remaining occurrences were visualised in QGIS software 3.14 (QGIS Development Team, 2020), and suspicious records that could not be confirmed or corrected were excluded. The dataset was then filtered to minimise the influence of spatial autocorrelation (Boria et al., 2014). These analyses were performed using the packages 'CoordinateCleaner' (Zizka et al., 2019), 'ecospat' (Di Cola et al., 2017), and 'spThin' (Aiello-Lammens et al., 2015) in R software 3.6.1 (R Development Core Team, 2019).

Bioclimatic predictors were obtained from WorldClim 2.1 (Fick & Hijmans, 2017) at a resolution of 2.5arcmin. Climatic data were then extracted from all raster layers at each occurrence point, and Pearson's correlation coefficients were computed for each pair of variables. A selection was made, amongst highly correlated variables ($|r| > 0.75$), based on their model contribution (i.e. jackknife analysis) and on the authors opinion regarding their biological relevance to the distribution of *I. pseudacorus*. Variables known to limit plant species distribution, such as thermal extremes, water stress and their interaction, were prioritized. The bioclimatic variables chosen as predictors for the model were: minimum temperature of the coldest month (bio6), mean temperature of the warmest quarter (bio10), annual precipitation (bio12), precipitation seasonality (bio15), and precipitation of the warmest quarter (bio18).

The analyses were performed in MaxEnt 3.4.1 (Phillips et al., 2017). Occurrences from both the native and introduced range of I. pseudacorus were used for model training and testing. This method allows to take into account the climatic variability acquired by the species in newly colonized areas, and is believed to yield more reliable outputs than using native or invaded range records alone (Beaumont et al., 2009). MaxEnt modelling settings were set as follows: convergence = 105, number of iterations = 500, prevalence = 0.5; regularization multiplier = 1; features = automatic. Model output was set as logistic, thus expressing suitability scores ranging from 0 (no suitability) to 1 (maximum suitability). Ten bootstrap replicates were computed, each allocating 70% of occurrences (n = 798) to model calibration and the remaining 30% (n = 342) to model evaluation. The average of all replicate models was used as final output. The minimum training presence threshold was used for graphical representation, as it includes all known areas where climate could potentially allow the species to establish, an important aspect in risk management of invasive species.

As *I. pseudacorus* has a wide geographic distribution, both in its native range and at a global scale, the background used for modelling was defined based on broad bioclimatic zones (Hill & Terblanche, 2014). Background data representative of the climate of the study area were drawn from a customized mask generated by selecting Köppen-Geiger climate zones (Beck et al., 2018) containing at least one occurrence record for the species (see Minuti et al., 2021 for details). The Multivariate Environmental Similarity Surface (MESS) was used to assess coverage of environmental gradients upon model projection and identify areas of uncertainty (et al., 2010). Where detected, the respective 'out-of-range' environmental variables were extrapolated from the dissimilarity maps (MoD) provided by the program output (Elith et al., 2011). The Continuous Boyce Index (CBI) was employed as a measure of model accuracy (Hirzel et al., 2006). This threshold-independent metric is considered more reliable than AUC when it comes to validating predictions and transferability of models built with presence-only data (Manzoor et al., 2018). CBI values were calculated using the package 'ecospat' (Di Cola et al., 2017) in R software 3.6.1.