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Biology of Invasive Plants

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Biology of Invasive Plants 7. *Iris pseudacorus* L. (Iridaceae)

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Scientific Classification

Domain: Eukaryota
Kingdom: Plantae
Phylum: Magnoliophyta
Class: Angiospermae
Order: Asparagales
Family: Iridaceae
Subfamily: Iridoideae
Genus: *Iris*
Species: *Iris pseudacorus* L. (Linnaeus 1753)
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* ssp. *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.
EPPO Code: IRIPS

Names and Taxonomy

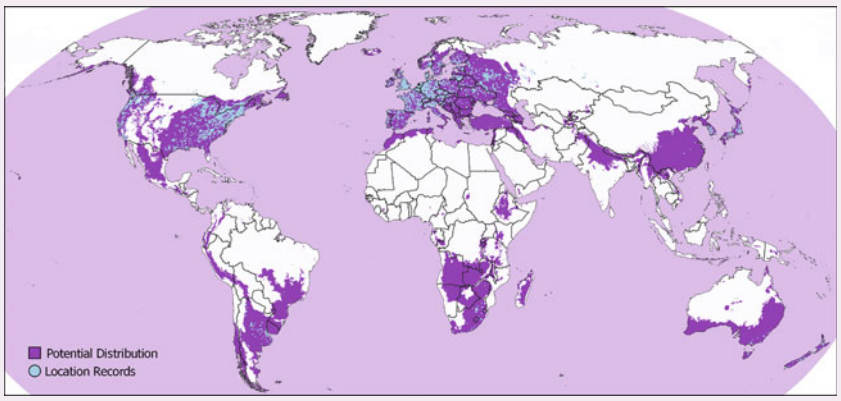
Among the plethora of common names used to identify *Iris pseudacorus*, the most common ones are yellow iris, yellow flag, yellow flag iris, pale-yellow iris, water iris, and water flag. In other languages, the species is referred to as *iris de marais*, *iris faux-acore*, and *iris jaune* (France); *giaggiolo acquatico* and *iris palustre* (Italy); *lirio amarillio* and *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 more than 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 (Boltenkov et al. 2020; Wheeler and Wilson 2014).

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

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 before seed production and manually removing rhizomes
- Herbicide application
- Existing methods often unsafe and unsustainable at the ecosystem level
- Biological control program 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.

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, semiarid, 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 the stinking iris [*Iris foetidissima* L.], a close relative of *I. pseudacorus*, which is reported to be invasive in New Zealand (Howell 2008).

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Importance

Negative Impacts

Iris pseudacorus becomes readily established and colonizes new habitats due to its very prolific nature (Alpert et al. 2000; Silvertown 2008) and the presumed absence of specialized 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 (Global Invasive Species Database 2022; Stone 2009; Thomas 1980; USDA-APHIS 2013).

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 bullrushes (*Typha* spp.) (Poaceae) (Raven and Thomas 1970) and other marsh plants such as sedges (*Carex* spp.), common tule (Schoenoplectus acutus (Muhl. ex Bigelow) Á. Löve & D. Löve) (both Cyperaceae), and water horsetail [*Equisetum fluviatile* L.] (Equisetaceae) (Stone 2009). This impact also includes threatened native irises, such as zigzag iris [*Iris brevicaulis* Raf.], dwarf iris [*Iris verna* L.], and dixie iris [*Iris hexagona* Walter] (Mopper et al. 2016; USDA-APHIS 2013; Weatherbee et al. 1998), as well as arrow arum [*Peltandra virginica* (L.) Schott] (Araceae), whose fruits are an important food source for wood ducks (*Aix sponsa*) 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 2009).

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 the 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, USA, 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 hypothesized 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 (Global Invasive Species Database 2022; Hayasaka et al. 2018; Jacobs et al. 2011; King County Noxious Weed Control Program 2009; Preece 1964; Stone 2009; Thomas 1980; USDA-APHIS 2013; 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 on 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* (Morgan et al. 2020; Sutherland 1990; Thomas 1980; Tu 2003). In Montana, USA, *I. pseudacorus* was shown to reduce stream width by up to 25 cm annually by trapping sediment and creating new stream banks dominated by *I. pseudacorus* seedlings (King County Noxious Weed Control Program 2009). 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 seedbed, *I. pseudacorus* contributes to the conversion of riparian marshes into swamps and mesic forests dominated by ashes (*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 (King County Noxious Weed Control Program 2009; Preece 1964; Stone 2009; USDA-APHIS 2013; Van Slooten 2016). Ecosystem processes and services provided by native aquatic and riparian vegetation can also be detrimentally altered by invasion (USDA-APHIS 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 United Kingdom, gastroenteritis occurred after livestock consumed *I. pseudacorus* leaves, and acute diarrhea occurred in domestic cattle (*Bos taurus*) after rhizome consumption (Sutherland 1990 and references therein). Conversely, extensive grazing of *I. pseudacorus* by wild horses (*Equus ferus*), cattle, sheep (*Ovis aries*), and goats (*Capra hircus*) 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 4 have international conservation status (Gervazoni et al. 2020). The invasion of this species in Argentina also represents a threat to the artificial rice (*Oryza sativa* L.) wetlands that cover large areas of land in the

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northeastern region of the country. This is especially relevant, considering that *I. pseudacorus* has previously been reported as a weed of this crop inGen 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 socioeconomic costs of *I. pseudacorus* invasions in natural and human-modified wetland ecosystems are scarce (Zilio et al. 2025).

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; Larue et al. 2010; Wu et al. 2013; Yousefi and Mohseni-Bandpei 2010; Zhang et al. 2007; Zhao et al. 2015; Zhou et al. 2010), 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 (Jacobs et al. 2011; Sutherland 1990) in these systems. It is also a suitable plant for use in erosion control, and for phyto-stabilization of contaminated soils in its native range (Pérez-Sirvent et al. 2017; Tu 2003). 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 [*Pontederia crassipes* Mart.] (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 (Bharthi et al. 2015; Mandal and Mondal 2011; 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 its diuretic properties and its 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, while roasted seeds are used as a substitute for coffee (*Coffea* spp.) (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 comes in contact with the skin (King County Noxious Weed Control Program 2009).

Description, Identification, and Diagnostic Characteristics

Iris pseudacorus is an emergent aquatic macrophyte, ~0.5 to 2.17 m in height (Chambers et al. 2008). Although *I. pseudacorus* is a perennial species, under unfavorable 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 color of its 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).

It can be difficult to distinguish *I. pseudacorus* from other similar iris species or cultivars when it is not in bloom (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 (Campbell et al. 2010; Kalesnik and Malvárez 2004; King County Noxious Weed Control Program 2009).

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 naturalized or invasive in parts of Canada, the United States, Argentina, Chile, Uruguay, South Africa, Australia, New Zealand, China, Japan, and the Korean Peninsula (POWO 2022; USDA-APHIS 2013), and it is also present in Mexico and Zimbabwe (Hyde et al. 2022; Naturalista 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), although 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 U.S. border (USDA-APHIS 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; Jaca and Mkhize 2015; NEMBA 2014; Sandenbergh et al. 2024; Figure 2C). Australian *I. pseudacorus* infestations are confined to Tasmania and the southeast region of the mainland (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).

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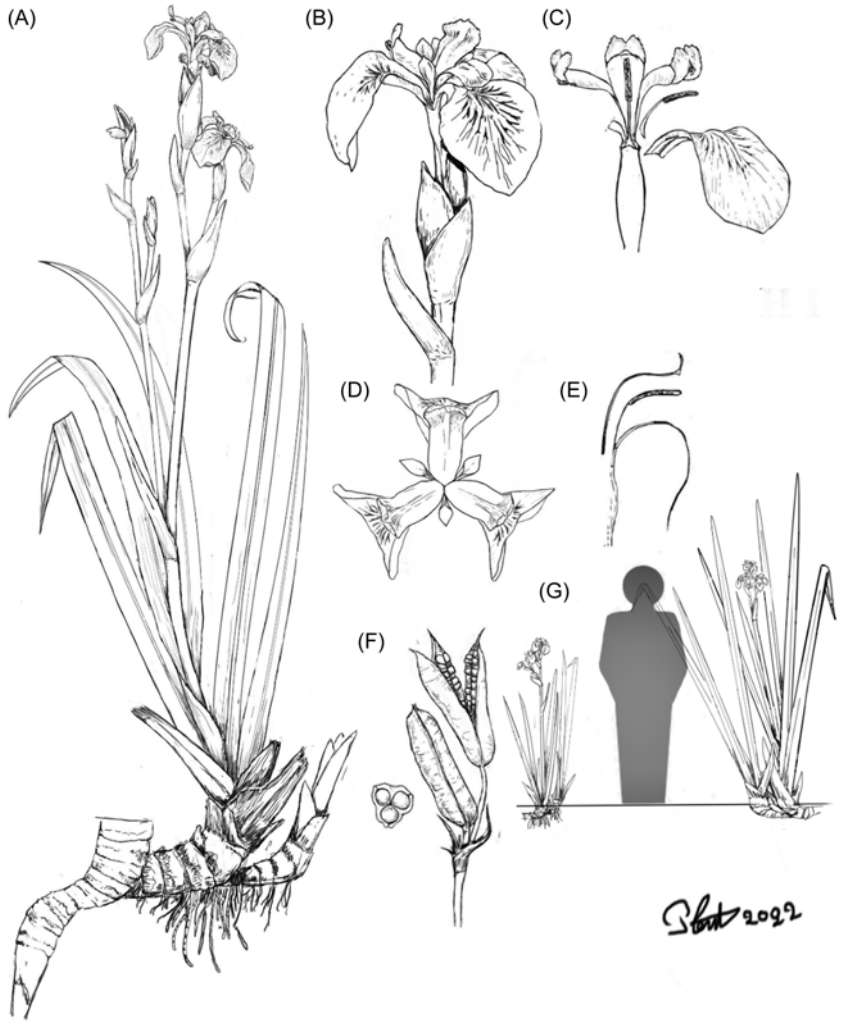


Figure 1. Morphology of *Iris pseudacorus* (Iridaceae) and its reproductive structures. (A) *Iris pseudacorus* general structure, (B–E) details of the flowers, (F) detail of the fruit, and (G) plant size.

Invasion Risk

A potential distribution model of *I. pseudacorus* was developed in order to identify areas with climatic suitability for this species and to prioritize areas at risk of invasion. The model was developed with the software Maxent v. 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, 2011).

The model showed areas at high risk of invasion by *I. pseudacorus* across different continents, in both the Northern and Southern Hemispheres (Figure 3). In the Northern Hemisphere, in addition to the climatic suitability across Europe (native range), the eastern regions of China and Japan also show a high probability of the plant thriving in Asia. 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 southeastern 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 to 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 northward, but in the Southern Hemisphere (South America, southern Africa, and Australasia), the future distribution is predicted to be reduced in response to climate change (Minuti et al. 2023).

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 (Cody 1961; Jaca and Mkhize 2015; USDA-APHIS 2013). Likewise, the use of this plant for its phytoremedial

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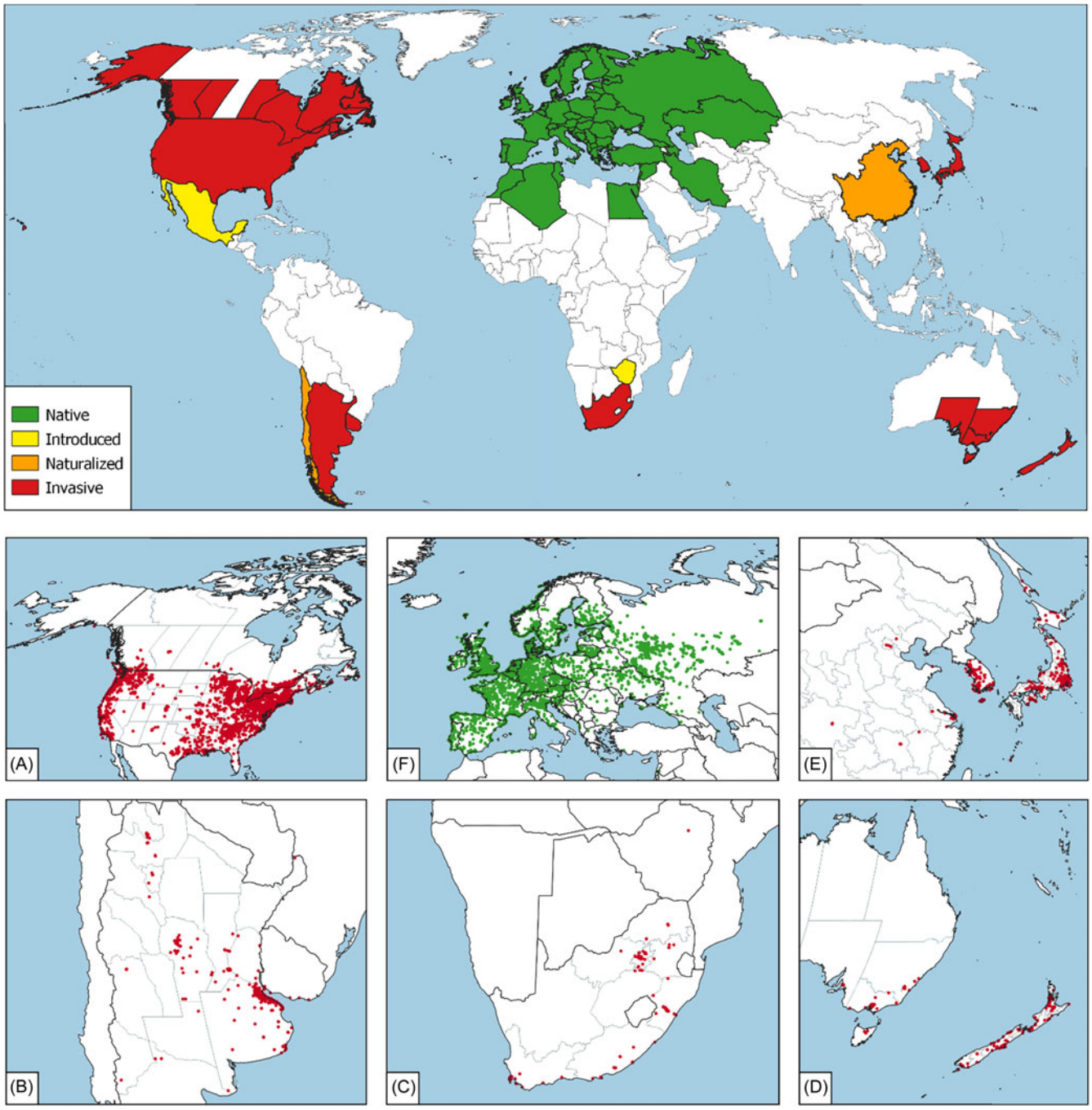


Figure 2. Worldwide distribution of *Iris pseudacorus*. Top: political map of regions where *I. pseudacorus* is reported to occur (invasion status inferred from the literature; see text for details). Bottom: introduced (A–E, red) and native (F, green) range records for *I. pseudacorus* downloaded from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

properties constitutes another anthropic factor that induces the introduction of this plant to new sites (Ediviani et al. 2018; Mohsin et al. 2023).

The exchange of specimens for gardens together with its use for water purification enabled extensive human-mediated distribution of *I. pseudacorus*. For instance, in Argentina, a citizen science study demonstrated its association with urban centers, 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 2 yr), floating in the water and consequently arriving at new, distant sites, promoting new invasions (Coops and Van Der Velde 1995; Gaskin et al. 2016), allowing 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

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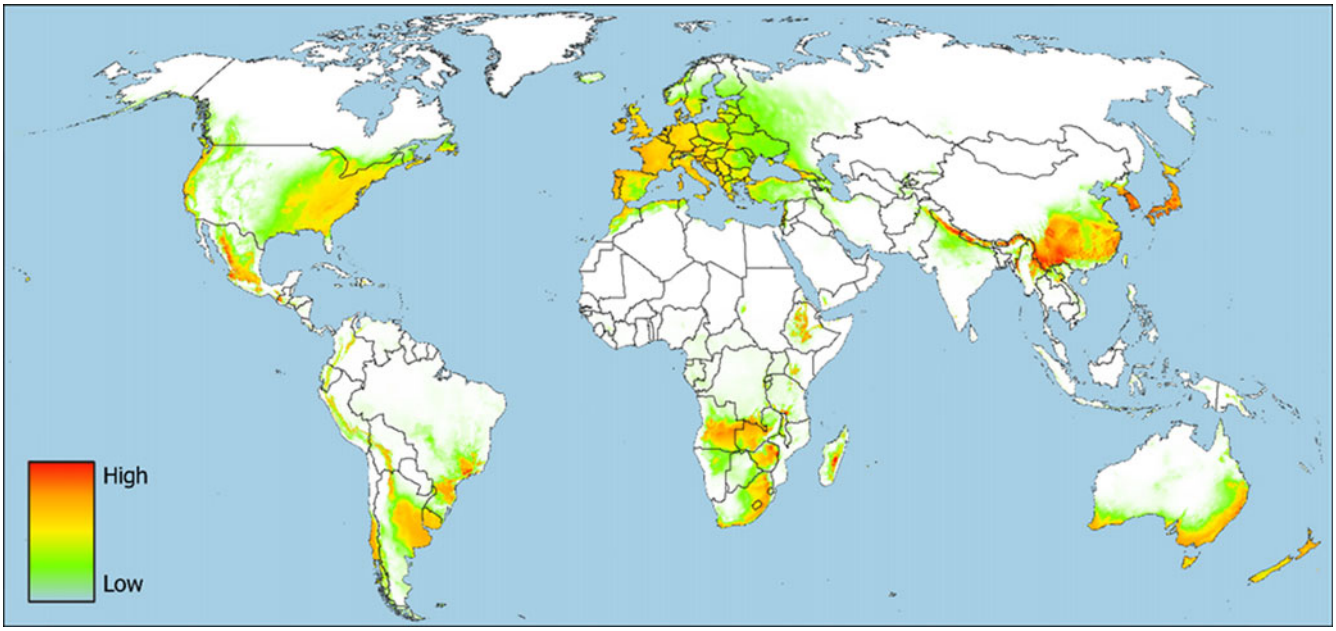


Figure 3. Global climatic suitability for *Iris pseudacorus* computed in Maxent (see methods in the Appendix).

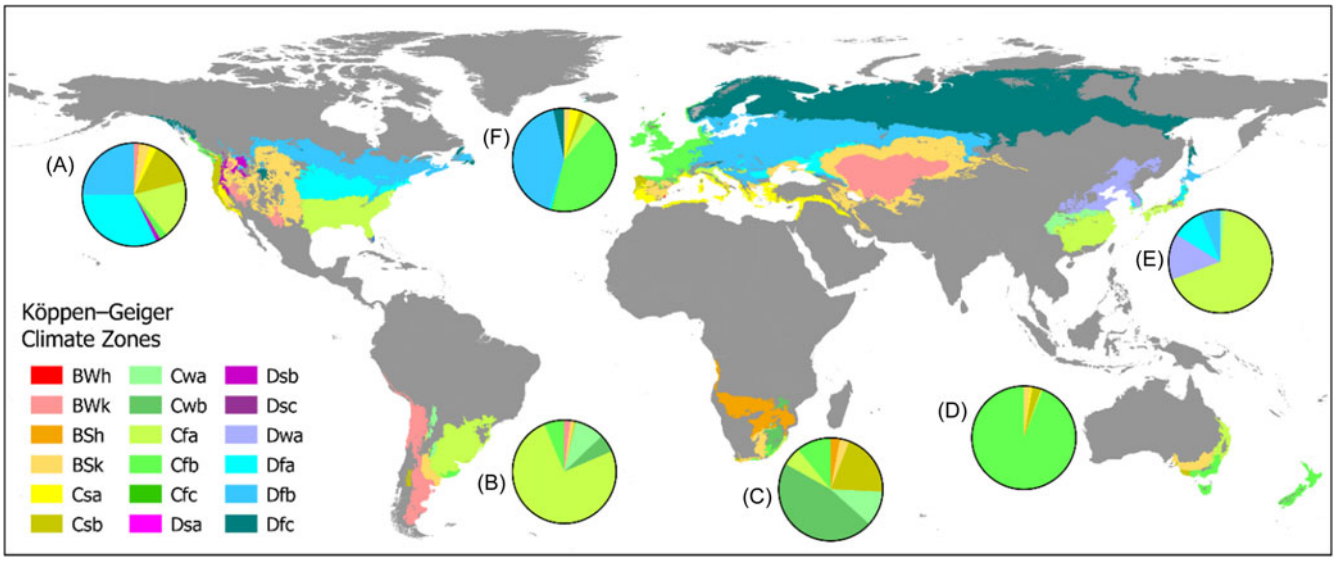


Figure 4. Köppen-Geiger climate zones occupied by *Iris pseudacorus* worldwide. The map was created based on *I. pseudacorus* distribution and the climate classification provided by Beck et al. (2018). Pie charts represent the relative density of occurrence points within each range: (A) North America,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

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 semiarid (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 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 it is also observed within the semiarid (BSk) and Mediterranean (Csa, Csb) climates of the western United States (Figure 4A). In South America, the most invaded regions 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

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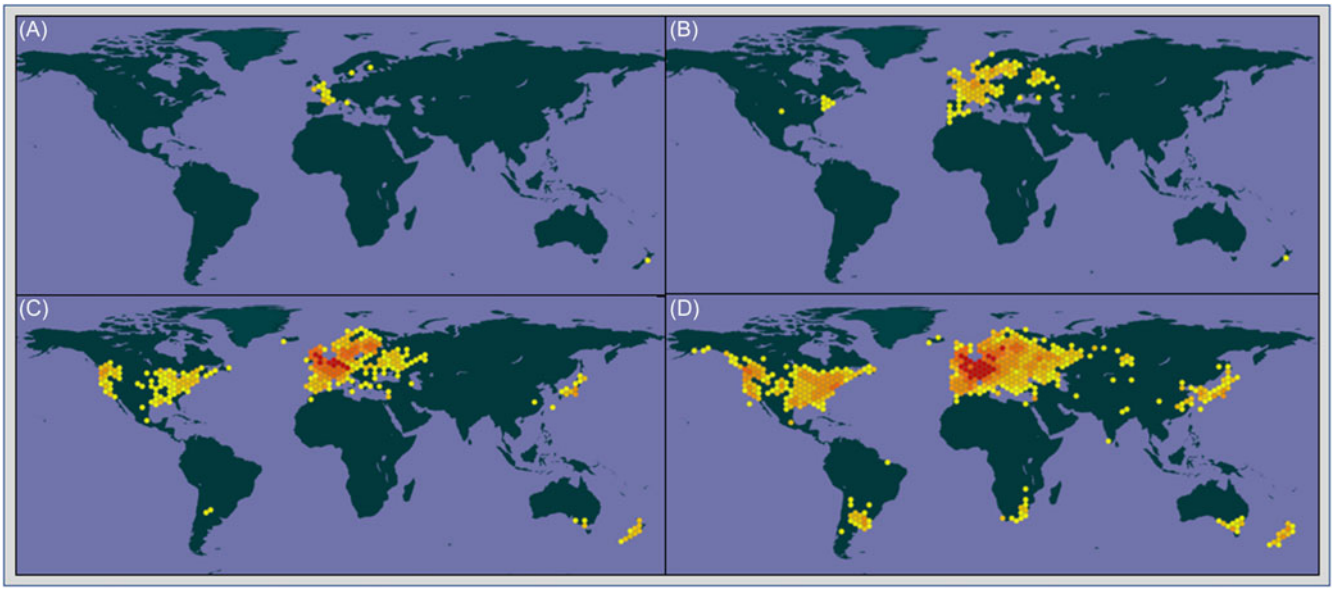


Figure 5. Records of occurrence of *Iris pseudacorus* in the Global Biodiversity Information Facility (GBIF) platform. Although this open database does not provide all existing records of *Iris pseudacorus*, it allows for the visualization of the increase over time in its geographic distribution (GBIF 2022). (A) 1600 to 1800, (B) 1900, (C) 2000, and (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.

African range (Figure 4C). In Australasia, *I. pseudacorus* has invaded the oceanic climates (Cfb) of New Zealand and southeastern Australia, with a slight expansion toward semiarid (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 above sea level (m asl), but has been recorded at elevations over 1,000 m asl (Sutherland 1990). In its invaded South African range, it occurs in the elevated interior, well above 1,200 m asl.

Land Use Associations

Iris pseudacorus occurs in habitats associated with water. It is found on the banks of lakes and 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 (Stone 2009; Sutherland 1990). 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 (Jacobs et al. 2010a; Sutherland 1990). 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 (Mulqueen and Gleeson 1988; Stone 2009; Sutherland 1990). *Iris pseudacorus* occurs in fens and fen woodland, but is less frequent in areas of chalk (Sutherland 1990). It can colonize 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 (Gerwing et al. 2021; Sutherland 1990). It persists in the higher zones of salt marshes and can tolerate soil acidity (at 0- to 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 (Stone 2009; Sutherland 1990; Tu 2003).

Invasion History

Early occurrence records (17th to 19th century) of *I. pseudacorus* are scant and are mainly limited to herbarium records from the United Kingdom and France. The species has been introduced from the Palearctic ecozone into many areas worldwide, including the Neotropics, Afrotropics, Nearctic, Indomalaya, and Australasia. 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; 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 before 1800 were intentional, as *I. pseudacorus* was used as an ornamental pond plant to the United States (Champion et al. 2022; Natural History Museum 2014; Wells and Brown 2000). 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 harbors (Torrey Botanical Club 1888), suggesting ship ballast water is a likely introduction source elsewhere.

The oldest report in this region corresponds to 1771, with *I. pseudacorus* being cultivated in Virginia (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 River in Delaware and the Hudson River valley in New York. It was naturalized at Lake Ontario in the Great Lakes

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region in 1886, and by 1900, herbarium 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 (Cody 1961; Fernald 1950). The species was well naturalized in southern Nova Scotia by at least 1915 (Fernald 1921; Roland 1945).

Written records and herbarium specimens suggest the *I. pseudacorus* invasion in North American was a result of multiple independent introductions. It was established in far western Canadian wetlands in British Columbia in 1931 before 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 (https://www.calflora.org/) and California Department of Food and Agriculture (https://doi.org/10.15468/phc373) herbaria databases), but the first naturalized 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 et al. 1969; Raven and Thomas 1970), and it has now invaded 8 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 (McGrannachan and Barton 2019; Wildland Consultants 2011). 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 conditions, 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 naturalized population of this plant in the Afrotropics was reported in 2004 in South Africa, where it was growing along the Vaal River in 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 categorized as a 1A invader under the National Environmental Management: Biodiversity Act and is listed 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).

Life-Form and Life History

Iris pseudacorus is categorized 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 (Jacobs et al. 2010a; Sutherland 1990). Leaves have aerenchyma, and they are always above the waterline. *Iris pseudacorus* typically occurs on high ground on the shore and wetlands, because seeds and seedlings require exposed soil conditions (Coops and Van der Velde 1995).

Iris pseudacorus individuals take 2 (unpublished data) to 3 yr (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), although the timing varies among climate zones and hydrological settings. Bloom time is from September to December in the Southern Hemisphere (Gervazoni 2024; Sandenbergh 2021).

After the reproductive period, depending on climatic and environmental conditions, the plant may remain green over winter (King County Noxious Weed Control Program 2009). Above- and belowground biomass increases seasonally, with the highest values of aboveground biomass in summer and negligible in winter (Larue et al. 2010). The seasonal accumulation of storage materials in the

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belowground 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 (Rakhimov et al. 2006; Sutherland 1990). The plant biomass of *I. pseudacorus* in the native range was estimated at 0.7 to 0.8 kg m^{-2} (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 (Gaskin et al. 2016; Lamote et al. 2002; Sutherland 1990). 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 in both the native and introduced ranges compared populations of *I. pseudacorus* and found genetic divergence between them, indicating that the propagation and spread of this species are predominantly a result of sexual reproduction (Gallego-Tévar et al. 2024; Gaskin et al. 2016; Lamote et al. 2002).

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 (Gaskin et al. 2016; Lamote et al. 2002). However, Gallego-Tévar et al. (2024) found higher genetic diversity in the native range (Spain) than was the case for the invaded range (California).

In tidal wetlands, floating wrack mats composed 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 seedbank and can germinate and emerge in disturbance-generated gaps or as wrack decomposes.

Anthropogenic dispersal also plays an important role in facilitating the spread of *I. pseudacorus* due to its high ornamental value. 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 (Mercado Libre 2022; Raghu et al. 2017). In South Africa, for example, the species was promoted for use in the trout (*Oncorhynchus mykiss*) farm industry, as well as for phytoremediation and the prevention of soil erosion, further promoting its dispersal and establishment (Sandenbergh et al. 2024; personal observations). "Escaping" cultivation has been reported as a main pathway for the establishment and subsequent invasion of *I. pseudacorus* (Minuti et al. 2021; Morgan et al. 2020; Sandenbergh et al. 2024).

Once dispersed, *I. pseudacorus* propagules, being disturbance adapted, can take advantage of undesirable conditions in novel environments. Disturbance favors *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* (Stone 2009; Sutherland 1990). 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 favorable conditions for *I. pseudacorus* establishment (Stone 2009; Tu 2003). In contrast, 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 that 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 naturalized in wet environments away from gardens (Goodridge et al. 2011; Henderson 2002). 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 (Flora Europaea 2022; Henderson 2002; Klinkenberg 2010; Lui et al. 2010; NatureGate 2022; Stone 2009; Sutherland 1990; Tutin et al. 1980; World Flora Organization 2022). Descriptions that follow reflect cross-referencing among published descriptions.

Iris pseudacorus is an emergent aquatic angiosperm from the rhizomatous, beardless subgenera *Limniris* sect. *Limniris* (Wilson 2006). Aboveground, the plant typically ranges in height from 0.5 to 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- to 4-cm wide and 40-cm to 1.5-m long and sword-shaped with pointed tips and may be downward-curved near the top (Negrut et al. 2018; Sutherland 1990).

The plant has bisexual pale to bright yellow flowers (8- to 10-cm diameter; flowers larger than 10 cm across are reported in Finland) (NatureGate 2022). Flowers are radially symmetrical, actinomorphic, and grouped as an inflorescence. The cyme-like inflorescences may each include 4 to 12 (often 5 to 10) flowers partially enclosed by inner and outer green spathes (bracts) with brown margins, the outer being strongly keeled and the inner unkeeled. There are 4 to 12 flowers per inflorescence, which are arranged on round, erect 2- to 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 to 80 by 20 to 45 mm, with a broadly ovate blade, sharply attenuated at the base and recurved, and bright yellow in color, with short radiating brownish lines. Internal tepals are 10 to 30 by 3 to 8 mm, erect, yellow, spatulate to oblanceolate, obtuse, and

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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- to 20-mm long, triangular in cross-section with concave sides; the pedicel is 3- to 5-cm long. There are three keeled styles and three stigmas per flower. The style is filiform, ending in three petal-like yellow branches arched over the external tepals and a small rounded stigma with a prominent tongue on the underside (Figure 1E). The three stamens are hidden under the three style branches (Figure 1C). Floral tubes are 6- to 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- to 8.5-cm long with a 5-mm beak, and most often described as three-angled with an obvious groove at each angle (but see World Flora Organisation (2022) and Gleason and Cronquist (1991) for reports of six-angled capsules). Developing capsules are yellow-green to green in color 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 to 7 mm), lustrous corky seeds. When mature, the capsule splits and releases seeds which, when growing in or near to waterbodies, disperse directly into or near the 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, and 34 (Choi et al. 2020; Dyer et al. 1976; Henderson 2002).

Below the surface, *I. pseudacorus* can produce a woody crown below the leaf base, from which dense, freely branching pink rhizomes (1- to 5-cm 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 (Jacobs et al. 2010a; Sutherland 1990; Yu et al. 2022). Fleshy roots (10- to 30-cm long) extend into the soil (Sutherland 1990; Figure 1A). Belowground biomass, comprising rhizomes and roots, may represent greater than 99% of the total biomass, which is evidence of this weed's resilience and ability to compete for space and resources (Minuti et al. 2021; Mopper et al. 2016; Sutherland 1990). Rhizomes make up most of the belowground biomass, with roots representing just greater than 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, and canals, or in dry wetland soil, suggesting a degree of tolerance to 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 8 wk) (Hetherington et al. 1982; Hunter et al. 2001; Mulqueen and Gleeson 1988; Sutherland 1990). 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 belowground tissues may also allow the plants to survive extended drought (Fitter and Hay 2012). Greater allocation of biomass to belowground structures than shoots could also provide some degree of protection to prevent juvenile plants from being washed away in high flows (Sutherland 1990; Whitehead 1971).

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 water (Dutton and Thomas 1991; Grewell et al. 2021; Strong and Kelloff 1994), 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 with 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 naturalized 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 colonizing 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 colonizing 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 prioritize freshwater tidal habitat, because 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 (PG, personal observations), 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 to 28°S, and with differences in altitude (sea level to 1,315 m asl; Welsh et al. 1987), climate, and hydrological regimes all playing a role. Even so, there are many common aspects of this species' life history.

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 (flooding, bank erosion, etc.) that create gaps that promote its rapid colonization of systems (Barrat-Segretain and Bornette 2000; Grewell et al. 2019; Pyšek and Prach 1993).

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

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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 the seedbank during the early spring season (Fitter and Hay 2012; Jacobs et al. 2010b). Annual rhizome growth typically continues through each growing season until branching begins after flowering (Jacobs et al. 2010b). Sutherland (1990) studied the species in Ireland and reported that when rhizomes reach about 10 yr 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 to 40 yr with continued incremental growth (Whitehead 1971), and some extant naturalized population patches in the invasive California range have been present for at least 50 yr (Consortium of California Herbaria 2022; BG, personal observations). While genetic studies reveal the primary dispersal and colonization is from seeds (Gaskin et al. 2016), local spread by radially spreading clones produces dense stands that displace resident vegetation (Falińska 1986; Preece 1964; Thomas 1980).

During pre-reproductive growth, the plants also store carbohydrates in roots, leaf bases, and pre-flowering shoot tissues (Grewell et al. 2021; Sutherland 1990). 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 colonization when there is significant investment of resources toward belowground growth and carbon reserves (Jacobs et al. 2010a; Sutherland 1990).

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 as in 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 to 10 mm above the corresponding outer perianth segment and are pollinated by bumblebees large enough to enter in contact with stamens and stigma (Figure 1 A and 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 (McGrannachan and Barton 2019; Sutherland 1990). Observations made in the native range included mainly bumblebees of the genus *Bombus*, as well as *Apis mellifera* (Apidae) and *Osmia rufa* (Megachilidae) bees. Syrphid flies, including *Rhingia campestris*, *Episyrphus balteatus*, and *Eristalis* spp., were also included, as were the scathophagids *Scatophaga stercoraria*; the Hepialidae moth *Hepialus humuli*; and the Noctuidae moths *Apamea monoglypha*, *Noctua 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* (Stratyomidae), and some coleopteran species, including the coccinellid predator *Eriopis connexa* (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 square meter (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 (PG, unpublished data).

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).

Seedbanks

Iris pseudacorus forms soil seedbanks, but longevity of these belowground 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 seedbank (Vecrin et al. 2007), while in the Netherlands, *I. pseudacorus* emerged from 25% of soil seedbank studies in an emergence assay, although the species was present in standing vegetation at 84% of sampled fens (van der Valk and Verhoeven 1988). In the invaded range, Leck and Leck (2005) recorded seedbank 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 that 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).

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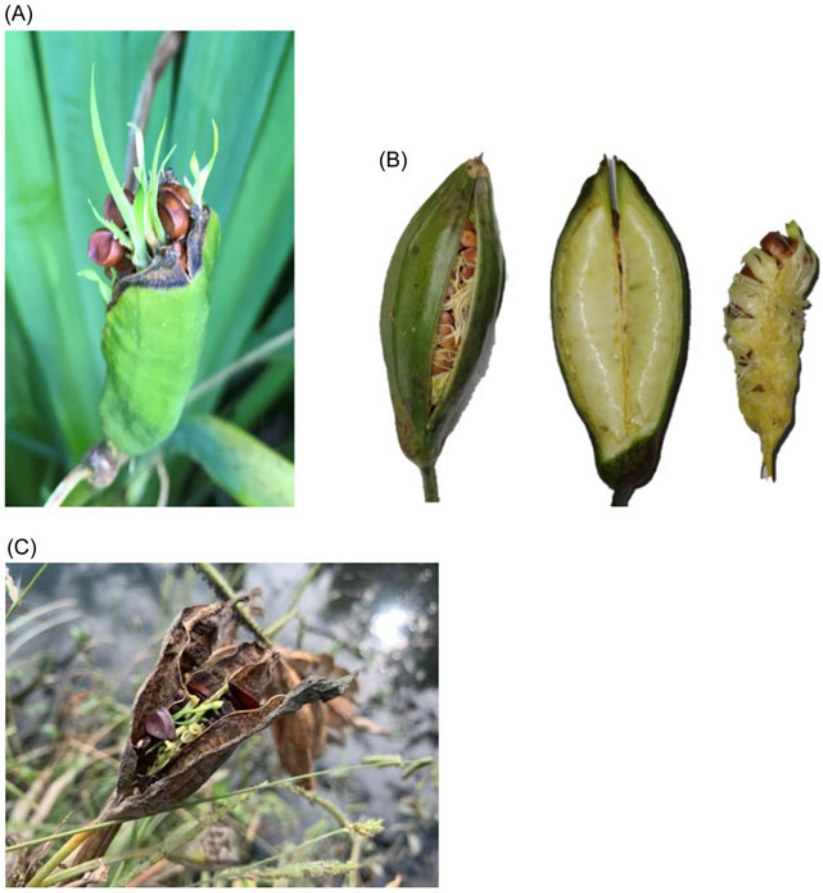


Figure 6. Vivipary in (A) South African, (B) Argentinian, and (C) Californian *Iris pseudacorus* seed capsules (Photos: E Sandenbergh, Johannesburg, 2020; P Gervazoni, Misiones, 2023; J Futrell, Brannon Island, 2018).

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, although 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 1 mo. A review by Sutherland (1990) suggests seeds from the Netherlands achieved 25% germination during 6 wk in drained soil, while 40% to 48% germination was recorded for non-scarified seeds from the United Kingdom. Germination of *I. pseudacorus* is hypogeal and cryptocotylar (unpublished data). Vivipary has been observed in the field in California (Gillard et al. 2021), Argentina, and South Africa (Gervazoni 2024; Sandenbergh 2021; Figure 6), whereby seeds have germinated inside recently dehisced seed capsules, providing evidence that dormancy may not be required. Accordingly, in Argentina, a germination experiment showed that seeds with a cold pretreatment for dormancy breaking, had a lower germination percentage than the control (Gervazoni 2024; Gervazoni et al. 2023).

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 to 25 C, with a photoperiod of 12-h light/12-h dark, 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 h 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 with an average temperature of 21.4 ± 5.1 C, showed that, under freshwater conditions, approximately 96% of seed could germinate—a proportion that 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 a combination of fluctuating temperatures and light is 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 pretreatment) for seeds collected at different sites across South Africa. In Argentina, 60.56% of germination was obtained for seeds with the cold pretreatment and

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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.

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) ranges in order to achieve a more comprehensive dataset for the germination potential of *I. pseudacorus* (unpublished data).

Sexual reproduction can be expected to be increasingly more important as climate change drives changes in water levels that promote increased seedbank emergence from greater exposure of moist soil in wetlands. *Iris pseudacorus* seeds germinate best in moist soil, rather than water-logged soils (Coops and Van Der Velde 1995; Lenssen et al. 1998; Thomas 1980). 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 versus 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 the 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).

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 geographic 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 (Gallego-Tévar et al. 2024; Gaskin et al. 2016; Lamote et al. 2002). 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) reported that *I. pseudacorus* populations in the northwest United States reproduce almost solely by seed, with 98% unique genotypes observed throughout the invasion, and Gallego-Tévar et al. (2024) reported high rates of intrapopulation 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 organizations, 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 United States with a long history of invasion, *I. pseudacorus* occurs in red maple (*Acer rubrum* L.)-river birch (*Betula nigra* L.)-green ash (*Fraxinus pennsylvanica* Marshall) swamp forest associations; shrub–swamp communities with bog-myrtle (*Myrica gale* L.), swamp rose (*Rosa palustris* Marshall), and hazel alder]*Alnus serrulata* (Aiton) Willd.]; natural and constructed freshwater marshes in association with rice cutgrass [*Leersia oryzoides* (L.) Sw.], pickerelweed (*Pontederia cordata* L.), and *Typha* spp.; marshes and swamps with emergent macrophytes such as Appalachian arrowhead [*Sagittaria australis* (J.G. Sm.) Small] and *Carex* spp. and with trees typical in swamp forests (see review in Stone 2009). In West Virginia, southern USA, it occurs in diverse fringed sedge table wetlands with mostly native *Carex* spp., club-rushes (*Scirpus* spp.), and soft rushes (*Juncus* spp.); in regularly inundated floodplain and riparian sycamore(Platanus sp.)–birch (Betula sp.) forests; and riverine wetlands with wild celery (*Vallisneria americana* Michx.)-pondweed (*Potamogeton* spp.) associations (Suiter and Evans 1999). In Central and Northern Plains states, *I. pseudacorus* is reported to occur in monocultures or intermixed with sandbar willow (*Salix interior* Rowlee)-broadleaf cattail (*Typha latifolia* L.) communities (Preece 1964 in Stone 2009). *Iris pseudacorus* invasions in freshwater wetlands of California and Oregon impact native emergent *T. latifolia*, broadleaf arrowhead (*Sagittaria latifolia* Willd.), and clubrush (*Schoenoplectus* spp). communities. In tidal wetlands of North American Pacific estuaries, *I. pseudacorus* occurs with baltic rush (*Juncus balticus* Englem.), hardstem bulrush (*Schoenoplectus acutus* (Muhl. ex Bigelow) Á. Löve & D. Löve), narrowleaf cattail (*Typha angustifolia* L.), water parsley (*Oenanthe sarmentosa* C. Presl ex DC.), 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 *T. latifolia* (in South Africa and Argentina), common bulrush (*Typha capensis* Rohrb.) (in South Africa), and Asian bulrush (*Typha orientalis*

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Figure 7. *Iris pseudacorus* invasion in Buenos Aires Province, Argentina. (Photo: A Faltlhauser).

Presl.) (in New Zealand), as well as with species from the Cyperaceae and Pontederiaceae families, among others (Gervazoni 2024; McGrannachan and Barton 2019; personal observations).

Due to its ability to form dense rhizomatic mats that exclude co-occurring species, *I. pseudacorus* has been described as an aggressive competitor, capable of engineering ecosystems and drastically reducing native plant diversity (Lamote et al. 2002; Thomas 1980). 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 *T. orientalis* and *Carex* sp. (CM, personal observations), and in South Africa with *T. capensis* and *Pontederia cordata* L. (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 preexisting native vegetation having been displaced (Gervazoni et al. 2020; PG, personal observations; Figure 7).

Management Options

Mechanical/Physical Control

Iris pseudacorus control by mechanical or manual means is often problematic, as such processes are 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 before seed production may help to reduce viable seed capacity and prevent cross-pollination, but do not kill the plant (DiTomaso and Kyser 2016; Tu 2003). 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 labor-intensive, and requires repeated efforts over several years (Tu 2003). Benthic barriers such as rubber matting have proven effective against partly submerged populations, with rhizomes killed within 70 d and no detection of regrowth after 200 d (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 *I. pseudacorus* rhizomes (personal communication). This is consistent with Stoneburner et al. (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 (DiTomaso and Kyser 2016; Global Invasive Species Database 2022; Wildland Consultants 2011). Glyphosate is commonly used in a 5% to 8% solution with a surfactant during late spring or early summer, to prevent seed development. During fall, a 2% to 8% 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

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control (99.2%) compared with 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 labor, time, equipment, and chemical costs all contributing to high expenditures. In New Zealand, chemical control costs (including labor and herbicide) of *I. pseudacorus* were estimated to be NZ$100 to NZ$340 (± US$60 to $210) per hectare for isolated patches, and more than NZ$1,350 (± US$830) per hectare 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 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 program.

The aim of any biological control program 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 economic 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 the United Kingdom, Belgium, and Italy (Minuti et al. 2021; Sutherland 1990). 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 herbivorous species are leaf miners and defoliators, while some are associated with flowers, fruits, and rhizomes (Minuti et al. 2021; Sutherland 1990).

The assessment of the prioritization 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* (Coleoptera: Chrysomelidae) (Figure 8A), the seed weevil *Mononychus punctumalbum* (Coleoptera: Curculionidae) (Figure 8B), and the sawfly *Rhadinoceraea micans* (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).

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. The larvae are believed to sequester and store secondary plant metabolites, which could be an effective defense against generalist predators, as well as the strongly hydrophobic cuticle which allows them to move on the water's surface to reach new plants (Boevé et al. 2013; Voigt et al. 2011). The occurrence of this species is associated with temperate and cold areas (GBIF 2021b), 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 colonization 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 2021a).

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 that feed on the rhizome. Currently, a quarantine population of *A. nonstriata* is under evaluation in South Africa, and preliminary results indicate that it is feasible for rearing 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 northeast Argentina, Uruguay, southern Brazil, southern South Africa, southeast Australia, and New Zealand. Therefore, these wetland areas should be prioritized when releasing *A. nonstriata* to allow for the its establishment 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 2024; Gervazoni et al. 2021). 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 2024; Gervazoni et al. 2021, 2022). 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 (unpublished data). Fruits and seeds present consistent damage by borer insects, but taxonomic identification and their inferred host range are under evaluation (Gervazoni 2024; Gervazoni et al. 2022). 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 (unpublished data).

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,

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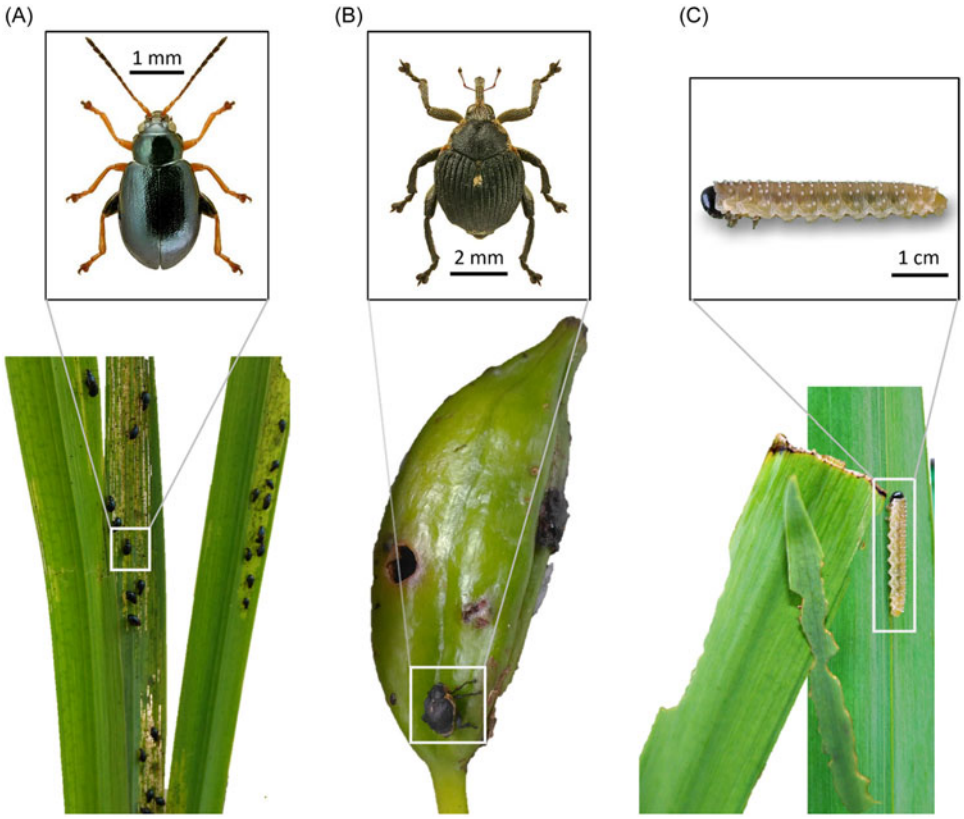


Figure 8. Representation of damage caused to *Iris pseudacorus* by three potential biological control agents. (A) *Aphthona nonstriata* (Coleoptera: Chrysomelidae), (B) *Mononychus punctumalbum* (Coleoptera: Curculionidae), and (C) *Rhadinoceraea micans* larvae (Hymenoptera: Tenthredinidae).

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, for example, golf courses and trout farms. To minimize 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 devising successful integrated management strategies that address those mechanisms. Recent studies highlighting the efficacy of the potential biocontrol agent, *A. nonstriata*, in reducing seedling establishment are promising, because the main pathway of spread is through seed dispersal and seedling establishment (GM, unpublished data). Further suppression of seed production could be realized 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 laws and regulations that aim to prohibit its commercialization and avoid new areas of invasion.

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References

[AVH] Australasian Virtual Herbarium (2022) *Iris pseudacorus*. https://avh.ala.org.au/occurrences/search?q=lsid:https://id.biodiversity.org.au/node/apni/2914189&fq=country:%22Australia%22&sort=occurrence_date&dir=asc&qualityProfile=ALA&disableAllQualityFilters=true. Accessed: June 12, 2022

[GBIF] Global Biodiversity Information Facility (2021a) *Aphthona nonstriata* (Goeze, 1777) in GBIF Secretariat (2021). GBIF Backbone Taxonomy Checklist Dataset. https://doi.org/10.15468/39omei. Accessed: June 29, 2022

[GBIF] Global Biodiversity Information Facility (2021b) *Mononychus punctumalbum* (J.F.W.Herbst, 1784) in GBIF Secretariat (2021). GBIF Backbone Taxonomy Checklist Dataset. https://doi.org/10.15468/39omei. Accessed: June 29, 2022

[GBIF] Global Biodiversity Information Facility (2021c). *Rhadinoceraea micans* (Klug, 1816) in GBIF Secretariat (2021). GBIF Backbone Taxonomy Checklist Dataset. www.gbif.org/es/species/4490342. Accessed: June 29, 2022

[GBIF] Global Biodiversity Information Facility (2022). *Iris pseudacorus* L. in GBIF Secretariat (2021). GBIF Backbone Taxonomy Checklist Dataset. available at https://doi.org/10.15468/39omei. Accessed: June 26, 2022

[IUCN] International Union for Conservation of Nature (2012) Assessment of the Socio-economic Value of Freshwater Species for the Northern African Region. Gland, Switzerland; Málaga, Spain: IUCN. https://portals.iucn.org/library/efiles/documents/2012-042.pdf. Accessed: March 8, 2024

[NEMBA] National Environmental Management: Biodiversity Act (2014) National Environmental Management: Biodiversity Act (10/2004) Alien and Invasive Species Regulations (GG 37885 – GN 598). 32 p

[POWO] Plants of the World Online (2022) *Iris pseudacorus* L. *In* Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. https://powo.science.k,ew.org/taxon/urn:lsid:ipni.org:names:438992-1#bibliography. Accessed: June 18, 2022

[USDA-APHIS] U.S. Department of Agriculture–Animal and Plant Health Inspection Service (2013) Weed Risk Assessment for *Iris pseudacorus* L. (Iridaceae). Technical Bulletin 1. 17 p. https://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/wra/Iris_pseudacorus_WRA.pdf

Ahmed S, Ahsan Maliick I, Hasan MM (2017) Exploring globally used antiurolithiatic plants of A to L families: Asteraceae, Fabaceae and Lamiaceae revisited. J Pharmacogn Phytochem 6:1780–1787

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38:541–545

Alpert P, Bone E, Holzapfel C (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect Plant Ecol 3:52–56

Ansola G, De Luis E (1994) Concentración de nutrientes en helófitos acuáticos utilizados en depuración de agua residual. Limnética 10:33–36

Barrat-Segretain MH, Bornette G (2000) Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality. Hydrobiologia 421:31–39

Barrett SCH (2015) Influences of clonality on plant sexual reproduction. Proc Natl Acad Sci USA 112:8859–8866

Baskin CC, Baskin JM (2014) Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. 2nd ed. San Diego, CA: Academic Press. 734 p

Beaumont LJ, Gallagher RV, Thuiller W, Downe PO, Leishman MR, Hughes L (2009) Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. Divers Distrib 15:409–420

Beck HE, Zimmermann, NE, McVicar TM, Vergopolan N, Berg A, Wood EF (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci Data 5:180214

Bharthi V, Kavya B, Shantha TR, Prathapa Reddy M, Kavya N, Rama Rao V, Kalpeshkumar B. Ishnawa, Venkateshwarlu G (2015) Pharmacognostical evaluation and phytochemical studies on Ayurvedic nutritional fruits of Trapa natans L. Int J Herb Med 3:13–19

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošik J, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Boevé JL, Voigt D, Gorb SN (2013) Integument and defense in larva and prepupa of a sawfly living on a semi-aquatic plant. Naturwissenschaften 100:107–110

Boltenkov E, Artyukova, E, Kozyrenko M, Erst A, Trias-Blasi A (2020) *Iris sanguinea* is conspecific with *I. sibirica* (Iridaceae) according to morphology and plastid DNA sequence data. PeerJ 8:e10088

Boria RA, Olson LE, Goodman SM, Anderson RP (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecol Model 275:73–77

Bossuyt B, de Fre B, Hoffmann M (2005) Abundance and flowering success patterns in a short-term grazed grassland: early evidence of facilitation. J Ecol 93:1104–1114

Branković S, Glišić R, Topuzović M, Marin M (2015) Uptake of seven metals by two macrophytes species: potential for phytoaccumulation and phytoremediation. Chem Ecol 31:583–593

Briese DT (2004) Weed biological control: applying science to solve seemingly intractable problems. Aust J Entomol 43:304–317

Campbell S, Higman P, Slaughter B, Schools E (2010) A Field Guide to Invasive Plants of Aquatic and Wetland Habitats for Michigan. Lansing: Michigan DNRE, Michigan State University Extension, Michigan Natural Features Inventory. 90 p

Castillo JM, Gallego-Tévar B, Grewell BJ (2023) Wrack burial limits germination and establishment of yellow flag iris (*Iris pseudacorus* L.). Plants 12:150

Chambers PA, Lacoul P, Murphy KJ, Thomaz SM (2008) Global diversity of aquatic macrophytes in freshwater. Hydrobiologia 595:9–26

Champion P, Wong LJ, Pagad S (2022) Global Register of Introduced and Invasive Species—New Zealand. Version 1.6. Invasive Species Specialist Group (ISSG) Checklist Dataset. https://doi.org/10.15468/o5dv6e accessed via GBIF.org on 2022-07-28

Champion PD, de Winton MD, de Lange PJ (1993) The Vegetation of the Lower Waikato Lakes. Vol. 2, Vegetation of Thirty-Eight Lakes in the Lower Waikato. NIWA Ecosystems Publication No. 8. Hamilton, NZ: NIWA. 137 p

Chang CS, Kim H, Chang, KS (2014) Provisional Checklist of Vascular Plants for the Korea Peninsula Flora. Version 1.0. 660 p. https://www.researchgate.net/publication/280010996_Provisional_Checklist_of_Vascular_Plants_for_the_Korea_Peninsula_Flora_KPF. Accessed: February 25, 2024

Choi B, Weiss-Schneeweiss H, Temsch EM, So S, Myeong H, Jang T (2020) Genome size and chromosome number evolution in Korean *Iris* L. species (Iridaceae Juss.). Plants 9:1284

Cody WJ (1961) *Iris pseudacorus* L. escaped from cultivation in Canada. Can Field Nat 75:139–142

Coetzee JA, Hill MP (2012) The role of eutrophication in the biological control of water hyacinth, *Eichhornia crassipes*, in South Africa. BioControl 57:247–261

Consortium of California Herbaria (2022) Plant Accession Results. Portal CCH 1, Version 3. https://www.ucjeps.berkeley.edu/consortium. Accessed: August 4, 2022

Coops H, Van Der Velde G (1995) Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Freshwater Biol 34:13–20

Cox GW (1999) Alien Species in North America and Hawaii: Impacts on Natural Ecosystems. Washington, DC: Island Press. 387 p

Crocker W (1906) Role of seed coats in delayed germination. Bot Gaz 42:265–291

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, d'Amen M, Randin C, Guisan A (2017) ecospat: an R package to support spatial analyses and modelling of species niches and distributions. Ecography 40:774–787

Dieringer G (1982) The pollination ecology of *Orchis spectabilis* L. (Orchidaceae). Ohio J Sci 82:218–225

DiTomaso JM, Kyser GB (2016) Shoreline drizzle applications for control of incipient patches of yellow flag iris (*Iris pseudacorus*). Invasive Plant Sci Manag 9:205–213

Dutton BE, Thomas RD (1991) The vascular flora of Cameron Parish, Louisiana. Castanea 56:1–37

Dyer AF, Ellis THN, Lithgow E, Lowther S, Mason I, Williams D (1976) The karyotype of *Iris pseudacorus* L. Trans Bot Soc Edinb 42:421–429

https://doi.org/10.1017/inp.2024.35 Published online by Cambridge University Press

Dykes WR (1974) The Genus Iris. Cambridge: Cambridge University Press. 245 p
Ediviani W, Priadi CR, Moersidik S (2018) Nutrient uptake from liquid digestate using ornamental aquatic macrophytes (*Canna indica*, *Iris pseudacorus*, *Typha latifolia*) in a constructed wetland system. J Phys Conf Ser 1022:012052
Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342
Elith J, Phillips J, Hastie T, Dudík M, Chee YE, Yates J (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57
Evergreen (2007) Invasive Plant Profile: Yellow Flag Iris, Yellow Flag. Iris pseudacorus. Vancouver, BC, Canada: Evergreen. 2 p
Falińska K (1986) Demography of *Iris pseudacorus* L. populations in abandoned meadows. Ekol Pol-Pol J Ecol 34:583–613
Fernald ML (1921) The Gray Herbarium expedition to Nova Scotia, 1920. Rhodora 23:89–111
Fernald ML (1950) Gray's Manual of Botany. 8th ed. New York: American Book Company. 1632 p
Fick SE, Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315
Fitter AH, Hay RKM (2012) Environmental Physiology of Plants. 3rd ed. San Diego: Academic Press. 367 p
Flora Europaea (2022) Flora Europaea website. Royal Botanic Garden Edinburgh, and European Environmental Agency. https://eunis.eea.europa.eu/references/1780/species https://eunis.eea.europa.eu/species/186664. Accessed: July 22, 2022
Forsyth AA (1976) British Poisonous Plants. London: H.S.M.O. 131 p
Fryxell PA (1957) Mode of reproduction of higher plants. Bot Rev 23:135–233
Fuller TC, McClintock E (1986) Poisonous Plants of California. Berkeley: University California Press. 433 p
Gallego-Tévar B, Grewell BJ, Gaskin JF, Castillo JM (2024) Genetic and phenotypic differentiation in functional traits of *Iris pseudacorus* L. in native and introduced Mediterranean climate ranges. Biol Invasions 26:2869–2882
Gallego-Tévar B, Grewell BJ, Whitcraft CR, Futrell JC, Bárcenas-Moreno G, Castillo JM (2022) Contrasted impacts of yellow flag iris (*Iris pseudacorus*) on plant diversity in tidal wetlands within its native and invaded distribution ranges. Diversity 14:326
Gaskin JF, Pokorny, ML, Mangold, JM (2016) An unusual case of seed dispersal in an invasive aquatic; yellow flag iris (*Iris pseudacorus*). Biol Invasions 18:2067–2075
GBIF.org (2022a) GBIF Occurrence Download. https://doi.org/10.15468/dl.ksvrrh
GBIF.org (2022b) GBIF Occurrence Download. https://doi.org/10.15468/dl.7tchjb
Gervazoni P (2024) Ecology, Distribution and Natural Enemies of the Invasive exotic Species *Iris pseudacorus*: Feasibility for Biological Control. Doctoral thesis. Cordoba, Argentina: National University of Cordoba. 127 p
Gervazoni P, Fuentes-Rodríguez D, Sosa A, Coetzee J, Bertucci S, Kramarz D, Franceschini Chayasa (2022) Preliminary assessment of potential biocontrol agents of *Iris pseudacorus* L. in the invaded range. V Chilean Symposium on Biological Control, 30 of August to September 1, Chillán, Chile (Dissertation)
Gervazoni P, Fuentes-Rodriguez D, Sosa A, Del Río G, Sabater L, Franceschini C (2021) Ensamble de insectos asociados a Especie Exótica Invasora *Iris pseudacorus* en el rango introducido Argentina. XXIX Reunión Argentina de Ecología, Tucumán, Argentina, 4 al 6 de agosto (Virtual)
Gervazoni P, Sosa A, Coetzee J, Cabañas A, Franceschini C (2023) Invasive capacity of *Iris pseudacorus* L. in the introduced range, Argentina. VII National Congress on Biodiversity Conservation (CNCB), April 24 to 28, Misiones, Argentina
Gervazoni P, Sosa A, Franceschini C, Coetzee J, Falthauser A, Fuentes-Rodriguez D, Martínez A (2020) The alien invasive yellow flag (*Iris pseudacorus* L.) in Argentinian wetlands: assessing geographical distribution through different data sources. Biol Invasions 22:3183–3193
Gerwing TG, Thomson HM, Brouard-John EK, Kushneryk K, Davies MM, Lawn P, Nelson KR (2021) Observed dispersal of invasive yellow flag iris (*Iris pseudacorus*) through a saline marine environment and growth in a novel substrate, shell hash. Appl Wetl Sci 41:1
Gillard MB, Castillo JM, Mesgaran MB, Futrell CJ, Grewell BJ (2021) High aqueous salinity does not preclude germination of invasive *Iris pseudacorus* from estuarine populations. Ecosphere 12:e03486
Gillard MB, Castillo JM, Mesgaran MB, Futrell CJ, Grewell BJ (2022) Germination niche breadth of invasive *Iris pseudacorus* (L.) suggests continued recruitment from seeds with climate warming. Am J Bot 109:1108–1119
Gioria M, Pyšek P (2017) Early bird catches the worm: germination as a critical first step in plant invasion. Biol Invasions 19:1055–1080
Gleason HA, Cronquist A (1991) Manual of Vascular Plants of Northeastern United States and Adjacent Canada. 2nd ed. New York: New York Botanical Garden. 190 p
Global Invasive Species Database (2022) Species profile: *Iris pseudacorus*. http://www.iucngisd.org/gisd/species.php?sc=873. Accessed: June 17, 2022
Goldblatt P (2000) Phylogeny and classification of the Iridaceae and the relationships of *Iris*. Ann Bot 58, https://doi.org/10.4462/annbotrm-9059
Goldblatt P, Rodriguez A, Powell MP, Davies JT, Manning JC, Van der Bank M, Savolainen V (2008) Iridaceae "Out of Australasia"? Phylogeny, biogeography, and divergence time based on plastid DNA sequences. Syst Bot 33:495–508
Good JA (1986) Insect visitors to *Iris pseudacorus* (Iridaceae) in Ireland. Ir Nat J 22:71–74
Goodridge J, Bixby M, Winter-Gorsline L, Tu M, Anderson S, Harber R, Douglas J, McMahan L, Chan S (2011) GardenSmart Oregon: A Guide to Non-invasive Plants. Portland: Nature Conservancy, Oregon Invasive Species Council. 54 p
Grewell BJ, Futrell CJ, Iannucci MT, Drenovsky RE (2019) Resprouting potential of rhizome fragments from invasive macrophyte reveals superior colonization ability of the diploid congener. AoB PLANTS 11:plz071
Grewell BJ, Gallego-Tévar B, Bárcenas-Moreno G, Whitcraft CR, Thorne KM, Buffington KJ, Castillo JM (2023) Phenotypic trait differences between *Iris pseudacorus* in native and introduced ranges support greater capacity of invasive populations to withstand sea level rise. Divers Distrib 29:834–848
Grewell BJ, Gallego-Tévar B, Gillard MB, Futrell CJ, Reicholf R, Castillo JM (2021) Salinity and inundation effects on Iris pseudacorus: implications for tidal wetland invasion with sea level rise. Plant Soil 466:275–291
Guppy HB (1912) Studies in Seeds and Fruits. London: Williams and Norgate. 528 p
Hayasaka D, Fujiwara S, Uchida T (2018) Impacts of invasive *Iris pseudacorus* L. (yellow flag) establishing in an abandoned urban pond on native semi-wetland vegetation. J Integr Agric 17:1881–1887
Henderson NC (2002) Iris. Pages 374, 388, 390 *in* Flora of North America Editorial Committee, eds. Flora of North America North of Mexico. Vol. 26. http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=116503. Accessed: July 27, 2022
Henn JJ, Anderson CB, Pastur GM (2016) Landscape-level impact and habitat factors associated with invasive beaver distribution in Tierra del Fuego. Biol Invasions 18:1679–1688
Hetherington AM, Hunter MIS, Crawford RMM (1982) Contrasting effects of anoxia on rhizome lipids in *Iris* species. Phytochem 21:1275–1278
Hill MP, Terblanche JS (2014) Niche overlap of congeneric invaders supports a single-species hypothesis and provides insight into future invasion risk: implications for global management of the *Bactrocera dorsalis* complex. PLoS ONE 9:e90121
Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199:142–152
Hitchcock CL, Cronquist A, Ownbey M, Thompson JW (1969) Vascular Plants of the Pacific Northwest. Vol. 1. Seattle: University of Washington Press. P 925
Howell CJ (2008) Consolidated List of Environmental Weeds in New Zealand. Wellington, New Zealand: Science & Technical Publications, Department of Conservation. P 26
Huertas Herrera A, Lencinas MV, Toro Manríquez M, Miller JA, Martínez Pastur G (2020) Mapping the status of the North American beaver invasion in the Tierra del Fuego archipelago. PLoS ONE 15:e0232057
Huiskes AHL, Koutstaal BP, Herman PMJ, Beeftink WG, Markusse MM, de Munck W (1995) Seed dispersal of halophytes in tidal salt marshes. J Ecol 83:559–567
Hunter RG, Combs DL, George DB (2001) Nitrogen, phosphorous, and organic carbon removal in simulated wetland treatment systems. Arch Environ Contam Toxicol 41:274–281

https://doi.org/10.1017/inp.2024.35 Published online by Cambridge University Press

Hyde MA, Wursten BT, Ballings P, Coates Palgrave M (2022) Flora of Zimbabwe: Cultivated Plants: Species Information: *Iris pseudacorus*. https://www.zimbabweflora.co.zw/cult/species.php?species_id=231910. Accessed: June 25, 2022

InBUy (2011) *Iris pseudacorus* L. http://inbuy.fcien.edu.uy/fichas_de_especies/DATAonline/DBASEonline/Iris_pseudacorus_w.pdf. Accessed: July 27, 2022

Jaca T, Mkhize V (2015) Distribution of *Iris pseudacorus* (Linnaeus, 1753) in South Africa. BioInvasions Rec 4:249–253

Jaca TP (2013) *Iris pseudacorus* L.: an ornamental aquatic with invasive potential in South Africa. S Afr J Bot 86:174

Jacobs J, Graves M, Mangold J (2010a) Ecology and Management of Yellow Flag Iris (*Iris pseudacorus* L.). Bozeman: USDA–Natural Resources Conservation Service, Montana State Office. 12 p

Jacobs J, Graves M, Mangold J (2010b) Plant Guide for Pale Yellow Iris (*Iris pseudacorus*). Bozeman: USDA–Natural Resources Conservation Service, Montana State Office. 3 p

Jacobs J, Pokorny M, Mangold J, Graves-Medley M (2011) Biology, Ecology and Management of Yellow Flag Iris (*Iris pseudacorus* L.). Bozeman: Montana State University. 12 p

Kadono Y (2004) Alien aquatic plants naturalized in Japan: history and present status. Glob Environ Res 8:163–169

Kalesnik F, Malvárez AI (2004) Las especies exóticas invasoras en los sistemas de humedales. El caso del Delta inferior del Río Paraná. Pages 131–138 *in* Aceñolaza FG, coordinating ed. Temas de la biodiversidad del Litoral Fluvial Argentino. Miscelanea 12. Tucumán, Argentina: INSUGEO

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

King County Noxious Weed Control Program (2009) Best Management Practices: Yellow-Flag Iris (*Iris pseudacorus*) Iridaceae. Seattle, WA: King County Department of Natural Resources and Parks, Water and Land Resources Division, Noxious Weed Control Program. http://your.kingcounty.gov/dnrp/library/water-and-land/weeds/BMPs/yellow-flag-iris-control.pdf

Klinkenberg B, ed (2010) *Iris pseudacorus* L. *In* E-Flora BC: Electronic Atlas of the Plants of British Columbia. Vancouver: Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia. https://ibis.geog.ubc.ca/biodiversity/eflora. Accessed: July 25, 2022

Lamote V, Roldán-Ruiz I, Coart E, De Loose M, Van Bockstaele E (2002) A study of genetic variation in *Iris pseudacorus* populations using amplified fragment length polymorphisms (AFLPs). Aquat Bot 73:19–31

Larue C, Korboulewsky N, Wang R, Mevy JP (2010) Depollution potential of three macrophytes: exudated, wall-bound and intracellular peroxidase activities plus intracellular phenol concentrations. Bioresource Technol 101:7951–7957

Leck MA, Leck CF (2005) Vascular plants of a Delaware River tidal freshwater wetland and adjacent terrestrial areas: seed bank and vegetation comparisons of reference and constructed marshes and annotated species list. J Torrey Bot Soc 132:323–354

Lenssen JPM, Menting FBJ, van der Putten, WH, Blom CWPM (1999) Effects of sediment type and water level on biomass production of wetland plant species. Aquat Bot 64:151–165

Lenssen JPM, ten Dolle GE, Blom CWPM (1998) The effect of flooding on the recruitment of reed marsh and tall forb plant species. Plant Ecol 139:13–23

Linnaeus C (1753) Species Plantarum. Vol. 1. London. 38 p

Liu H, Stiling P, Pemberton RW, Peña J (2006) Insect herbivore faunal diversity among invasive, non-invasive and native *Eugenia* species: implications for the enemy release hypothesis. Fla Entomol 89:475–484

Lui K, Butler M, Allen M, Snyder E, da Silva J, Brownson B, Ecclestone A (2010) Field Guide to Aquatic Invasive Species: Identification, Collection and Reporting of Aquatic Invasive in Ontario Waters. 3rd ed. Ontario, Canada: Ministry of Natural Resources. 201 p

Mandal A, Mondal AK (2011) Studies on antimicrobial activities of some selected ferns and lycophytes in Eastern India with special emphasis on ethno-medicinal use. Afr J Plant Sci 5:412–420

Manning J, Goldblatt P (2008) The Iris Family: Natural History and Classification. Portland, OR: Timber Press. Pp 200–204

Manzoor SA, Griffiths G, Lukac M (2018) Species distribution model transferability and model grain size—finer may not always be better. Sci Rep 8:1–9

Masciadri S, Brugnoli E, Muniz P (2010) InBUy database of invasive and alien species (IAS) in Uruguay: a useful tool to confront this threat to biodiversity. Biota Neotrop 10:205–213

Maw R (2010) Section 72 Analysis for 5-Year Review Results: Canterbury Regional Pest Management Strategy 2005–2015. Canterbury, UK: Canterbury Regional Council. 145 p

McGrannachan C, Barton J (2019) Feasibility of Biological Control of Yellow Flag Iris, *Iris pseudacorus* L. (LC3487). Auckland, New Zealand: Manaaki Whenua–Landcare Research. 63 p

Mercado Libre (2022) Lirios amarillos. https://listado.mercadolibre.com.ar/lirios-amarillos. Accessed: April 30, 2022

Ministry of Environment and Sustainable Development of Argentina (2022) Lista de especies exóticas invasoras, potencialmente invasoras y criptogénicas. https://www.argentina.gob.ar/ambiente/biodiversidad/exoticas-invasoras/buscador-especies. Accessed: June 17, 2022

Minuti G, Coetzee JA, Ngxande-Koza S, Hill MP, Stiers I (2021) Prospects for the biological control of *Iris pseudacorus* L. (Iridaceae). Biocontrol Sci Technol 31:314–335D

Minuti G, Coetzee JA, Stiers I (2023) Contrasting effects of climate change on the invasion risk and biocontrol potential of the invasive *Iris pseudacorus* L. between Northern and Southern Hemisphere. Biol Control 184:105290

Minuti G, Stiers I, Coetzee JA (2022) Climatic suitability and compatibility of the invasive *Iris pseudacorus* L. (Iridaceae) in the Southern Hemisphere: considerations for biocontrol. Biol Control 169:104886

Mohsin M, Nawrot N, Wojciechowska E, Kuittinen S, Szczepańska K, Dembska G, Pappinen A (2023) Cadmium accumulation by *Phragmites australis* and *Iris pseudacorus* from stormwater in floating treatment wetlands microcosms: insights into plant tolerance and utility for phytoremediation. J Environ Manag 331:117339

Mopper S, Wiens KC, Goranova, GA (2016) Competition, salinity, and clonal growth in native and introduced irises. Am J Bot 103:1575–1581

Morgan VH, Berent L, Fusaro A (2020) *Iris pseudacorus* L. U.S. Nonindigenous Aquatic Species Database. https://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=1115. Accessed: June 17, 2022

Mulqueen J, Gleeson TN (1988) Association of the yellow flag (*Iris pseudacorus* L.) with ground-water seepage and its possible use as an indicator plant. Irish J Agric Res 27:106–110

Murphy K, Carvalho P, Efremov A, Grimaldo JT, Molina-Navarro E, Davidson TA, Thomaz SM (2020) Latitudinal variation in global range-size of aquatic macrophyte species shows evidence for a Rapoport effect. Freshwater Biol 65:1622–1640

Murphy K, Efremov A, Davidson TA, Molina-Navarro E, Fidanza K, Betiol TCC, Chambers P, Grimaldo JT, Martins SV, Springuel I, Kennedy M, Mormul RP, Dibble E, Hofstra D, Lukács BA, et al. (2019) World distribution, diversity and endemism of aquatic macrophytes. Aquat Bot 158:103127

Natural History Museum (2014) Collection specimens [*Iris pseudacorus* L.]. https://doi.org/10.5519/0002965. Accessed: January 31, 2023

Naturalista (2022) Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. https://www.naturalista.mx/taxa/47779-Iris-pseudacorus. Accessed: June 24, 2022

Nature Conservation Decree (1997) 160/1997 as Amended by 916/1997, 14/2002 and 913/2005, Finlex

NatureGate (2022) Yellow Iris *Iris pseudacorus*. Helsinki: Nature Gate Working Research Group, University of Helsinki, Finland. https://luontoportti.com/en/t/403/yellow-iris. Accessed: July 26, 2022

Negrut G, Nicolin A, Neacşu A (2018) The study of some anatomical features in stems and leaves of macrophytes (*Hippuris vulgaris* L., *Iris pseudacorus* L. and *Nuphar lutea* (L.) Sm.). Res J Agric Sci 50:420–429

Neiff JJ (1990) Aspects of primary productivity in the lower Paraná and Paraguay riverine system. Acta Limnol Bras 3:77–113

Pérez-Sirvent C, Hernández-Pérez C, Martínez-Sánchez J, García-Lorenzo M, Bech J (2017) Metal uptake by wetland plants: implications for phytoremediation and restoration. J Soils Sediments 17:1384–1393

Phillips SJ, Anderson RP, Dudík M, Schapire E, Blair ME (2017) Opening the black box: an open-source release of Maxent. Ecography 40:887–893

Preece SJ (1964) *Iris pseudacorus* in Montana. Proc Mont Acad Sci 24:1–4

Puliafico KP, Schwarzlaender M, Harmon BL, Hinz HL (2008) Effect of generalist insect herbivores on introduced *Lepidium draba* (Brassicaceae): implications for the enemy release hypothesis. J Appl Entomol 132:519–529

https://doi.org/10.1017/inp.2024.35 Published online by Cambridge University Press

Pyšek P, Prach K (1993) Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J Biogeogr 20:413–420
QGIS Development Team (2020) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org
R Development Core Team (2019) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing
Raghu S, Morin L, Pratt P (2017) Prioritizing Weed Targets for Biological Control in the Western USA. Canberra, Australia: CSIRO. P 45
Rahimi V, Grouh H, Solymani A, Bahermand N, Meftahizade H (2011) Assessment of cytological and morphological variation among Iranian native *Iris* species. African J Biotechnol 10:8805–8815
Rakhimov DA, Kholmuradova TN, Shoyakubov RS (2006) Polysaccharide accumulation dynamics in *Iris pseudacorus*. Chem Nat Compd 42:259–261
Ramey V, Peichel B (2001) Yellow flag (*Iris pseudacorus*). Gainesville: Center for Aquatic and Invasive Plants, University of Florida. http://plants.ifas.ufl.edu/plant-directory/iris-pseudacorus. Accessed: June 17, 2022
Raunkiaer C (1934) Life Forms of Plants and Statistical Plant Geography [English translation of collected papers by C. Raunkiaer 1903]. Oxford: Calderon Press. 648 p
Raven PH, Thomas JH (1970) *Iris pseudacorus* in western North America. Madrono 20:390–391
Roland AE (1945) The flora of Nova Scotia. Proc Nova Scotia Inst Sci 21:95–642
Rosbakh S, Phartyal SS, Poschlod P (2020) Seed germination traits shape community assembly along a hydroperiod gradient. Ann Bot 125:67–78
Sandenbergh E (2021) The Invasion Autecology of *Iris pseudacorus* L. (Iridaceae) in South Africa. Master's thesis. Makhanda, South Africa: Rhodes University. 101 p
Sandenbergh E, Petruzzella A, Coetzee J (2024) Distribution and sexual reproductive potential of *Iris pseudacorus* L. (Iridaceae) in South Africa. S Afr J Bot 167:31–39
Sarver M, Treher A, Wilson L, Naczi R, Kuehn FB (2008) Mistaken Identity? Invasive Plants and Their Native Look-Alikes—An Identification Guide for the Mid-Atlantic. Dover: Delaware Department of Agriculture and USDA Natural Resources Conservation Service. 68 p
Schlüter U, Crawford RM (2001). Long-term anoxia tolerance in leaves of *Acorus calamus* L. and *Iris pseudacorus* L. J Exp Bot 52:2213–2225
Sharma S, Raval AJ, Koneri R, Sharma GK, Chandrul KK (2022) An exploration for protective effect of rhizome extract of *Iris pseudacorus* L. and seed extract of *Dolichos biflorus* L. in sodium oxalate induced urolithiasis in rat model. Int J Pharm Sci Rev Res 74:187–197
Silvertown J (2008) The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. Int J Plant Sci 169:157–168
Sonntag E (2021) Overcoming Adversity: Promise of Recovery of Native Plants in a Temperate Wetland Community Following Removal of Yellow Flag Iris (*Iris pseudacorus* L.) Using Benthic Barriers. Doctoral dissertation. Colwood, Canada: Royal Roads University. 103 p
Stone KR (2009) *Iris pseudacorus*. *In* Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. https://www.fs.fed.us/database/feis/plants/forb/iripse/all.html. Accessed: June 24, 2022
Stoneburner AL, Meiman PJ, Ocheltree TW, Nissen SJ, Bradfield SJ (2021) Simulated trampling by cattle negatively impacts invasive yellow-flag iris (*Iris pseudacorus*) when submerged. Invasive Plant Sci Manag 14:232–239
Strong MT, Kelloff CL (1994) Intertidal vascular plants of Brent March, Potomac River, Stafford County, Virginia. Castanea 59:354–366
Suiter DW, Evans DK (1999) Vascular flora and rare species of New River Gorge National River, West Virginia. Castanea 64:23–49
Sutherland WJ (1990) Biological flora of the British Isles, no. 169. J Ecol 78:833–848
Sutherland WJ, Walton D (1990) The changes in morphology and demography of *Iris pseudacorus* L. at different heights on a saltmarsh. Funct Ecol 4:655–659
Suzuki H, Yamagata H (1980) Promotion of *Iris* seed germination. Jpn J Breed 30:161–169
Tanner CC, Clayton JS, Coffey T (1990) Submerged-vegetation changes in Lake Rotoroa (Hamilton, New Zealand) related to herbicide treatment and invasion by *Egeria densa*. NZ J Mar Fresh 24:45–57
Tarasoff CS, Streichert K, Gardner W, Heise B, Church J, Pypker TG (2016) Assessing benthic barriers vs. aggressive cutting as effective yellow flag iris (*Iris pseudacorus*) control mechanisms. Invasive Plant Sci Manag 9:229–234
Te Waihora Co-Governance (2019) Weed Watch—Yellow Flag Iris. https://tewaihora.org/weed-watch-yellow-flag-iris. Accessed: June 17, 2022
Thomas LK Jr (1980) The Impact of Three Exotic Plant Species on a Potomac Island. National Park Service Scientific Monograph Series No. 13. Washington, DC: U.S. Department of the Interior, National Park Service. 179 p
Thomson HM, Davies MM, Lawn PT, Kushneryk K, Brouard-John EK, Nelson KR, Gerwing TG (2021) Spread of an aquatic invasive plant, *Iris pseudacorus*, following replacement of a hydraulic structure. Ecol Restor 39:238–246
Torrey Botanical Club (1888) Preliminary Catalog of Anthophyta and Pteridophyta, Reported as Growing Spontaneously Within One Hundred Miles of New York City. New York: Columbia College Herbarium. 90 p
Tu M (2003) Element Stewardship Abstract for *Iris pseudacorus* L. (Yellow Flag Iris, Water Flag). Arlington, VA: Nature Conservancy. http://www.invasive.org/weedcd/pdfs/tncweeds/irispse.pdf. Accessed: June 17, 2022
Tulika T, Mala A (2015) Pharmaceutical potential of aquatic plant *Pistia stratiotes* (L.) and *Eichhornia crassipes*. J Plant Sci 3:10–18
Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH, Walters SM, Webb DM, eds (1980) Flora Europaea: Alismataceae to Orchidadeae (Monocotyledones). Vol. 5. Cambridge: Cambridge University Press. 476 p
Tyron P (2006) Yellow Flag Iris Control, in the Mission Valley of Western Montana. Presented at the 2006 Washington State Weed Conference, Yakima, WA. St Ignatius, MT: Lake County Weed Control
Ugarte E, Lira F, Fuentes N, Klotz S (2011) Vascular alien flora, Chile. Check List 7:365–382
van den Broek T, van Diggelen R, Bobbink R (2005) Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. J Veg Sci 16:579–586
van der Valk AG, Verhoeven JTA (1988) Potential role of seed banks and understory species in restoring quaking fens from floating forests. Vegetatio 76:3–13
van Klinken RD, Raghu S (2006) A scientific approach to agent selection. Aust J Entomol 45:253–258
van Slooten L (2016) Invasives: yellow flag iris (*Iris pseudacorus*). WNY Gardening Matters. https://erie.cce.cornell.edu/resources/article-1-invasive-yellow-flag-iris. Accessed: June 12, 2024
Vecrin MP, Grevilliot F, Muller S (2007) The contribution of persistent soil seed banks and flooding to the restoration of alluvial meadows. J Nat Conserv 15:59–69
Voigt D, Gorb S, Boevé JL (2011) Superhydrophobic cuticle with a "pinning effect" in the larvae of the iris sawfly, *Rhadinoceraea micans* (Hymenoptera, Tenthredinidae). Zoology 114:265–271
Wang Q, Yang J, Li C, Xiao B, Que X (2013) Influence of initial pesticide concentrations in water on chlorpyrifos toxicity and removal by *Iris pseudacorus*. Water Sci Technol 67:1908–1915
Weatherbee PB, Somers P, Simmons T (1998) A Guide to Invasive Plants in Massachusetts. Westborough: Massachusetts Division of Fisheries and Wildlife. 23 p
Wells EF, Brown RL (2000) An annotated checklist of the vascular plants in the forest at historic Mount Vernon, Virginia: a legacy from the past. Castanea 65:242–257
Welsh SL, Atwood ND, Goodrich S, Higgins LC, eds (1987) A Utah Flora. The Great Basin Naturalist Memoir No. 9. Provo, UT: Brigham Young University. 894 p
Wheeler AS, Wilson CA (2014) Exploring phylogenetic relationships within a broadly distributed Northern Hemisphere group of semi-aquatic *Iris* species (Iridaceae). Syst Bot 39:759–766
Whitehead FH (1971) Comparative autecology as a guide to plant distribution. Pages 167–176 *in* Duffey EO, Watt AS, eds. The Scientific Management of Animal and Plant Communities for Conservation: Proceedings of the 11th Symposium of the British Ecological Society. Oxford: Blackwell Scientific
Wildland Consultants (2011) Current Extent and Potential Distribution of Yellow Flag Iris in Parts of the Lower Waikato River Catchment. Hamilton,

https://doi.org/10.1017/inp.2024.35 Published online by Cambridge University Press

New Zealand: Prepared for Department of Conservation and Waikato Regional Council. 33 p
Williams PA, Champion PD (2008) Biological Success and Weediness of Existing Terrestrial Pest Plants and Aquatic Weeds in Northland. Landcare Research Contract Report LC0708/080. Lincoln, New Zealand: Prepared for Northland Regional Council. 55 p
Wilson CA (2006) Patterns in evolution in characters that define *Iris* subgenera and sections. Aliso: J Syst Flor Bot 22:425–433
Wilson CA (2011) Subgeneric classification in *Iris* re-examined using chloroplast sequence data. Taxon 60:27–35
World Flora Organization (2022) *Iris pseudacorus* L. http://www.worldfloraonline.org/taxon/wfo-0000783754. Accessed: July 30, 2022
Wu J, Cui N, Cheng S (2013) Effects of sediment anoxia on growth and root respiratory metabolism of *Iris pseudacorus*: implications for vegetation restoration of eutrophic waters in China. Ecol Eng 53:194–199
Xiong W, Wang H, Wu Z, Xiao K, Li T, Bowler PA (2023) Ecological and economic impacts of alien invasive yellow flag (*Iris pseudacorus* L.) in China. Sustainability 15:5905
Yousefi Z, Mohseni-Bandpei A (2010). Nitrogen and phosphorus removal from wastewater by subsurface wetlands planted with *Iris pseudacorus*. Ecol Eng 36:777–782
Yu X, Yue L, Wu Q, Yang L, Fan C, Wang Z, Hu J (2022) Transcriptome analysis and morphological changes in response to waterlogging in *Iris pseudacorus*. Phyton 91:2136–2162
Zhang XB, Liu P, Yang YS, Chen WR (2007) Phytoremediation of urban wastewater by model wetlands with ornamental hydrophytes. J Environ Sci 19:902–909
Zhao H, Wang F, Ji M (2015) Brackish eutrophic water treatment by *Iris pseudacorus* L. in planted microcosms. Int J Phytoremediat 17:814–821
Zhou YQ, Huang SZ, Yu SL, Gu JG, Zhao JZ, Han YL, Fu JJ (2010) The physiological response and sub-cellular localization of lead and cadmium in *Iris pseudacorus* L. Ecotoxicology 19:69–76
Zilio M, Restrepo AFS, Gervazoni P, Minuti G, Muzón J, Djeddour D, Sosa A (2025) Economic loss of ecosystem services caused by yellow flag iris and white ginger lily, two invasive alien plants in natural ecosystems of Argentina. J Nat Conserv 84:126789
Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Antonelli A (2019) *CoordinateCleaner*: standardized cleaning of occurrence records from biological collection databases. Methods Ecol Evol 10:744–751

Appendix

Species Distribution Model

Occurrence records for *I. pseudacorus* were sourced from the Global Biodiversity Information Facility portal (GBIF.org 2022a; GBIF.org 2022b). 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 visualized in QGIS software v. 3.14 (QGIS Development Team 2020), and suspicious records that could not be confirmed or corrected were excluded. The dataset was then filtered to minimize 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 v. 3.6.1 (R Development Core Team 2019).

Bioclimatic predictors were obtained from WorldClim 2.1 (Fick and Hijmans 2017) at a resolution of 2.5 arcmin. 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, among highly correlated variables ($|r| > 0.75$), based on their model contribution (i.e., jackknife analysis) and in 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 one 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 modeling settings were 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 modeling was defined based on broad bioclimatic zones (Hill and 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 (for details, see Minuti et al. 2021). The Multivariate Environmental Similarity Surface (MESS) was used to assess coverage of environmental gradients upon model projection and identify areas of uncertainty (Elith 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 Area Under the Curve (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 v. 3.6.1.

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