Biological Flora of Central Europe: *Impatiens glandulifera* Royle

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1. Abstract

This paper presents all current knowledge on the biology of the invasive therophyte *Impatiens glandulifera* Royle (Himalayan Balsam), and covers aspects of taxonomy, morphology, distribution, habitat requirements, ecology, life cycle, genetics, history of invasive spread, ecological impact and management. Although a few review papers have been published on this species in previous decades, a great deal of insights have been gained in the last three decades, owing to the species' notorious reputation as one of the most problematic invasive species in Europe. This study consequently focusses on this novel information, with a particular focus on information from Central Europe.

2. Introduction

The therophyte *Impatiens glandulifera* Royle (Himalayan Balsam) is considered one of the most problematic invasive plant species in Europe. Consequently, much research has been performed on this species in the last decades. The last reviews on this species, however, data back to the last two decades (Beerling and Perrins, 1993; Clements et al., 2008; Cockel and Tanner, 2011). Consequently, this study aims at synthesizing the latest research on this species, combining information on the species' general biology and its invasive spread, impact and management across its full range. More specifically, we firstly update the information provided in Beerling and Perrins (1993) on *I. glandulifera*'s taxonomy, morphology, distribution, habitat requirements, ecology, life cycle, biotic interactions and genetic data. Secondly, we combine this information with an overview of the insights gained on the species' invasive behaviour, ecosystem impact and management; research fields that have received particular research attention during the last decades.

3. Taxonomy and morphology

3.1. Taxonomy

Impatiens glandulifera Royle is a balsam species of the genus *Impatiens*, within the Balsaminaceae family. The family includes only two genera: *Impatiens* L. (c. 900 species) and *Hydrocera* Blume (1 species). The family Balsaminaceae was formerly treated as a separate order, i.e. the Balsaminales, or classified as a member of the order Geraniales. Recent molecular phylogenetic analyses revealed that Balsaminaceae is part of the Ericales (which currently comprises 22 families in the APG IV system (Stevens, 2001)), and sits as sister group to all other Balsaminoid Ericales (Marcgraviaceae, Pellicieraceae and Tetrameristaceae families) (Anderberg et al., 2002; Geuten et al., 2004). *Impatiens* species are mostly native to tropical mountain forests of the old world. Only one species (*I. noli-tangere* L.) is native to Europe. *I. glandulifera* is part of a basal clade within the Balsaminaceae, containing species that are mainly distributed in the Himalaya and regions of Eurasia with a temperate climate (Janssens et al., 2006). The family includes many species of ornamental interest, with *Impatiens walleriana* Hook.f. and *I. hawkeri* W. Bull being among the most sold ornamentals worldwide (Grey-Wilson, 1983). Some of these ornamentals have become highly invasive, such as *I. capensis* Meerb., *I. parviflora* D.C., *I. balfouri* Hook.f and *I. glandulifera* in Europe; I. *walleriana* in the tropics and *I. niamniamensis* Gilg in New Zealand (Adamowski, 2008).

The Plant List currently mentions 5 resolved synonyms of *I. glandulifera* Royle, including *I. macrochila* Lindl., *I. roylei* Walpers, *Balsamina glandulifera* (Royle) Ser., *B. macrochila* (Lindl.) Ser. and *B. roylei* (Walp.) Ser. (The Plant List, 2013). Special attention should be paid to the author abbreviation since *I. glandulifera* Arn. is a distinct species, synonym of *I. taprobanica* Hiern, native to Sri Lanka. Three infraspecific taxa (i.e. forms) of *I. glandulifera* have furthermore been distinguished according to the colour of flowers: *albida* (Hegi) B. Boivin: white flowers; *pallidiflora* (Hook. f.) Weath.: light pink flowers; and *glandulifera* Vahl: dark pink flowers (Ebel and Mikhailova, 2016; Missouri Botanical Garden, 2008).

Common names include Himalayan balsam, Indian balsam, Policeman's helmet, Gnome's hatstand, Bobby tops, Kiss-me-on-the-mountain, and Ornamental jewelweed (English); Drüsiges Springkraut, Indisches Springkraut, Drüsenspringkraut, Drüsentragendes Springkraut, Riesenspringkraut (German); Netýkavka žláznatá (Czech); Netýkavka žliazkatá (Slovak); Žlezava nedotika (Slovene); Nedirak (Croatian); Bíbor nebáncsvirág (Hungarian); Niecierpek gruczołowaty, Niecierpek himalajski, Niecierpek Roylego (Polish).

Hybrids between *I. glandulifera* and other *Impatiens* species have not been reported to date. However, natural pollen transfer between *I. glandulifera* and *I. balfourii* by pollinators has been observed in France and artificial pollination between the two species results in seed production, although these seeds germinated only occasionally (Ugoletti et al., 2013).

3.2. Morphology

I. glandulifera has an erect, solitary, tall, thick stem, green to reddish in colour, usually simple or sometimes branching, usually 5-50 mm in diameter (Fig. 1A) (Beerling and Perrins, 1993). Plants can usually reach 1-2 (2.5) meter in height, and even 3 m plants have occasionally been reported, making it the tallest annual species in the UK and likely also in the rest of Europe (Andrews et al., 2005; Chittka and Schürkens, 2001; Grime et al., 1988; Willis and Hulme, 2004). The whole plant is glabrous (Balogh, 2008). The stems are hollow and thickened at the nodes, with strengthening elements (a ring of lignified vascular tissue containing lignin and holocellulose) located in the periphery, which increases the mechanical resistance to bending

(Beerling and Perrins, 1993; Ennos et al., 1993; Spatz et al., 1990). How tall *I. glandulifera* individuals grow depends on many abiotic and biotic factors, including soil nutrients and moisture (Grime et al., 1988), temperature (growing degree hours) (Helsen et al., 2017), latitude (length of the growing season, photoperiod) (Helsen et al., 2020a; Kollmann and Bañuelos, 2004), and the level of irradiance (see parts 5.6, 5.9 and 6.3). In its native range the species was found to have a smaller plant height than in Europe in some (Gruntman et al., 2020; Tanner et al., 2008), but not all studies (Tanner et al., 2014b).

I. glandulifera has two contrasting root forms: 2-4 cylindrical primary or seminal roots of 2-3 mm diameter, with an anatomy typical of dicot roots, and numerous (146 ±35) tapered, fleshy adventitious roots, of an average length of 15-20 cm, showing a stem-like anatomy, with similar peripheral strengthening elements. The adventitious roots emerge from the hollow, wide stem base. Roots grow downwards, and form the shape of an inverted cone with top diameter reaching c. 6 cm, and length c. 8 cm. The adventitious roots grow in irregular concentric circles (rows), emerging progressively higher up the stem, therefore the large, upper ones are the youngest. Numerous, narrow lateral roots emerge from the upper parts of the main roots, which are responsible for resource acquisition (Ennos et al., 1993). The rooting depth ranges from 10 to 50 cm (Fitter and Peat, 1994). Plants can also form adventitious roots on the stem when wounded, allowing re-rooting of broken or bent stems (Fig. 1D) (Beerling and Perrins, 1993; McClatchie, 1917).

Leaves are set opposite or arranged in whorls of 2-5 (Tanner, 2011), although more whorls develop in shaded conditions (Kostrakiewicz-Gierałt, 2015). The leaves are lanceolate to elliptic-ovate, serrulate to sharply toothed, with 18-50 teeth on each side, cuneate, glandular and shortly decurrent at base and acuminate at their apex (Fig. 1B) (Beerling and Perrins, 1993). Purple headed glands located on their base are extrafloral nectaries, which contain high levels of antimicrobial naphthoquinones (Fig. 1B) (Balogh, 2008; Block et al., 2019) (see part 5.10).

On average, leaves are 5-18 cm long and 2.5-7 cm wide, and have – not so common for terrestrial dicots – an equal amount of stomata on the adaxial (upper) and abaxial (downward) side (Beerling and Perrins, 1993) or higher on the abaxial side (277 mm^{-2}) than the adaxial side (137 mm^{-2}) (Fitter and Peat, 1994) (Fig. 2). The average leaf area is 119.10 cm^2 with a mean mass of 312 mg and average leaf dry matter content (LDMC) of 137 mg g^{-1}, resulting in an average specific leaf area (SLA) of 38.3 mm^2 mg^{-1} (Kleyer et al., 2008). The average leaf area seems to gradually decrease, and SLA gradually increase, with increasing temperature (decreasing latitude) in Europe (Helsen et al., 2020b, 2018b) (Table 1). More specifically, SLA has been found to vary between 25 and 40 mm^2 mg^{-1} in situ, and can even reach 100 mm^2 mg^{-1} under low-light greenhouse conditions (Helsen et al., 2018b; Gruntman et al., 2020). Smaller leaves have been reported to develop in well-illuminated sites (Maule et al., 2000) and in dry habitats (Grime et al., 1988), and large leaf area variation within populations seems to occur in both dry and very wet locations (Helsen et al., 2017) (see part 5.9).

The inflorescences are axillary, standing, clustering racemes, containing 2-14 dorsal flowers that are 25-40 mm long (Fig. 1A) (Beerling and Perrins, 1993). The petals are variable in colour, usually lilac, pink or purple and occasionally white (Beerling and Perrins, 1993); the latter being an anthocyanin-free form (Ebel and Mikhailova, 2016). Flowers are zygomorphic and of pungent, sweet scent (Fitter and Peat, 1994; Tanner, 2011). The five stamens are fused by their anthers and form a brush covering the stigma, with both suspended downward from the roof of the lower sepal (Kostrakiewicz-Gierałt, 2015; Vervoort et al., 2011). A lower, posterior sepal forms a sac (12–20 mm long and 9–17 mm wide) abruptly ending in an incurved spur, 2-7 mm long. Two lateral sepals are oblique cordate, and small (Balogh, 2008; Beerling and Perrins, 1993; eFloras, 2020). There are five, broad petals, the upper (dorsal) is strongly arched, and the lateral ones are joined in pairs, forming the lower lip - the landing site of pollinators, while the upper petal forms a characteristic hood above the stamens (Fig. 1C) (Balogh, 2008; Beerling and Perrins, 1993).

The fruit is a fleshy capsule, 1.5-3.5 (5.0) cm long and 0.4-1.5 cm wide, lanceolate, distinctively widening to the apex, slightly five-angled (Fig. 1A&C) (Balogh, 2008). Seeds are oval-globose and discolour from pale grey-brown to black at maturity. The seeds are 3–4 (7) mm long, 2–4.8 mm wide and 1.5–2 mm thick (Balogh, 2008; Fitter and Peat, 1994; Helmisaari, 2010) and have a rugose, ruminate seed coat type (Maciejewska-Rutkowska and Janczak, 2016). Part 5.4 contains more details on fruit and seed morphology.

4. Distribution and habitat requirements

4.1. Distribution and invasion history

I. glandulifera is reported as native to three countries in the foothills of the western Himalaya, i.e. northeast Pakistan, northwest India (Jammu and Kashmir, Himachal Pradesh, Uttarakhand) and likely western Nepal (Fig. 3A) (Beerling and Perrins, 1993; CABI, 2020; Fitter and Peat, 1994; Stace, 2019). In this relatively small range (estimated at approximately 800 km in length and 50 km in width, Tanner et al. (2008)), the species grows in the elevational belt with a temperate climate between 2000 and 4000 m above sea level (a.s.l.) (Beerling and Perrins, 1993; Hagenblad et al., 2015).

The first reported introduction of *I. glandulifera* into Europe was from Kashmir into England in 1839, where it was introduced as an ornamental plant to the Botanic Gardens at Kew (Beerling and Perrins, 1993). Within the following decade the species was also introduced across the European continent (e.g. in Sweden (1842), Austria (1845) and Czech Republic (1846)) (Čuda et al., 2020). In the late 1800s, roughly 40 years after these initial introductions, the species became naturalised, further spreading across the European continent (Britten, 1900; Čuda et al., 2020; Pyšek and Prach, 1995), and most likely also to other continents (Čuda et al., 2020; Mills et al., 1993; Nagy and Korpelainen, 2015). Population genetic analyses have indicated that *I. glandulifera* has been introduced to the UK at least 3 times from different locations in its native range (Ellison et al., 2020; Kurose et al., 2020) (see part 6.2).

The species now occurs in at least 32 countries across Europe, from the British Isles in the west to Poland, Belarus and Russia in the east, and from northern Italy, northern Spain, in the south to northern Scandinavia (Fig. 3B) (CABI, 2020; GBIF Secretariat, 2019). The species is largely absent from truly Mediterranean vegetation types. The species has recently also spread in the Balkans and the Caucasus (Fayvush and Tamanyan, 2011; GBIF Secretariat, 2019; Komzha and Popov, 1990; Pacanoski and Saliji, 2014), and is naturalized in Russia (European part, far East and, recently, the Altai Republic), China (Hunan), Japan, New Zealand, Argentina and both western and eastern Canada and USA (Fig. 3A) (Artemov and Zykova, 2019; CABI, 2020; Čuda et al., 2020; EPPO, 2020; GBIF Secretariat, 2019; Vinogradova et al., 2020). In the USA, the species was first reported from Norwich (Connecticut) in 1883 and in Canada from Ottawa in 1901, with initial introductions possibly through ship's ballast from Europe (Clements et al., 2008; Mills et al., 1993; Tabak and Von Wettberg, 2008).

Since the 1960's, *I. glandulifera* has strongly increased in abundance across most European countries (Čuda et al., 2020; Zając et al., 2011) (e.g. Fig. 4). Interestingly, increased abundances seem independent from the time of introduction, with a shorter lag phase in locations of later introduction (Pyšek and Prach, 1995). The species has furthermore strongly advanced its northern range limits in the last decades, with a c. 1400 km expansion along the entire Atlantic coast of Norway and a c. 300 km shift along the Baltic coast of Sweden (Fig. 3B&C). Remarkably, this poleward expansion was almost perfectly predicted by a species distribution model in 1993, under a 1.5 °C warming scenario (Beerling, 1993). This model included only the minimum winter temperature and the heat sum (growing degree days) as predictor variables, of which just the latter seemingly controlled the northern distribution limit. Winter temperatures nonetheless limited the species’ germination, growth and fecundity in a sowing experiment along an elevational gradient in northeast England, suggesting some importance of minimum temperatures on its European distribution (Willis and Hulme, 2002). Currently, the northernmost observation is a population northwest of Alta in northern Norway (70.2°N) (GBIF Secretariat, 2019). The spread is thus likely to continue with global warming toward higher latitudes and altitudes. It has, on the other hand, been suggested that the southern distribution boundary might move northwards in response to increasing summer drought (Beerling, 1993).

The climatic amplitude across the species' vast European range of 2,926,000 km² is wide: the mean temperature range is 8.4 °C for the whole year and 13.9 °C for the growing season (April – September) for the period 1970-2000 (Vangansbeke et al., 2020). The cold mean annual temperature limit is 5.5 °C (5 percentile of occupied grid cells) and the warm limit is 11.6 °C (95 percentile). The mean precipitation across the European range is 725 mm, with a 5 and 95 percentile of 520 and 1278 mm, respectively (Vangansbeke et al., 2020). Across the 10 km²-hectads occupied by the species in Britain, the January mean temperature was 3.7 °C, the July mean temperature 15.1 °C, and the mean precipitation 957 mm over the period 1961-1990 (Hill et al., 2004).

Unlike in its native range, *I. glandulifera* mainly occurs in lowland locations in Europe, with observations near sea level and only up to 1200 m in the Austrian Alps (Drescher and Prots, 2000) and 800 m in the Polish Carpathians (Zając et al., 2011; Zając and Zając, 2015). The mean elevation of occurrence of the species across 2954 resurveyed vegetation plots in temperate European forests, for example, was 259 m a.s.l., with a minimum of 19 m, and a maximum of 330 m a.s.l. (Zellweger et al., 2020).

4.2. Habitat

In Europe, *I. glandulifera* is most typical for river valleys and its associated riparian habitats. It grows on riverbanks, in reeds, in and along alder and willow thickets, in fens and, increasingly, also in moist deciduous or coniferous forests, as well as along forest paths (Beerling and Perrins, 1993; Čuda et al., 2020; Mossberg and Stenberg, 2018). In the latter habitats, the species often co-occurs with its congeners *I. parviflora* and *I. noli-tangere*, which, under most conditions, are competitively inferior to *I. glandulifera* (Čuda et al., 2015; Skálová et al., 2013). *I. glandulifera* occasionally colonizes roadsides in several European countries (Follak et al., 2018), and can also occur in (sub-montane) meadows, field borders and fallow, and anthropogenically disturbed land (Kiełtyk and Delimat, 2019; Kostrakiewicz-Gierałt, 2015; Prowse, 2001). In Canada, the species occurs along riverbanks, marshes, bogs, ditches and roadsides, and thus appears to occupy similar habitats as in Europe (Clements et al., 2008). With its affinity to riparian zones, *I. glandulifera*'s habitat preference in its invaded range differs from that in the Himalayas, where it is most frequent in high altitude (> 2000 m a.s.l.) meadows, ditches between fields, along roads and in fringes and openings of deciduous and coniferous forests (Cockel and Tanner, 2011; Čuda et al., 2020; Drescher and Prots, 2000).

I. glandulifera prefers moist to wet, base- and nutrient-rich soils across its European range, as reflected in its (central European) Ellenberg species indicator values for soil moisture F (8), soil acidity R (7) and soil nutrients N (7) (Ellenberg and Leuschner, 2010) and similar Swedish ecological soil indicator values for moisture (7), pH (6) and nitrogen availability (8) (Tyler et al., 2021). The latter source also provides an indicator value of 5 for soil phosphorus availability, on a scale from 1 to 5 (Tyler et al., 2021). However, the species also tolerates drier, more acidic and less fertile conditions and a broad range of soil types and textures, growing on fine or coarse alluvial soils, shingle, free-draining mineral soils and peat (Beerling and Perrins, 1993) (see part 4.4).

4.3. Communities

In Central Europe, *I. glandulifera* mainly occurs in the following communities (Drescher and Prots, 1996; Klotz et al., 2002; Tokarska-Guzik et al., 2012) (the nomenclature follows Mucina et al. (2016)):

- Hydrophilous, semi-natural, tall herb fringe communities of riverbanks and other water bodies of both lowlands and uplands (*Convolvuletalia sepium* and *Adenostylion alliariae*)
- Reed swamps of mesotrophic and eutrophic, slowly flowing or stagnating freshwater bodies (*Phragmitetalia*)
- Sedge-bed marsh vegetation (*Magnocaricetalia*)
- Willow scrub and open forests of riparian habitats (*Salicetalia purpureae*, *Salicion albae*)
- Mesotrophic, regularly flooded alder carr (*Alnetalia glutinosae*)

I. glandulifera is also regularly found in anthropogenic, disturbed habitats assigned to:

- Ruderal semi-natural fringe vegetation (*Galio-Alliarietalia*)
- Semi-natural fringe vegetation of rivers and other waters (*Convolvuletalia sepium*)
- Perennial ruderal, xerophylous vegetation (*Artemisietea vulgaris*)
- Tall herb semi-natural vegetation of forest edges and clearings (*Galeopsio-Senecionetalia sylvatici*, *Epilobion angustifolii*)

In Poland the species has been encountered in nine different Natura 2000 habitat types, largely comprising the communities described above (Adamowski et al., 2018). A distinct *I. glandulifera* dominated association termed *Impatienti-Calystegietum* has been recognized (Dajdok et al., 2003), and the species was also found in sub-montane fresh meadows and road verges of the *Molinio-Arrhenatheretea* class (Kiełtyk and Delimat, 2019). In the UK, four main communities with *I. glandulifera* were distinguished: riverine, partly inundated communities, *Phragmites-Urtica* fens, mesotrophic grasslands, and different types of woodland, including

Alnus glutinosa-Urtica dioica woodland, both the typical and *Sambucus nigra* subtypes (i.e. NVC classification type W6a and W6d) (Beerling and Perrins, 1993; Fitter and Peat, 1994). For Sweden, the following broad vegetation types containing *I. glandulifera* are distinguished: Tall herb/sedge/reed meadows; Eutrophic water & shores; Ruderal communities; Hedgerows, thickets, wood-margins and groves; and *Alnus glutinosa* swamps (Tyler et al., 2021).

The species most frequently co-occurring with *I. glandulifera* in riparian habitats are relatively constant across Europe and consist mostly of perennial, tall forbs and grasses (Table 2) (e.g. Beerling and Perrins, 1993; Dajdok et al., 2003; Diekmann et al., 2016; Drescher and Prots, 1996; Helsen et al., 2018b; Kiełtyk and Delimat, 2019; Prowse, 2001). Species of other life forms, such as vines and woody species, are less often associated. Among the frequent and/or abundant associates of *I. glandulifera* in Central Europe are also *Carduus crispus*, *Glyceria maxima*, *Lamium maculatum*, *Myosoton aquaticum* and *Symphytum officinale* (Hejda and Pyšek, 2006; Helmisaari, 2010; Oberdorfer, 1983). In the UK, *I. glandulifera* additionally occurs quite frequently with *Lamium album* (Hulme and Bremner, 2006).

Woody species most often co-occurring with *I. glandulifera* are *Alnus* sp., *Fraxinus excelsior* and *Salix* sp. (Kostrakiewicz-Gierałt and Zajac, 2014; Vinogradova et al., 2020). Especially at disturbed fertile sites, *I. glandulifera* may co-occur with other neophytes such as *Solidago gigantea*, *I. parviflora*, *Aster* sp., *Fallopia* sp. and *Echinocystis lobata*, the latter occurring solely in Eastern Europe (Drescher and Prots, 1996). Such communities were described as a separate *Impatienti-Solidaginetum* for the hilly and (sub-) montane regions in Switzerland (Moor, 1958) and in the Czech Republic (Kopecký, 1967; Lhotska and Kopecký, 1966).

The most frequent companion of *I. glandulifera* in Europe is *Urtica dioica* (Table 2). The two species compete strongly: while the perennial *Urtica* starts to grow in early spring and has a fast growth rate, *I. glandulifera* germinates later, but is capable of withstanding the shade and root competition and, with an even higher growth rate, overtops *U. dioica* by mid-summer, before flowering. Although the dominant aspect of *I. glandulifera* suggests that the species has a strong negative effect on species diversity, it appears to fill the niche that otherwise *U. dioica* would have taken up (Gruntman et al., 2014; Koenies and Glavac, 1979; Tickner et al., 2001).

In its native range, *I. glandulifera* often occurs in tall herb communities in the scrublands and pastures of the Himalayan cedar (*Cedrus deodara*) mixed forest zone (Balogh, 2008). Here the species can be considerably smaller than in Europe, and forms small populations of 30-60 individuals, mixed in with other native vegetation (Tanner et al., 2008, but see Tanner et al., 2014b). Co-occurring species include representatives of the Asteraceae, Cannabaceae (e.g. *Cannabis* sp.), Fabaceae, Poaceae, Polygonaceae (e.g. *Persicaria wallichii, Rumex* sp.) and Ranunculaceae. It also co-occurs with several congeners, including *I. radiata*, *I. scabrida* and *I. sulcata* (Tanner et al., 2014b).

4.4. Response to abiotic factors

The species clearly prefers moist to wet soils. A high soil moisture is especially favourable for germination, which furthermore requires more or less bare soil. Germination, seedling establishment and survival are consequently facilitated by some disturbance as frequently found along rivers and shorelines. However, too high soil moisture seemingly reduces *I. glandulifera* cover (Pattison et al., 2019), and early season flooding can strongly reduce seedling survival (Tickner et al., 2001). Measurements of soil moisture have furthermore shown that the species can also grow on soils that are, at least temporarily, relatively dry (Table 3) (also indicated by the vegetation types in which it occurs, see part 4.3) (Maule et al., 2000). The species is nonetheless sensitive to drought, which can cause wilting, and has been shown to cause vivid red anthocyanin coloration of plants (Beerling and Perrins, 1993; Fitter and Peat, 1994).

I. glandulifera tolerates a wide spectrum of environmental factors. Soil pH (measured in $CaCl_2$) varies between c. 3.4 (Perrins et al., 1993) and 7.5 (Beerling and Perrins, 1993) (Table 3), with an ecological optimum at moderately high values. In exceptional cases, the species was recorded at pH values of up to 7.6 – 7.7 on calcareous deposits (Beerling and Perrins, 1993). While the upper limit appears to be defined by the availability of sites, the lower limit is possibly an effect of increasing aluminium toxicity and low nitrate availability at high soil acidity. The species is nonetheless tolerant to Mg, with a 19-fold variation in soil Mg concentrations observed for Belgian sites invaded *by I. glandulifera* (Dassonville et al., 2008). *I. glandulifera* furthermore shows hypertolerance for cadmium (Cd), with no effects on biomass and germination after exposure to, respectively 150 mg kg^{-1} and 1000 mg kg^{-1} Cd (Coakley et al., 2019).

The species also has a broad range in soil nutrient availability, occurring on sites with both low and high soil C/N ratios and cation concentrations (Table 3), but as reflected in the ecology of the main habitats, the species mainly occurs in sites with relatively high soil fertility. The ecological optimum of *I. glandulifera* at sites with high soil moisture, pH and fertility (also see part 4.2) may reflect its physiological optimum enabling its high growth.

Although *I. glandulifera* can occur in open, unshaded vegetation, especially at higher latitudes in Europe, it often occurs in (partly) shaded areas. The species is indeed quite shade tolerant and often found in light *Salix* and *Alnus* woodlands, and it can locally be abundant even under closed canopies (Table 3) in forest interiors (Čuda et al., 2020, 2017b; Gaggini et al., 2018; Kostrakiewicz-Gierałt and Zajac, 2014). In fact, *I. glandulifera* shows an optimum curve along the gradient of light availability, being most frequent and healthy at moderate levels of shade (Čuda et al., 2014; Diekmann et al., 2016; Maule et al., 2000), which coincides with its Ellenberg light value of 5. This is furthermore reflected in the highest population biomass (up to 559 g dry weight m^{-2}) for *I. glandulifera* growing in locations with 20-30%

relative irradiance compared to more shaded and open populations in England (Andrews et al., 2005). See part 5.9 for its physiological adaptation to shade.

I. glandulifera is sensitive to frost, and late spring and early autumn frost can kill seedlings and adult plants, especially smaller and unsheltered plants (Beerling and Perrins, 1993; Fitter and Peat, 1994). An experimental cold treatment of 1h at -9°C on *Impatiens* seedlings from the Czech Republic indicated that *I. glandulifera* (57% seedling survival) is more frost-resistant than *I. parviflora* (40% survival), but less than *I. noli-tangere* (72% survival) (Skálová et al., 2011). Although it has been suggested that native populations might be more frost-resistant than European populations, this has not yet been formally tested (Beerling and Perrins, 1993). Disturbances, such as mowing, can lead to mortality of adult plants and negatively impact population dynamics, if the disturbance occurs before seed dispersal (Beerling and Perrins, 1993).

5. Life cycle and biology

5.1. Life cycle

I. glandulifera is a summer-annual herb (therophyte, according to the Raunkiær classification). Reproduction occurs exclusively through sexual reproduction, without clonal propagation (Helmisaari, 2010). Population persistence and establishment is consequently fully dependent on annual seed germination (see also part 5.4). Although seedling densities can be up to 350 individuals m^{-2}, density-dependent seedling mortality and plant growth usually results in lower densities in adult *I. glandulifera* stands (see part 5.2) (Beerling and Perrins, 1993).

This dependence of population persistence on annual seed germination has made the species vulnerable to boom-bust dynamics (cf. Strayer et al. 2017), i.e. strong population size fluctuations (Diekmann et al., 2016; Helsen et al., 2019). For example, across 80 permanent vegetation plots monitored between 1989 and 2001 in Germany, *I. glandulifera* showed strong colonization of reed communities in certain years, followed by total regression in following years (Kasperek, 2004). These fluctuations were related to changes in the ground-water table and river flooding events (Kasperek, 2004). In another German study, *I. glandulifera* abundance changed with more than 30% after 1 year for 10% of the 114 studied plots (Bieberich et al., 2020). These dynamics can also cause populations to 'wander' through the landscape from year to year. In the Czech Republic, for instance, the population invasion front advanced 2.0 ± 1.4 m after 1 year, followed by a retreat of 3.8 ± 1.8 m in the second year (Čuda et al., 2017b).

Concerning the species' growth patterns, plants can grow very fast after germination, with reported vertical growth of 1.3 m in 72 days (Perrins et al., 1993), and maximum stem growth rates reaching 3.0 ± 0.5 cm day^{-1} SE (Fig. 5) (Mujuni et al., 2015; Ugoletti et al., 2011). Plants tend to invest primarily in aboveground biomass and usually obtain around 500 cm^2 total leaf area, but can reach up to 2000 cm^2 in woodland populations (Tanner et al., 2014b). Root:shoot ratios are consequently relatively low (0.1-0.3), but seem variable between populations, in both the native (India) and invaded (UK) range, and can nevertheless increase to c. 0.65 in response to low nutrient availability (Andrews et al., 2009; Skálová et al., 2012; Tanner et al., 2014b). Reproductive allocation (ratio of reproductive to vegetative biomass) was furthermore found to be higher for populations from more northern latitudes, when grown together in a greenhouse (Helsen et al., 2020a) (also see part 6.3).

5.2. Spatial distribution of plants within populations

In Europe, densities in adult *I. glandulifera* stands can reach up to 100-170 individuals m^{-2}, but more commonly range between 20 and 50 individual m^{-2} (Čuda et al., 2017a; Greenwood and Kuhn, 2014; Maule et al., 2000; Rusterholz et al., 2014; Tanner et al., 2014b; Titze, 2000). Densities vary between habitat types, and low density populations (<5 individuals m^{-2}) occur across Europe, but seem to be especially common in southern Poland (Kostrakiewicz-Gierałt, 2015; Kostrakiewicz-Gierałt and Zajac, 2014). A similar density range (1-177 individuals m^{-2}) has also been observed for invasive populations in Québec (Canada) (Leblanc and Lavoie, 2017). Native (Indian) populations nevertheless show lower densities (20-30 individuals m^{-2}), potentially due to population thinning through natural enemy damage of seedlings (Tanner et al., 2014b).

5.3. Phenology

In Europe, *I. glandulifera* seeds germinate synchronously during 1-3 weeks from February to March in the oceanic regions (Beerling and Perrins, 1993; Prowse, 2001) or in March-April in more continental and cooler regions (Čuda et al., 2015; Janczak, 2013; Perglová et al., 2009; Perrins et al., 1993). The cotyledon stage lasts until early April and is followed by rapid shoot extension and leaf expansion (Beerling and Perrins, 1993; Ugoletti et al., 2011). Plants will usually reach their mature height in August (Andrews et al., 2009; Tanner et al., 2014b), but can continue to grow until autumn frosts occur (Kostrakiewicz-Gierałt and Zajac, 2014; Skálová et al., 2012; Willis and Hulme, 2002).

Flowering onset occurs at the end of June in oceanic temperate European regions and in July in continental and northern Europe, and British Columbia (Canada) (Clements et al., 2008; Čuda et al., 2015; Perrins et al., 1993; Tyler et al., 2021). In shaded habitats and under strong competition, the flowering can be delayed by 2-3 weeks (Beerling and Perrins, 1993; Mujuni et al., 2015). Flowering normally continues until autumn frosts in October. In the UK, this results in an average flowering season length of 122 days (Baude et al., 2016; Fitter and Peat, 1994). In a common garden experiment in Denmark, flowering started 65-93 days after seedling emergence, with flowering onset being gradually earlier for plants originating from higher latitudes (Kollmann and Bañuelos, 2004). In a greenhouse experiment, a similar latitudinal gradient in flowering onset was observed (from approx. 90-120 days after germination), indicating that this variation is genetically regulated (Helsen et al., 2020a). In a greenhouse experiment in Belgium, flowering was exceptionally fast, and most populations flowered within 40-45 days after radicle emergence (unpublished data). In the native range, the species is reported to flower in July and August (eFloras, 2020).

Seeds are released over an extended period from mid-July (UK) or from August (continental Europe) until autumn frosts (Chmura et al., 2013; Perrins et al., 1993; Willis and Hulme, 2004). In the UK, average seed mass increases towards the end of the vegetation season, while the number of seeds per capsule is greatest both at the start and close to the end of the fruiting season (Perrins et al., 1993; Willis and Hulme, 2004).

5.4. Reproduction

I. glandulifera flowers are hermaphroditic, but markedly protandrous. Stamens create a closed sleeve around the stigma, and pollen deposition can start only after the sleeve covering the stigma has fallen off. The male and female reproductive phases normally last around 24 and 6-7 hours, respectively. The latter phase can double in length in the absence of pollination (Fitter and Peat, 1994; Titze, 2000; Vervoort et al., 2011). The species has no incompatibility system, and is considered facultative allogamous (Baude et al., 2016; Fitter and Peat, 1994). Cleistogamy does not occur (Beerling and Perrins, 1993; Fitter and Peat, 1994). Experimental autonomous selfing yielded very low fruit set (9.3%) in a study by Vervoort et al. (2011). Hand self-pollination nonetheless indicated high self-compatibility, with seed viability equally high as for hand cross-pollinated plants (84.9 ± 1.0%). This resulted in a self-fertility index (i.e. proportion fruit/seed set for autonomous selfed and hand outcrossed plants) of 0.12 ± 0.03 for fruit set and 0.94 ± 0.19 for seed set, and a self-compatibility index (i.e. proportion fruit/seed set for hand selfed and hand outcrossed plants) of 0.97 ± 0.06 for fruit set and 0.95 ± 0.02 for seed set (Vervoort et al., 2011).

The high flower densities (up to 130 flowers m^{-2}) observed in large *I. glandulifera* populations combined with high quantities of pollen (1306 × 10^{3} grains per flower) and nectar (7667.8 µg flower^{-1} day^{-1} ± 4268.3 SD or 357.0-607.4 kg ha^{-1} year^{-1}) attracts large numbers of pollinators (Baude et al., 2016; Emer et al., 2015; Jabłoński, 1986), mostly honey bees (*Apis mellifera*), common wasps (*Vespa vulgaris*), bumblebees (*Bombus sp.*) and Hemiptera (Bartomeus et al., 2010; Lopezaraiza-Mikel et al., 2007; Nienhuis et al., 2009a; Starý and Tkalcu, 1998; Titze, 2000; Vervoort et al., 2011). While honey bees collect both pollen and nectar, bumblebees and wasps predominantly forage for nectar (Titze, 2000). The nectar has high sugar content (48-53%) and can result in >10 mg sugar flower^{-1} day^{-1} (Chittka and Schürkens, 2001; Titze, 2000). *I. glandulifera* is consequently more rewarding to pollinators in terms of nectar than any known co-occurring native plant species in Europe (Chittka and Schürkens, 2001). The secretion begins soon after the flower opens and is highest during the morning, decreases during the day and ceases at night (Beerling and Perrins, 1993; Titze, 2000).

Pollen diameters are 20.9-28.3 µm (Fitter and Peat, 1994). In a study by Titze (2000), the average pollen production was 1,580,863 ± 368,746 pollen grains per flower, of which, on average 1.66% of the pollen grains remained in the five pollen chambers at the end of anthesis. Increases in humidity can result in increased pollen tube growth and anoxia of pollen tubes results in the cessation of elongation and bursting within 4 min (Beerling and Perrins, 1993). Under lab conditions, pollen germination (pollen tube development) decreased with age, from 50% at beginning of anthesis, to only 15% after 32 hours. Often, pollen grains already start germinating in the pollen chamber or on the pollinator (Titze, 2000). During field observations in Germany, the first pollinator-visit of a flower in female state, resulted in on average 256 pollen grains reaching the stigma, 18 forming a pollen tube and 10 pollen tubes penetrating the stigmatic tissue six hours after the pollinator visit. Stigmas furthermore reached saturation of up to 1200 pollen grains after, on average, 14 pollinator visits (Titze, 2000).

The ovary consists of five fused carpels, with 5-locular, axile placentation and on average eleven ovules per capsule (Titze, 2000). This results in a pollen to ovule ratio of around 144,000. The pollination of *I. glandulifera* has been described as highly efficient, especially by bumblebees. A 100% seed set can happen after one pollinator visit (Nienhuis et al., 2009b), although Titze (2000) found that at least 4 pollinator visits are necessary during the female phase to obtain average seed set of 9 seeds in a field assay. In this same study, flowers were visited 6 times/hour on average, whereas Vervoort et al. (2011) reported a total of 250 pollinator visits during a flower's lifespan. The pollination ecology of *I. glandulifera* has also been described in detail by Burquez (1988) and Daumann (1967).

Total seed production depends on plant size and number of capsules per plant (Kostrakiewicz-Gierałt and Zajac, 2014; Willis and Hulme, 2004). In gardens, plants can have 280 capsules over a season (Perrins et al., 1993), but in nature plants usually have about 40-120 capsules per plant (Kostrakiewicz-Gierałt and Zajac, 2014). Capsules can have (1) 6-10 (20) seeds (Fitter and Peat, 1994; Kostrakiewicz-Gierałt and Zajac, 2014; Perrins et al., 1993; Titze, 2000; Willis and Hulme, 2004). As a result, a single plant can produce (500) 800-1700 (2500) seeds over the extended period of seed release, depending on the biotic and abiotic environment as well as population density and origin (Hodgson et al., 2020; Koenies and Glavac, 1979; Perrins et al., 1993; Willis and Hulme, 2004). This results in high (density dependent) seed rain in autumn across Europe (e.g. 1400 seeds m^{-2} in the Czech Republic (Skálová and Pyšek, 2009), 5000-6000 seeds m^{-2} in England (Beerling and Perrins, 1993) and up to 32,000 seeds m^{-2} in Germany (Koenies and Glavac, 1979)). With increasing resources, *I. glandulifera* invests in more, rather than heavier seeds (Willis and Hulme, 2004). Reproductive allocation patterns across latitudes in Europe are explained in part 6.3. In dense *I. glandulifera* populations, seed rains of 5000-6000 (7977) seeds m^{-2} have been reported (Beerling and Perrins, 1993; Kleyer et al., 2008).

The seeds are explosively discharged from the capsule when ripe (i.e. ballistochory) (Grime et al., 1988), which transport the majority of seeds up to 1-2 (4) m from the parental plant, with even distances of 8-10 m being predicted by a seed dispersal model (Beerling and Perrins, 1993; Chapman and Gray, 2012). Seeds are also dispersed by water (hydrochory) along streams and rivers (see part 6.1). Seed mass is highly variable, both within and among populations, with population averages ranging between 2 and 35 mg (Table 1) (Chmura et al., 2013; Čuda et al., 2016; Helsen et al., 2017; Hodgson et al., 2020; Willis and Hulme, 2004). Seed mass can vary with climate, soil conditions and competition (Chmura et al., 2013; Kostrakiewicz-Gierałt and Zajac, 2014; Maciejewska-Rutkowska and Janczak, 2016; Skálová et al., 2012; Willis and Hulme, 2004).

5.5. Germination

I. glandulifera seeds have very high germination rates (58-95% of seeds) (Fitter and Peat, 1994; Janczak, 2013; Kollmann and Bañuelos, 2004; Skálová et al., 2019). Germination rates nonetheless strongly vary among years and populations (Willis & Hulme 2002), and are higher and more homogeneous under controlled experimental conditions (Perglová et al., 2009; Perrins et al., 1993; Willis and Hulme, 2002). Cold moist stratification of at least 30-45 days at 4-5°C is required to break the physiological dormancy (Andrews et al., 2009; Beerling and Perrins, 1993; Perglová et al., 2009). The time of chilling required declines logarithmically with time of dry storage at room temperature (Beerling and Perrins, 1993; Perglová et al., 2009). After dormancy is broken, seeds do not re-enter secondary dormancy when dry-stored

(Mumford, 1988). The optimal germination depth in the soil is 5-15 mm (Beerling and Perrins, 1993; Janczak, 2013).

Gibberellic acid, winter minimum temperature and soil nitrogen do not seem to influence dormancy (Andrews et al., 2009; Beerling and Perrins, 1993; Skálová et al., 2019), but seed survival does depend on soil moisture conditions (Janczak, 2013). Seed germination is greater under high irradiance and increased nitrogen availability, both in the field (Skálová et al., 2019) and under laboratory conditions (Andrews et al., 2009). The effect of high nitrogen availability is only visible for seeds subjected to short chilling conditions, suggesting that nitrogen effects will be most important at the southern end of *I. glandulifera*'s range in Europe, where winters are shorter and milder (Andrews et al., 2009). A study in the UK furthermore observed earlier germination of heavier seeds (Prowse, 2001).

Microclimatic conditions affect germination in the field (Skálová et al., 2011), with germination rates negatively correlated with the minimum field temperature in April in Czech Republic. However, sub-zero temperatures did not affect seed germination in a field experiment (Skálová et al., 2019). Microclimatic effects likely also explain the earlier emergence of more shallow buried seeds (Beerling and Perrins, 1993).

Fully imbibed (i.e. water-saturated) seeds stored under laboratory conditions at 20 °C can remain viable for at least 3 years, but the percentage of germination decreases with time (Beerling and Perrins, 1993; Perglová et al., 2009). Also in the field, *I. glandulifera* is able to create a short-term persistent soil seed bank (Bakker et al., 1996; Beerling and Perrins, 1993; Mumford, 1988; Skálová et al., 2019), with some seeds able to survive up to four years (Skálová et al., 2019). However, some studies observe no or very limited germination and/or dormant seeds after the first winter (Janczak, 2013; Perglová et al., 2009; Perrins et al., 1993). This suggests that the formation of a soil seed bank is dependent on environmental conditions, such as flooding, since seeds seem to have a limited ability to survive when submerged in water (Janczak and Zieliński, 2012).

5.6. Response to competition

While several European native species seemingly have no competitive effects on *I. glandulifera* (e.g. *Arabidopsis thaliana*, *Chelidonium majus*, *Tanacetum vulgare*) (Power and Sánchez Vilas, 2020), more competitive European species, such as *Urtica dioica* can reduce *I. glandulifera*'s biomass (Čuda et al., 2015; Gruntman et al., 2014), reproductive output (Gruntman et al., 2014) and seedling recruitment and survival (Bastl et al., 1997; Čuda et al., 2015; Prowse, 2001; Tickner et al., 2001). Experimental work also showed that *I. glandulifera*'s growth and reproduction is more strongly reduced by graminoid-dominated vegetation than by riparian herb-dominated vegetation (Fig. 5) (Mujuni et al., 2015). Dense native vegetation was even found to prevent the establishment of *I. glandulifera* on Scottish river banks (Pattison et al., 2019). Competition can furthermore reduce *I. glandulifera*'s plant height and leaf dry matter content (LDMC) and increase its leaf area and specific leaf area (SLA) (Helsen et al., 2018a; Koenies and Glavac, 1979), reflecting trait responses to competition for light.

Despite the observed competitive effects on *I. glandulifera*, the species nevertheless often appears to be the more dominant competitor in its European range, which is reflected in strong competitive effects on co-occurring species. The species has shown to reduce both above- and belowground growth and biomass of several co-occurring herbaceous species (Beerling and Perrins, 1993; Bieberich et al., 2018; Bottollier-Curtet et al., 2013), including its congeners *I. noli-tangere* and *I. parviflora* (Čuda et al., 2015; Skálová et al., 2013). The reproductive output (Chittka and Schürkens, 2001; Gruntman et al., 2014) and seedling survival (Ruckli et al., 2014b) of co-occurring species is also often reduced. *I. glandulifera* furthermore showed negative effects on tree seedling growth in some studies (Maule et al., 2000; Ruckli et al., 2014b), but not in others (Ammer et al., 2011). Effects on plant community level diversity and composition are explained in detail in part 7.1.

Several mechanisms contribute to the competitive success of *I. glandulifera* and enable this species to achieve dominance in many European plant communities and habitats. First, *I. glandulifera* is a tall statured plant exhibiting several resource acquisitive functional traits (Helsen et al., 2020b; Van Cleemput et al., 2020a), indicating adaptation to fast growth and fast pre-emption of most available light and nutrients (cf. the leaf economics spectrum, Díaz et al. (2016); Wright et al. (2004)). The early synchronized seed germination and fast seedling growth likely further increase the species' success, allowing it to pre-empt resources before the co-occurring species finish their development (Beerling and Perrins, 1993). An experiment with *Urtica dioica* furthermore showed that *I. glandulifera* was more tolerant to nutrient deprivation than the competitive European-native *U. dioica,* thus suggesting an additional competitive advantage under low nutrient conditions (Beerling and Perrins, 1993). It has been hypothesized that *I. glandulifera*'s competitive success might be partly caused by its allelopathic capacities (see part 5.10), against which plants in its introduced range are not adapted (cf. the novel weapons hypothesis, Callaway and Ridenour (2004)). This mechanism has been invoked to explain observed negative effects of direct competition and soil legacy effects of *I. glandulifera* on the growth and survival of European plant species (Gruntman et al., 2014; Power and Sánchez Vilas, 2020), and their arbuscular and ecto-mycorrhizal symbionts (Gaggini et al., 2019a; Ruckli et al., 2014b; Tanner and Gange, 2013). Also the reduced number of herbivores and parasites in *I. glandulifera*'s invaded range compared to its native range (see part 5.7) might allow the plants to allocate more resources to growth and reproduction, thus enhancing their competitive capacity (cf. the 'enemy release' hypothesis, Keane (2002)) (Najberek et al., 2018).

5.7. Herbivores and pathogens

I. glandulifera experiences much lower levels of leaf damage by natural pests and invertebrate herbivory in invasive UK populations (<15% of leaves damaged) than in native Indian populations (up to 65% of leaves damaged) (Tanner et al., 2008, 2014b). Recent field studies in Poland, however, found similar levels of herbivore/pest damage of *I. glandulifera* leaves than of (native) *I. noli-tangere* leaves (Najberek et al., 2020a, 2017). The pressure of herbivores/pests varied across several Central European populations, with old populations (established 65-85 years ago) subject to higher levels of leaf damage and aphid pressure than recently established populations (5-25 years old) (Gruntman et al., 2017). Moreover, these older populations showed a greater production of a specific naphthoquinone that acts as a secondary defence compound against herbivory (Gruntman et al., 2017) (see part 5.10). Detailed assessments of herbivore and pest damage of *I. glandulifera* leaves in one lowland (290 m a.s.l) and one mountain population (909 m a.s.l.) in the Polish Tatra Mountains nonetheless showed that respectively 58% and 45% of leaves showed at least one disease or damage symptom. Observed symptoms included spots, necrosis, mines, discoloration, deformation, wilting and herbivory damage (Najberek et al., 2020a, 2017). Experimental work using fungicide and insecticide treatments suggest that generalist invertebrate herbivores and pests have little negative effects on *I. glandulifera*’s fitness in Switzerland (Burkhart and Nentwig, 2008). Both sheep and cattle are known to graze on all aboveground parts (Beerling and Perrins, 1993). Detailed information on invertebrate herbivores, and fungal and viral parasites is provided in the following sections.

Invertebrates

In its native range, several invertebrate feeders have been observed on *I. glandulifera*, including the beetles *Altica himensis, Alcidodes westermanni, Languriophasma cyanea* and *Metialma scenica*, the leafhopper *Evacanthus repexus* and the thrip *Taeniothrips major* (Tanner et al., 2008; Tanner and Djeddour, 2010). Also in Europe, several invertebrate taxa have been observed on *I. glandulifera* leaves, of which the majority was classified as putative herbivores (Table 4) (Beerling and Perrins, 1993; Najberek et al., 2020a, 2017). However, only a few species have been clearly identified as herbivores of *I. glandulifera* in Europe, including the Hemiptera (aphids) *Aphis fabae*, *A. nasturtii* and *Impatientinum asiaticum* (Beerling and Perrins, 1993; Starý et al., 2014), the Hymenoptera saw fly *Siobla sturmii*, the Diptera leaf-miner fly *Phytoliriomyza melampyga* (Ellis, 2020; Fitter and Peat, 1994) and the Lepidoptera *Deilephila elpenor*, *Xanthorhoe quadrifasiata* and *Pristerognatha fuligana*, the latter a specialist species of the European native *Impatiens noli-tangere* (Burkhart and Nentwig, 2008; Gruntman et al., 2017; Lemurell, 2018; Meert and Nossent, 2019). Although *Impatientinum balsamines* has also been reported to feed on *I. glandulifera* (Beerling and Perrins, 1993), a more recent study found this species exclusively feeding on *I. noli-tangere* in Czech Republic (Starý et al., 2014). Prowse (2001) also observed severe leaf damage and reduction of flowering due to grazing by *Orthotylus* capsid bugs in the UK. Grazing by certain gastropods, including *Arion* sp. has been observed on cotyledons, seedlings and senescent leaves, but not on mature plant tissue, likely due to the production of secondary compounds (see part 5.10) (Prowse, 2001; Ruckli et al., 2013).

Fungi

In *I. glandulifera*'s native range, several mildews (*Plasmopara obducens*, *Sphaerotheca balsaminae*), Coelomycetes fungi (*Phomopsis* sp., *Phoma exigua*, *Ascochyta* sp.), Dothideomycetes fungi (*Septoria* sp.) and rust fungi (*Puccinia komarovii* var. *glanduliferae*) form important pathogens (Tanner et al., 2008, 2014a; Tanner and Djeddour, 2010; Tanner, 2007). Mildew (i.e. *Plasmopara obducens*, *Fibroidium balsaminae* and potentially *Podosphaera balsaminae*) and rust damage (i.e. *Cronartium flaccidum*) also occurs in European populations (Ellis, 2020; Fitter and Peat, 1994; Tanner et al., 2008), with the latter being the most commonly observed leaf damage type (80-90% of all damaged leaves) in two Polish populations (Najberek et al., 2020a, 2017). Seeds of *I. glandulifera* in Italy and Switzerland were furthermore found to be infected by the true fungal seed pathogen *Fusarium culmorum* and several secondary fungal pathogens (*Alternaria alternata*, *Aspergillus niger*, *Cladosporium cladosprioides*, *C. herbarum*, *Epicoccum nigrum*, *Penicillium notatum*, *Phoma leveillei* and *Trichoderma viridae*) (Najberek et al., 2018).

Viruses

Kollmann et al. (2007) found accidental viral infections of *I. glandulifera* individuals originating from different regions across Europe, grown in a common garden in Denmark. The infection frequency was region specific, but not related to the population’s latitudinal origin. The infection was systemic and could be transferred to different plant species. Although the virus remained unidentified, it caused symptoms resembling those of the Tobacco Rattle Virus. Plants with viral infection symptoms have also been observed in the UK, most likely through infection of the Tomato Spotted Wilt Virus (TSWV), which seemingly caused up to 70% seedling mortality. Symptoms were furthermore similar to those of Impatiens Necrotic Spot Virus, which is known from horticultural varieties of *Impatiens* sp. (Prowse, 2001)

5.8. Symbionts

In the MycoFLor (Hempel et al., 2013) and FungalRoot databases (Soudzilovskaia et al., 2020), *I. glandulifera* is classified as (facultative) arbuscular mycorrhizal, based on observations of vesicular-arbuscular mycorrhiza in British (Harley and Harley, 1987) and Czech (Štajerová et al., 2009) material. Arbuscular mycorrhizal fungi (AMF) root colonisation percentage was furthermore slightly higher for two native Indian populations (± 80% average) than three invasive British populations (± 60% average) (Tanner et al., 2014b). British, but not Indian populations, showed negative correlation between AMF colonisation percentage and plant height, total leaf area and aboveground biomass, suggesting that association with incompatible AMF species can negatively impact *I. glandulifera*'s fitness in the invaded range (Tanner et al., 2014b). In a pot experiment, AMF inoculation was furthermore found to reduce *I. glandulifera*'s biomass of separately grown plants, but to enhance biomass when grown in inter- and intra-specific competition (Ab Razak, 2019). Plant-soil feedbacks (soil conditioning by *I. glandulifera* plants that result in changes in the soil microbial community) seemingly decreased mean root AMF colonisation from 44.6 to 22.8% compared to unconditioned soil (Pattison et al., 2016).

Several leaf endophytes have been isolated from *I. glandulifera* under both field and greenhouse conditions, but endophyte communities are nonetheless species poor (Currie et al., 2020; Pattison et al., 2016). Plant-soil feedbacks furthermore increased endophyte species richness and the abundance of certain endophyte species (Pattison et al., 2016). Leaf endophytes have previously been found to protect plants against pathogens and insect herbivores, thus potentially increasing *I. glandulifera* fitness (Ab Razak, 2019; Currie et al., 2020; Gange et al., 2012).

5.9. Physiological data

I. glandulifera's preference for shaded locations is reflected in its shade-adapted trait set, such as a low leaf mass ratio and leaf area ratio (i.e. total leaf mass/leaf area per aboveground vegetative mass, respectively), and high SLA and photosynthetic rate (Ugoletti et al., 2011).

However, compared to the highly shade-tolerant *I. parviflora*, *I. glandulifera*'s traits indicate adaptation to only moderate levels of shading (Ugoletti et al., 2011).

Experimental shading results in both shade avoidance (i.e. increased height, reduced root:shoot ratio and basal diameter) and shade tolerance responses (i.e. increased leaf area, leaf area ratio, leaf mass ratio and SLA) (Andrews et al., 2009; Gruntman et al., 2020). This is supported by both field and experimental observations of increased plant height in the shaded populations (Kostrakiewicz-Gierałt and Zajac, 2014; Maule et al., 2000; Skálová et al., 2013, 2012), but see Kostrakiewicz-Gierałt (2015) who reported a decrease in plant height in very deep shade of a riparian forest interior. Plants also show physiological shade tolerance during experimental shading, through an increase in maximal photosynthetic efficiency, quantum efficiency and effective quantum yield of PS-II, under low light availability (Gruntman et al., 2020). Although some minor differences occurred, these trait responses to shading were generally comparable for *I. glandulifera* individuals from the native and invaded range (Gruntman et al., 2020). Not only relative irradiance (shade quantity), but also shade quality (red:far-red ratio) impacts *I. glandulifera*'s shade response. In a shading experiment, plants showed significantly higher increase in SLA and leaf area ratio under canopy shade compared to neutral shade using aluminium shading nets (50% lower red:far-red ratio for canopy shade). Plants furthermore had reduced chlorophyll levels under canopy shade, compared to both exposed and neutral shaded plants (Strømme, 2012).

Even under 10% relative irradiance, *I. glandulifera* can manage to retain fast apical extension growth, thanks to the accumulation of nitrate and potassium in the stems to retain osmotic pressure (up to 20% of the stem dry weight) (Andrews et al., 2009, 2005). This strategy can result in an osmotic concentration of 168 osmol m^{-3} and a water content of 95.8 – 97.3% in the stems. It has been calculated that the energetic cost of using KNO_3 as osmoticum at low irradiance is two to seven times more energetically efficient compared to alternative organic, photosynthesis-dependent osmotica such as hexose, glucose and malate (Andrews et al., 2005).

Several of *I. glandulifera*'s leaf traits, such as high maximum photosynthetic rate (>20 μmol CO_2 m^{-2} s^{-1}), SLA, chlorophyll content and leaf nitrogen content (Table 1) (Andrews et al., 2009; Helsen et al., 2020b; Ugoletti et al., 2011; Van Cleemput et al., 2020a) are furthermore linked to a fast growth and resource-acquisitive strategy (cf. the leaf economics spectrum, Díaz et al. (2016); Wright et al. (2004)). This fast growth is likely further promoted by the accumulation of boron (B), which helps with P uptake, and Cu, which is involved in photosynthesis and plant metabolism (Čuda et al., 2017b; Dassonville et al., 2008; Greenwood et al., 2020). The species' fast growth is likely also related to its relatively high stomatal conductance (Gs, >400 mmol m^{-2} s^{-1}), and thus increased photosynthesis, compared to other *Impatiens* species in Europe. *I. glandulifera* nevertheless has similar levels of assimilation per unit Gs (A/Gs, c. 0.03 μmol CO_2 $mmol^{-1}$) as other *Impatiens* species in Europe (Ugoletti et al., 2011). *I. glandulifera* is a C_3 plant in terms of its carbon fixation strategy (Fitter and Peat, 1994).

An overview of other nutrient levels in *I. glandulifera* leaves is provided in Table 1 for Belgium and in Beerling and Perrins (1993) for England. *I. glandulifera* also contains high levels of water in leaves (c. 84.3%), stems (c. 92.7%) and even roots (c. 75.2%) (Beerling and Perrins, 1993; Van Meerbeek et al., 2015), which is also reflected in its low values for leaf dry matter content and stem specific density across Europe (Table 1). Experimental nutrient deprivation furthermore induces similar symptoms in *I. glandulifera*, as observed for several other laboratory grown plants (Table 5) (Prowse, 2001). Concentrations of organic components, such as carbohydrates, starch, cellulose and lignin, are provided in Beerling and Perrins (1993), while foliar pigment concentrations (chlorophyll and carotenoids) are provided in Table 1.

5.10. Biochemical data

Aboveground parts of *I. glandulifera* contain a dozen identified polyphenols, including several flavonoids and phenolic acids with moderate antibiotic and antioxidant activities (Szewczyk et al., 2019, 2016; Vieira et al., 2016). Anti-microbial peptides (Miazga-Karska et al., 2017) and several slightly cytotoxic and antioxidant fatty acids, triterpenoids and sterols (Szewczyk et al., 2018) have been identified in above- and belowground plant parts. Flowers and seed capsules also contain an unsaturated fatty acid (trans-tetradec-2-enoic acid), that relates to specific *Apis mellifera* queen pheromones (Ortin and Evans, 2013). Five polyphenols, including ampelopsin, have been identified in *I. glandulifera* pollen with expected medicinal properties, potentially explaining the reduced infection of *Bombus pascuorum* bumblebees by *Apicystis bombi* when foraging on *I. glandulifera* (Vanderplanck et al., 2019).

I. glandulifera furthermore has allelopathic capacity, widely believed to be caused by the high concentrations of several naphthoquinone pigments present in all plant parts (Bieberich et al., 2018; Block et al., 2019; Lobstein et al., 2001). Naphthoquinones reach the highest concentrations in seedlings and gradually decline with plant age, and are furthermore found to be released from *I. glandulifera* plants by exudation from roots and leaching from leaves (Ruckli et al., 2014a; Smith, 2013). Isolates of these naphthoquinones directly inhibit (nectar) fungal growth and insect development (Block et al., 2019; Mitchell et al., 2007). Recently, other potential allelopathic substances have been isolated, including the unstable 1,2,4-trihydroxynaphthalene-1-O-glucoside and the glucosylated steroids glanduliferin A & B, with the latter exhibiting (human cancer) cell growth inhibition capacities (Cimmino et al., 2016; Tříska et al., 2013).

The allelopathic capacity of *I. glandulifera* has been demonstrated through a reduction in seed germination and seedling development of several other plant species in multiple controlled experiments using extracts and leachates of different *I. glandulifera* plant parts (Baležentienė, 2018; Bieberich et al., 2018; Csiszár et al., 2013; Loydi et al., 2015; Vrchotová et al., 2011). Similar experiments also showed inhibition of these extracts on ectomycorrhizal fungi mycelium development (Ruckli et al., 2014a). Both a field and a greenhouse experiment, however, found no stronger allelopathic effect of *I. glandulifera* than of European native plant species, suggesting that allelopathy does not strongly contribute to *I. glandulifera*'s invasion success (Del Fabbro et al., 2014; Gruntman et al., 2014). In a greenhouse competition experiment, *I. glandulifera*'s performance was higher in the presence of its litter, although this litter did not reduce the growth of co-occurring plant species (Mujuni et al., 2015). Leaf extracts were furthermore found to strongly increase repellency and mortality of *Myzus persicae* aphids in a controlled experiment (Pavela et al., 2009).

5.11 Genetic data

I. glandulifera is a diploid species throughout its native and invaded range (Song et al., 2003). Chromosome numbers of both 2n = 20 and 2n = 18 have been reported from multiple locations in both the native and invaded ranges (Singhal et al. 2017; Song et al. 2003, and references therein), with a 2C DNA content of 2.2-2.3 pg for plants with 2n = 18 (Fitter and Peat, 1994). In addition, 2n = 12 has been reported from India (Jeelani et al., 2010). Multiple studies have furthermore identified polymorphic microsatellite (SSR) markers for the species (Korpelainen and Pietiläinen, 2020; Provan et al., 2007; Walker et al., 2009) and chloroplast genome sequencing has also proven successful and informative for introduction history assessments (Cafa et al., 2020; Kurose et al., 2020).

6. History of invasive spread in Europe

6.1. Pathways of spread

After *I. glandulifera* was intentionally introduced as an ornamental and nectar-producing plant in Europe (Adamowski, 2008; Jernelöv, 2017; Pyšek and Prach, 1995), initial naturalisation occurred mainly through escape from gardens (Fig. 6) (Hejda and Pyšek, 2006). This was facilitated by *I. glandulifera*'s high propagule pressure, combined with its ballistic seed dispersal (see part 5.4). Naturalization was in some regions helped by the intentional release in grasslands and along riverbanks by beekeepers and the general public (Pihl, 1884; Rotherham, 2001).

Long-distance dispersal mostly occurs through (downstream) flowing water along river courses, since fresh seeds can roll on the river bed and dry seeds are buoyant and can float long distances (Fig. 6) (Čuda et al., 2017a; Najberek et al., 2020b). As such, waterways serve as major invasion corridors in the landscape (Pyšek and Prach, 1995). Due to the potential of long-distance dispersal, catchment colonization events have corresponded to major steps in the spread of *I. glandulifera* (Wadsworth et al., 2000). Waterways further serve as corridors for the invasion of adjacent non-riparian habitats, like grasslands and forest ecosystems (Čuda et al., 2020; Pyšek and Prach, 1993). Dispersal away from riverbanks happens predominantly through ballistochory, but flood events can also promote invasion of adjacent lands by inducing seed transport and creating open habitat patches and favourable nutrient conditions for seedling establishment (Čuda et al., 2017a). In Czech Republic, *I. glandulifera* takes around 20 years from initial establishment on a main river to start spreading along its tributaries (Malíková and Prach, 2010).

Other secondary vectors accounting for long-distance dispersal include human machineries (e.g. mower, tractor wheels), mud on workers' boots (Dawson and Holland, 1999), and transportation of garden waste, contaminated top soil or river gravel (Fig. 6) (CABI, 2020;

Hartmann, 1995; Jernelöv, 2017; Kurtto, 2000; Rusterholz et al., 2012). These secondary dispersal events likely explain the observed gradual upstream migration of the species along mountain streams such as in the Carpathians (Zając et al., 2011). Increasing anthropogenic disturbances of natural habitats furthermore favour the establishment of *I. glandulifera* in non-riparian habitats, such as forests (Čuda et al., 2020), and possibly roadsides (Follak et al., 2018). Spread of seeds by animals (e.g. rodents, ants) has been suggested, but remains uncertain (Beerling and Perrins, 1993; Helmisaari, 2010). *I. glandulifera*'s introduction history has been explained in part 4.1.

It has been hypothesized that the exponential invasion in riparian habitats of Central Europe in the last decades is caused by the cessation of traditional riverbank management practices (mowing, hay making, grazing) since the late 1930s. Together with river eutrophication, this resulted in the replacement of grass and sedge dominated vegetation by vegetation composed of competitive nitrophilous forbs (e.g. *Urtica dioica*). The absence of a dense sward in these new communities likely facilitated *I. glandulifera*'s establishment (Jernelöv, 2017; Mujuni et al., 2015; Pyšek and Prach, 1995).

6.2. Population genetics

Multiple introductions of *I. glandulifera* into Europe have been suggested, and seem supported by observed genetic clustering shown among countries (Hagenblad et al., 2015; Kupcinskiene et al., 2015; Nagy and Korpelainen, 2015), but in some instances also within countries (Hagenblad et al., 2015; Kurose et al., 2020; Love et al., 2013; Nagy and Korpelainen, 2015; Zybartaite et al., 2011). This diverse population origin seems furthermore to be derived from both India and Pakistan (Kurose et al., 2020; Nagy and Korpelainen, 2015). Canadian populations studied genetically by Nagy and Korpelainen (2015) clustered together with British and Finish populations, which supports the hypothesis that Canadian plants have originated from Europe. Despite these multiple introductions, many, but not all, European populations show a reduction in (neutral) genetic diversity compared to that of native populations (Hagenblad et al., 2015; Nagy and Korpelainen, 2015). However, note that only a limited number of (native) populations were evaluated in these studies.

A resampling study along a European latitudinal gradient found that *I. glandulifera* populations experienced no genetic diversity loss after 5 years, despite fluctuations in population sizes (Helsen et al., 2019). The study furthermore observed that annual population re-establishment is effectuated by a sufficiently high number of genetically diverse founders and that significant among-population gene flow occurs (Helsen et al., 2019). Temporal shifts in the genetic composition of populations (cf. founder effects) are common, however, especially for small populations (Helsen et al., 2019; Walker et al., 2009). Genetic studies also support that dispersal along river systems plays an important role for gene flow within the species, under some circumstances even more so than human mediated spread (Love et al., 2013; Walker et al., 2009).

6.3 Adaptation

Despite expected low potential for adaptation due to its low population-level genetic diversity (Hagenblad et al., 2015; Nagy and Korpelainen, 2015), two greenhouse experiments found that *I. glandulifera* shows clear patterns of local adaptation for several life-history traits across its European range. Flowering onset was progressively earlier for populations from higher latitudes in the greenhouse, which is likely an adaptive response to cope with the shorter growing season. Following allocation theory predictions, this was accompanied by a gradual decrease in both plant height and vegetative biomass (Helsen et al., 2020a; Kollmann and Bañuelos, 2004). In contrast to allocation theory predictions, however, reproductive output did not decrease with latitude, but remained constant (Helsen et al., 2020a). These patterns were hypothesized to be caused by the stress-gradient hypothesis, which predicts selection for higher reproductive allocation at high latitudes due to higher reproductive uncertainty and reduced levels of competition because of harsher climatic conditions. At lower latitudes, communities invaded by *I. glandulifera* are indeed characterized by a more competitive trait-composition and Grime C-signature, thus potentially driving selection for increased biomass (competitiveness) (Helsen et al., 2018b). In another greenhouse experiment, *I. glandulifera* individuals from France were indeed found to impose stronger competitive effects on co-occurring plants from more northern origin (Sweden and Norway) (Helsen et al., 2018a). *I. glandulifera*'s short generation time, absence of a long-term seed bank and considerable gene flow likely explain its potential for relatively rapid genetic adaptation. At smaller spatial scales in Germany (± 140 km^2), however, *I. glandulifera* did not show genetic adaptation to contrasting habitat types (Pahl et al., 2013). These results suggest that *I. glandulifera*'s successful invasion across its large invaded range might also be partly explained by its potential for fast genetic adaptation. Another study nevertheless showed high phenotypic plasticity of several traits in response to variation in nutrient and water availability levels, which might additionally attribute to its invasive success (Skálová et al., 2012).

A greenhouse experiment with native Indian and invasive Norwegian plants found no difference in vegetative and reproductive traits, nor in their plasticity in response to nitrogen availability. This suggests that the species did not acquire a more competitive trait set after introduction, but that it was pre-adapted for invasion (Elst et al., 2016). A recent greenhouse study nevertheless observed higher reproductive allocation for invasive Central European populations than for native Indian populations (Gruntman et al., 2020). Another study observed similar levels of resistance against a generalist herbivore for native populations and older populations from the invaded range, but lower resistance for young native populations. The authors interpret this as that the selection pressure for enemy release in the invaded range might attenuate over time (Gruntman et al., 2017).

7. Impact and management

7.1. Impact

Although several studies have recorded impacts of *I. glandulifera* on diversity and ecosystem functioning, these effects often seem context dependent, with many studies actually observing very little to no impact (detailed further), especially in comparison to other invasive species in Europe, such as *Reynoutria japonica*. Consequently, the perceived severity of *I. glandulifera*'s invasive impact is sometimes questioned (e.g. Flügel, 2017). A recent expert knowledge-based assessment of potential *I. glandulifera* impact on ecosystem functions and services nonetheless ranked the species as having potentially highly damaging impact on the environment (Martinez-Cillero et al., 2019), reflecting the general perception of *I. glandulifera* as a problematic invader (Kowarik and Schepker, 1998). The species is consequently included on the list of invasive alien species of Union concern of the European Union and the European and Mediterranean Plant Protection Organisation (EPPO) list of invasive alien plants (Tanner and Gange, 2020).

Plant communities

Most studies in Europe find no or limited effects of *I. glandulifera* invasion on plot-level plant species richness of riparian vegetation and woodlands (Čuda et al., 2017b; Diekmann et al., 2016; Gaggini et al., 2019b; Hejda et al., 2009; Hejda and Pyšek, 2006; Helsen et al., 2018b; Prowse, 2001). These limited effects might be caused by the relatively low diversity of some of these communities prior to invasion, or because *I. glandulifera* reaches full height late in the growing season, thus only imposing shade after many co-occurring species have already completed their life cycle (such as vernal geophytes). Grassland communities in both Poland and the UK and riparian vegetation in one British study have nonetheless shown strong reductions in species richness following invasion (Hulme and Bremner, 2006; Kiełtyk and Delimat, 2019; Prowse, 2001). Evenness is furthermore strongly affected in all invaded communities, with significant changes in community composition (Bieberich et al., 2020; Čuda et al., 2017b; Diekmann et al., 2016; Gaggini et al., 2019b) and even functional diversity (Hejda and de Bello, 2013). These changes, however, usually reflect changes in species abundances rather than species turnover, with mainly abundance losses of light-demanding species and species with low competitive abilities (Čuda et al., 2017b; Diekmann et al., 2016; Helsen et al., 2018b; Hulme and Bremner, 2006; Kiełtyk and Delimat, 2019). The shading effects are also reflected in the community weighted mean (CWM) functional trait shifts towards higher SLA and lower LDMC (Hejda, 2013; Hejda and de Bello, 2013; Helsen et al., 2018b; Scharfy et al., 2011). In Belgium, CWM SLA was, however, found to increase with higher abundance of *I. glandulifera* (Van Cleemput et al., 2020b). CWM plant height was furthermore reduced in the presence of *I. glandulifera* in a greenhouse experiment (Helsen et al., 2018a).

Pollination

The high flower densities observed in large *I. glandulifera* populations, combined with the high quantities of nectar and pollen produced, attract large numbers of pollinators, mainly bumblebees and bees (see part 5.4). *I. glandulifera*'s extended flowering season in early autumn, at a time of low flower abundance in the native European flora, likely contributes to pollinator survival (Starý and Tkalcu, 1998). Although flower visitation is often much higher for *I. glandulifera* than for co-occurring species in Europe, *I. glandulifera*'s presence only reduced honeybee, but not bumble bee, visitation rates of co-occurring plant species. Consequently, for most plant species, flower pollen loads and seed set are not affected, despite the deposition of high levels of *I. glandulifera* pollen on a subset of these plant species (cf. *Calystegia sepium, Circaea lutetiana, Epilobium angustifolium, Epilobium hirsutum, Silene dioica*) (Bartomeus et al., 2010; Cawoy et al., 2012; Emer et al., 2015; Lopezaraiza-Mikel et al., 2007; Nienhuis et al., 2009a). Two studies nonetheless found significant reduction in pollen load and seed set for the riparian plant species *Stachys palustris* and *Lythrum salicaria* when *I. glandulifera* was present (Chittka and Schürkens, 2001; Thijs et al., 2012).

Invertebrate communities

Invaded British riparian vegetation harboured a reduced abundance of herbivore, detritivore and predator invertebrates in both the foliage-dwelling and ground-dwelling communities, but not in the below-ground communities. Species richness of foliage-dwelling Coleoptera and Heteroptera was furthermore significantly reduced (Tanner et al., 2013). Another study found a similar reduction in the diversity and abundance of ground-dwelling invertebrates in Scottish riparian zones (Seeney et al., 2019). In Switzerland, both Collembola and Acari litter and soil community composition shifted with *I. glandulifera* forest invasion. Collembola richness and abundance was not affected, however, while Acari abundance was higher under invaded vegetation (Rusterholz et al., 2014). In the same region, gastropod species richness and abundance was also increased in invaded forest plots, most likely due to the higher and more constant soil moisture levels under *I. glandulifera* (Ruckli et al., 2013).

Carbon and nutrient pools and fluxes

I. glandulifera has been found to increase community-level aboveground dry biomass in the field (from 0.68 to 1.00 kg m^{-2}, Dassonville et al. (2008)) and in the greenhouse (Helsen et al., 2018a). This is likely caused by the high amounts of biomass produced by the invader itself, which was found to be 7.98 ± 4.58 kg m^{-2} SD wet biomass and 0.58 ± 0.32 kg m^{-2} SD dry biomass across fifteen 0.75 m^2 areas of densely invaded riparian vegetation in Belgium (Van Meerbeek et al., 2015). Along an invasion gradient in Belgium total aboveground biomass nonetheless decreased (Van Cleemput et al., 2020b). Invader-induced increases in total biomass were furthermore related to both functional traits of *I. glandulifera* and CWM traits of the invaded communities (Helsen et al., 2018a; Van Cleemput et al., 2020b). Belowground (root) biomass, however, was strongly reduced following invasion, potentially due to allelopathic effects (see part 5.10) (Gaggini et al., 2019b). Invasion increased nutrient stocks (N, P, K, Mg) in the aboveground biomass (Dassonville et al., 2008), which is likely partly due to high nutrient levels in aboveground *I. glandulifera* parts (cf. K, Mg, P, Andrews et al. (2005); Dassonville et al. (2008)) and increased nutrient levels in co-occurring plant species following invasion (cf. N, Mg, Ca, Van Cleemput et al. (2020b)).

Several studies found no effects of *I. glandulifera* invasion on soil carbon and nutrient levels (Dassonville et al., 2008; Gaggini et al., 2019b; Helsen et al., 2020b), with the exception of increased soil B and Cu in Czech Republic (Čuda et al., 2017b), increased soil P in Belgium (Van Cleemput et al., 2020b) and reduced soil K in Germany (Diekmann et al., 2016). Although no clear difference in litter decomposition rate was observed in Czech Republic (Čuda et al., 2017b), decomposition rates were significantly higher for invaded than control plots along a latitudinal gradient from northern France (Amiens) to central Sweden (Stockholm). Further north, in central Norway (Trondheim), litter decomposition rates were nonetheless lower in invaded communities (Helsen et al., 2018b). Although invasion effects were partly related to changes in CWM traits that are linked to high litter quality, such as high specific stem density and low LDMC, microclimatic changes and invasion impact on the soil decomposer communities were likely also important (Helsen et al., 2018b). *I. glandulifera* can indeed strongly impact the bacterial, fungal and invertebrate soil communities, most likely through the root exudation of secondary allelopathic compounds (see part 5.10) (Gaggini et al., 2019a, 2018; Pattison et al., 2016; Rusterholz et al., 2014; Stefanowicz et al., 2019). Because of the species’ hypertolerance for Cd, it has also been suggested as a potential candidate for phytoremediation of Cd polluted soils (Coakley et al., 2019).

Soil erosion

Although an initial study suggested increased soil erosion in the riparian zone of a Swiss river, inclusion of additional data of subsequent years of this river and a second river in the UK provided a more nuanced picture (Greenwood and Kuhn, 2014). While increased erosion was observed for around half of the time-points, research indicated much higher sediment fluxes for most time points (Greenwood et al., 2020, 2018). The authors argue that *I. glandulifera* most easily colonized riparian zones where localized river-flow conditions concentrate and deposit sediment and seeds. After colonization, the adventitious root system of *I. glandulifera* enhances sedimentation of fine sediments. At times of strong water flow fluctuations, those zones nonetheless become prone to higher-than-background sediment flux and erosion because of the absent root of *I. glandulifera* in winter and the competition-induced reduced native vegetation cover (Greenwood et al., 2020) and possibly root mass (Gaggini et al., 2019b).

7.2. Management

Since *I. glandulifera* is an annual plant with limited seed dormancy, management actions should aim at preventing seed formation (Dawson and Holland, 1999; Wadsworth et al., 2000). Best timing for plant removal (uprooting or mowing; the latter when there is a high risk of soil erosion) is consequently before or at early flowering, the latest before first seed set, since successful seed set has been observed from plants cut late in the growing season (Clements et al., 2008). Due to the species' ability to rapidly form large populations from a few individuals, efficiency of control must be very high (> 99%) to achieve successful eradication (Wadsworth et al., 2000). Consequently, follow-up visits during the growing season are often necessary (Adriaens et al., 2019). Continued management efforts during three consecutive years are recommended to make sure no regrowth or new germination occurs at the site (Adriaens et al., 2019; IRD Duhallow LIFE Report, 2015). Specifically for riparian systems, it is recommended to plan the management on the river catchment scale, working downstream to avoid upstream reinvasion through the influx of new seeds (Wadsworth et al., 2000). This is, however, often complicated due to fragmented land ownership and inaccessible locations (Tanner, 2017).

In forests, eradication is likely easier since recolonization is more limited than along rivers and *I. glandulifera* is outcompeted by woody species during succession in some cases (Čuda et al., 2020). However, here, soil disturbance by logging machinery and transport of soil contaminated by seeds should be minimized to prevent further spread of *I. glandulifera* in forests (Čuda et al., 2020). Raising public awareness about potential negative impacts, especially among beekeepers and growers of ornamental plants, is essential to increase support for management actions and prevent new infestations (Helmisaari, 2010; Novoa et al., 2017; Tanner and Gange, 2020).

Mechanical control

Due to *I. glandulifera*'s small and shallow rooting system, hand-pulling is a very effective management strategy (Adriaens et al., 2019; Leblanc and Lavoie, 2017; Tanner, 2017), but can result in increased soil erosion if removal leaves river banks bare. For larger stands, mowing (with handheld machinery or with heavy machinery if soil conditions allow) is a more feasible option. The cut should be as close to the ground as possible (below the lowest node) to avoid regrowth (Delbart et al., 2010; Howell, 2002). Following removal, the cut plant parts should be safely disposed or bagged to avoid re-rooting and prevent potential allelopathic leachate effects (Leblanc and Lavoie, 2017). Čuda et al. (2020) argues that this is likely less important for forest populations where re-rooting is less probable due to drier soils and a generally thicker litter layer compared to riparian habitats. Costs can nevertheless be high for this approach (e.g. Can\$21,000 ha^{-1} in Québec, Canada) (Leblanc and Lavoie, 2017). Spraying hot water of 80°C on the plants has also been tested as a management strategy, but cutting is more time and cost efficient (Oliver et al., 2020).

Grazing

Grazing is considered a potentially effective management option in grasslands, because sheep, cattle and horses are known to feed on *I. glandulifera* and trample the fragile stems (Beerling and Perrins, 1993; Larsson and Martinsson, 1998; Navchoo and Kachroo, 1995). Moreover, *I. glandulifera* is unable to invade areas densely covered by grass, which is promoted by generalist grazers such as cattle (Čuda et al., 2017a). The timing of grazing is crucial for control outcome, however, as grazing during seeding can result in further spread of *I. glandulifera* seeds through ballistochory and zoochory (Cockel and Tanner, 2011; Matthews et al., 2015).

Chemical control

Both selective (e.g. 2,4-Dichlorophenoxyacetic acid amine, triclopyr) and non-selective herbicides (e.g. glyphosate) are effective to control *I. glandulifera* (Beerling and Perrins, 1993; CABI, 2020; Wadsworth et al., 2000). However, the use of herbicides near watercourses should be avoided due to non-target effects and is often legally restricted (Adriaens et al., 2019; Clements et al., 2008).

Biological control

In a screening of the natural enemies of *I. glandulifera* in its native range, a number of insects and fungal pathogens were identified (Varia et al., 2016). From the natural enemies that were prioritized for further investigation (Tanner and Djeddour, 2010; Tanner, 2008), only the rust fungus *Puccinia komarovii* var. *glanduliferae* exhibited sufficiently high host specificity and was subjected to rigorous pest assessment (Pratt et al., 2013). Initial results from its release in the UK were promising, although low success rates of infection were observed for some *I. glandulifera* populations, caused by the high host specificity of the rust (Nagy and Korpelainen, 2015; Tanner et al., 2015; Varia et al., 2016). Although this resulted in complete resistance of certain *I. glandulifera* populations to the original *P. komarovii* strains from India, these populations nevertheless showed susceptibility to new *P. komarovii* strains from Pakistan (Ellison et al., 2020). Experimental work furthermore suggests that the presence of arbuscular mycorrhizal and endophytic fungi can reduce *I. glandulifera*'s susceptibility to *P. komarovii*, as coevolved fungi can offer protection against antagonists, potentially hampering biological control (Ab Razak, 2019; Currie et al., 2020; Gange et al., 2018). However, confirming the endophyte-enemy release hypothesis (Evans, 2008), plants in the introduced ranges have low foliar endophytic fungi diversity, which is promising for the success of biocontrol measures (Currie et al., 2020). The European phytophagous Lepidoptera *Pristerognatha fuligana* was also considered as a potential control agent, but has proven ineffective (Burkhart and Nentwig, 2008).

8. Conclusions

Although most details of *I. glandulifera*'s morphology and auto-ecology were already summarised in Beerling and Perrins (1993), important novel insights have been gained in the last decades. For example, the species' boom-bust population dynamics have been formally acknowledged in its invaded range, and research has increased our understanding of the species' biotic interactions, regarding competitors, symbionts, herbivores and parasites. Also our understanding of the species' functional traits, ecophysiology, genetics and biochemistry (allelopathic secondary compounds) has improved significantly. Our study furthermore provides an update of the species' current distribution across the globe, which has strongly expanded since the 1990s. We also present an overview of all research relating to the species' invasive behaviour and ecosystem impact, mainly in Europe. In this respect, for the first time, we compiled the information on the species' population genetic patterns and adaptation in Europe.

Despite these significant advances, several gaps in our knowledge do remain. Especially research on the species' herbivores, pathogens and symbionts remains fragmentary and also our understanding of *I. glandulifera*'s allelopathic biochemical compounds is still limited. Furthermore, most research on the species has been performed in Europe, while our knowledge on the species' ecology and invasive behaviour is less well understood across its current exotic range in the Americas, Asia and New Zealand, and its native Himalayan range. Finally, we also do not yet fully know how the species' population dynamics and spread will be affected by the ongoing changes in the climate system (e.g. in response to warming, droughts).

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Tables

Table 1. Overview of *Impatiens glandulifera*'s functional traits and leaf nutrient concentrations in several European regions (mean and standard error). Data from Van Cleemput et al. (2020a), Helsen et al. (2017) and Helsen et al. (2018b) is based on 6, 5 and 10 populations, respectively. Data of Van Cleemput et al. (2020a) is from unshaded populations across north Belgium. Data of Helsen et al. (2018b, 2017) is from semi-shaded plots near Amiens (France), Ghent (Belgium), Bremen (Germany), Landskrona (south Sweden), Stockholm (central Sweden) and Trondheim (Norway). SLA = specific leaf area, LDMC = leaf dry matter content, SSD = stem specific density, Chl = chlorophyll concentration, Carot = carotenoid concentration.

Source	**Van Cleemput et al. (2020a) (n=6)**	**Helsen et al. (2017, 2018b) (n=10, except *: n=5)**					
Country	BE	FR*	BE	DE	south SE	central SE	NO
Plant height (cm)	176.7 ± 11	164.0 ± 10.1	127.8 ± 9.2	159.8 ± 7.5	153.6 ± 5.1	155.8 ± 7.4	137.2 ± 4.7
Latitude (°N)/ longitude (°E)	50.8/ 4.8	49.9/ 2.3	51.1/ 3.7	53.1/ 8.8	55.7/ 13.2	59.3/ 18.1	63.4/ 10.4
Seed mass (mg)*		1.96 ± 0.24	2.13 ± 0.46	1.64 ± 0.07	1.93 ± 0.17	2.04 ± 0.15	2.17 ± 0.20
leaf area (mm^2)	4672 ± 398		6978 ± 495	6063 ± 450	6162 ± 350	5315 ± 566	4003 ± 579
SLA (mm^2 mg^{-1})	22.2 ± 1.6		40.5 ± 2.5	41.5 ± 2.1	44.8 ± 4.2	35.0 ± 2.0	34.3 ± 1.6
LDMC (mg g^{-1})	214.1 ± 6.6		141 ± 6.0	133.7 ± 4.6	140.4 ± 6.0	152.6 ± 3.0	144.3 ± 3.9
SSD (mg mm^{-3})			0.065 ± 0.003	0.074 ± 0.005	0.081 ± 0.004	0.085 ± 0.006	0.080 ± 0.003
Chl (mg g^{-1})	5.86 ± 1.63						
Chl a/b ratio	2.58 ± 0.04						
Carot (mg g^{-1})	1.18 ± 0.46						
C/N ratio	14.53 ± 1.44						
Leaf N (mg g^{-1})	30.11 ± 2.71						
Leaf P (mg g^{-1})	2.95 ± 0.21						
Leaf K (mg g^{-1})	10.61 ± 0.82						
Leaf Ca (mg g^{-1})	22.98 ± 2.68						
Leaf Mg (mg g^{-1})	3.09 ± 0.32						
Leaf S (mg g^{-1})	2.22 ± 0.19						
Leaf Na (mg g^{-1})	0.13 ± 0.03						
Leaf Zn (μg g^{-1})	96.6 ± 24.1						
Leaf Mn (μg g^{-1})	94.8 ± 32.2						

Table 2. Biotic conditions: the most frequent co-occurring species of *Impatiens glandulifera* in several European regions. Frequency (% of plots present) is given for each species. Data from Helsen et al. (2018b) is based on 10 vegetation plots near Ghent (Belgium), Bremen (Germany), Landskrona (south Sweden), Stockholm (central Sweden) and Trondheim (Norway). Data from Diekmann et al. (2016) based on 50 invaded sites from different habitats near Bremen.

Source	**Helsen et al. (2018b) (n=10 for each country)**					**Diekmann et al. (2016) (n=50)**
Country	BE	DE	south SE	central SE	NO	DE
Aegopodium podagraria	40	10	70	20	30	24
Agrostis stolonifera	10	10		30	30	
Alliaria petiolata				10		20
Anthriscus sylvestris	20	20		20	40	
Calystegia sepium	30	40	60	40		38
Cirsium arvense	20			50	50	
Dactylis glomerata	20	10	30	40	20	22
Elymus repens						12
Epilobium hirsutum	20	20	30			10
Filipendula ulmaria		30	20	60	50	28
Galeopsis tetrahit	10	20	10	20	30	
Galium aparine	70	50	60	20		54
Geum urbanum	20	20	50	30	10	10
Glechoma hederacea	50	60	40	30		50
Heracleum sphondylium	50		10			
Holcus lanatus	30	60	20			12
Humulus lupulus		20				16
Iris pseudacorus						10
Lolium perenne	10	20	20	30	70	
Lysimachia vulgaris				10		16
Lythrum salicaria		10		10		12
Phalaris arundinacea	30		20	30		36
Phleum pratense		20		20	50	
Phragmites australis	20	30	20	20		22
Poa trivialis	40	10	30	20	30	46
Ranunculus repens	20		30	10	40	14
Rubus fruticosus agg.	20	60	30			34
Rubus idaeus			20	40	50	16
Rumex obtusifolius	30	10	20	10	30	
Stachys sylvatica	50				30	
Urtica dioica	100	100	80	100	70	92

Table 3. Abiotic conditions in plots invaded by *Impatiens glandulifera*. Mean values with standard error (SE), median values or minima and maxima are given.

Source	**Diekmann et al. (2016) (n=50)**			**Čuda et al. (2013) (n=59)**		**Beerling and Perrins (1993) (n = 8[2])**		**Maule et al. (2000)**	
Country	NW Germany			Czech Republic		UK		NE England, UK	
	Median	Min	Max	Mean	±SE	Min	Max	Min	Max
Soil pH ($CaCl_2$)	5.0	3.35	7.17						
Soil pH (H_2O)						4.5	6.9	3.9	5.9
Soil Carbon (%)	6.7	1.8	23.5	8.26	0.51	3.8[3]	55.9[3]		
Soil Nitrogen (%)	0.4	0.1	1.5	0.54	0.03				
Soil Phosphate (µg g^{-1})	62	24	195			3.7	59.7	5.9	83.0
Soil C/N ratio	16.9	10.3	36.6						
Soil K (µg g^{-1})	92	19	474			49.9	167.3	46.1	267
Soil Ca (µg g^{-1})	1203	198	11747			1158	4017		
Soil water (%)						15.2	53.3	6.5	85.1
Canopy cover (%)	72.5[1]	0[1]	105[1]	70.9	1.85				
Irradiance (PAR in % of open-habitat radiation)								0.3	100

[1] Sum of percentage cover of trees and shrubs (can be higher than 100%), [2] Mean of five replicates, [3] Organic carbon only.

Table 4. Overview of invertebrate groups observed on leaves of *I. glandulifera* in the UK (presence) (Beerling and Dawah, 1993) and Poland (percentage of observed total invertebrate individuals) (Najberek et al., 2020a, 2017). For Poland, only groups with putative damaging effects on *I. glandulifera* are included.

Class	**Order**	**Taxon**	**Beerling & Dawah (1993)**	**Najberek et al. (2017) (%)**	**Najberek et al. (2020) (%)**
Arachnida	-	Acari		0.16	
Insecta	Coleoptera	-		0.16	1.02
		Chrysomelidae	×		
		Coccinellidae			0.31
		Curculionidae	×		0.86
	Diptera	-		3.20	1.57
		Agromyzidae	×		
		Drosophilidae		2.24	0.16
		Psychodidae			0.08
		Syrphidae		0.64	0.39
	Hemiptera	-		2.08	0.86
		Aphidoidea	× (Aphididae)	72.32	81.75
		Auchenorrhyncha		0.96	0.70
		Cicadellidae	×	0.16	0.08
		Coreidae		0.16	
		Nabiidae	×		
	Heteroptera	Pentatomidae		0.48	0.08
	Hymenoptera	-		1.60	3.84
		Symphyta (larvae)		0.16	
		Vespidae		0.16	
	Lepidoptera	- (larvae)		0.16	
		Sphingidae	×		
	Mecoptera	-		0.16	
	Orthoptera	-		0.16	
	Psocoptera	-		0.16	0.08
Gastropoda	Stylommatophora	-		14.88	8.22

Table 5. Mineral nutrient deficiency symptoms in laboratory grown I. *glandulifera*. Based on Prowse (2001).

Nutrient	**Symptoms**
Complete nutrient deficiency	Strong growth of lateral roots, leaves dark green, glands well developed. Root hairs along length of root.
Magnesium	Chlorosis evident in leaves, and leaves curling abaxially. Roots underdeveloped with prolific root hair production.
Calcium	Dead
Phosphorus	“Scorching” of leaf tips. Roots severely underdeveloped with poor lateral root growth and few root hairs.
Nitrogen	Shoot necrotic, apex still green. Root development comparable with control. Severe chlorosis in older leaves.
Potassium	Thinning of leaves and large areas of the leaf without colour. No glandular development.
Micronutrients	Normal shoot growth though leaves pale green; pronounced anthocyanin colouration in stem. Root development comparable with control. Glands present.
Sulphur	Slight chlorosis and deformation of older leaves. Roots well developed but with anthocyanin colouration. Extreme proliferation of root hairs all along the root length.
Iron	Severe interveinal chlorosis and leaf tip “scorch” in young leaves. Roots have “stubby” appearance. Glands present.

Figures

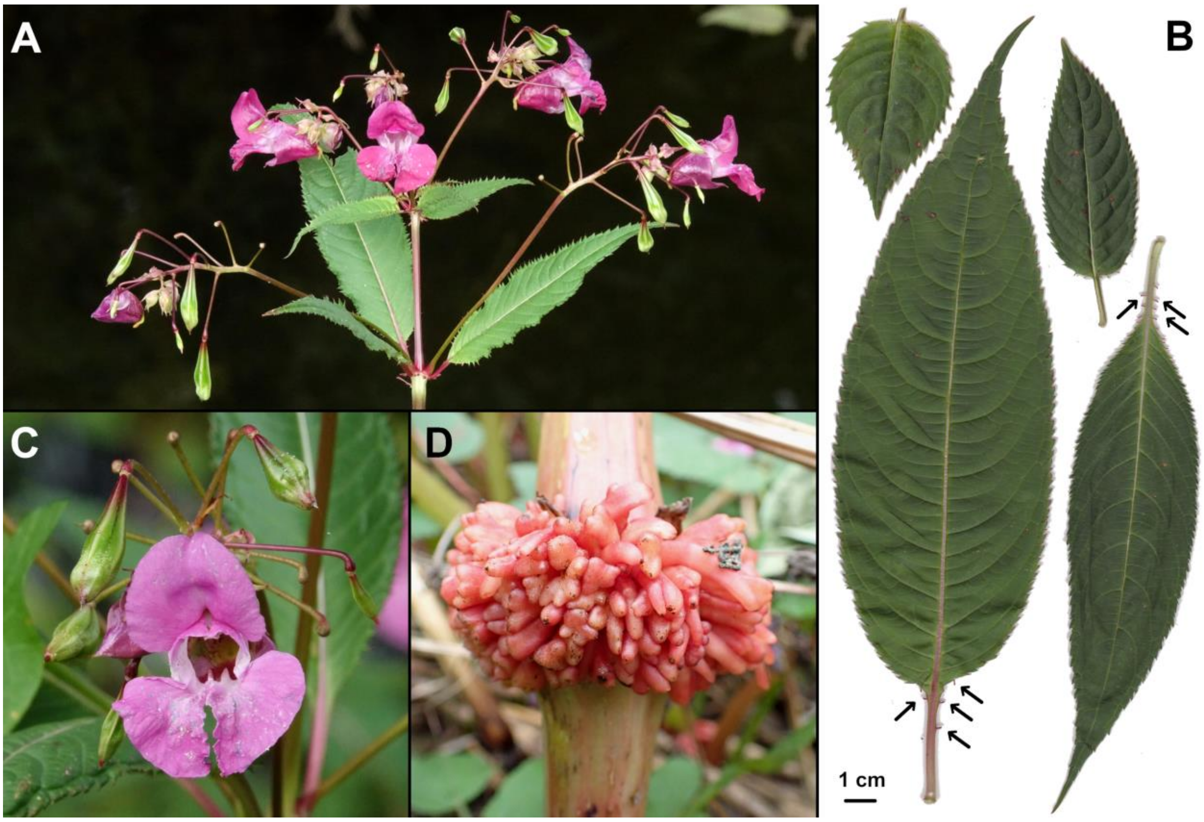

Figure 1. Illustration of *Impatiens glandulifera*'s morphology. A. Terminal inflorescence showing both flowers and capsules, B. Variation in leaf size and shape. Arrows indicate the extrafloral nectaries at the leaf base, C. Detail of flower and capsules, D. Detail of adventitious root formation on the stem after stem damage. A. & C. © Sanne Govaert, B. © Kenny Helsen, D. ©Heather A. Kelly

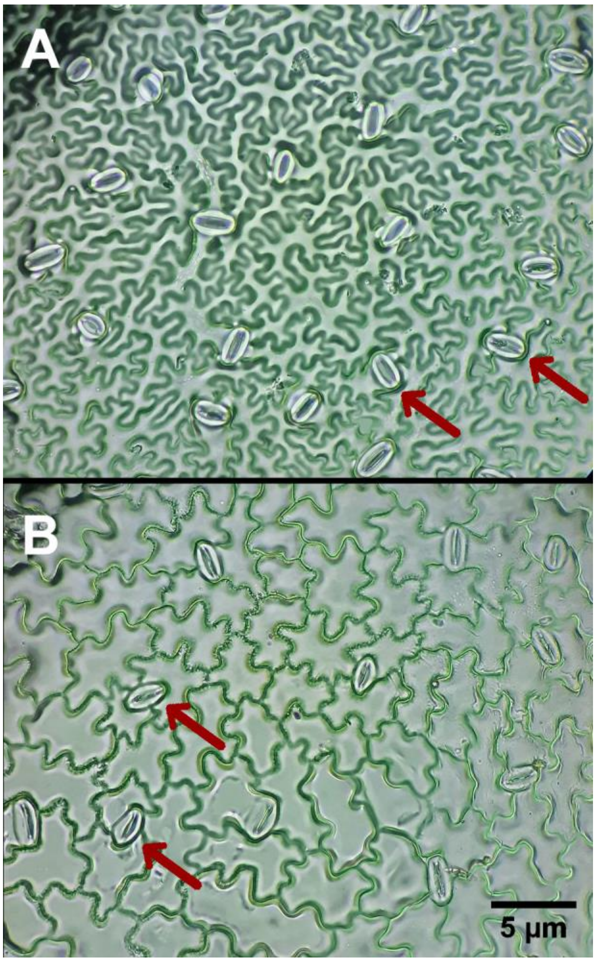

Figure 2. Microscope pictures of *Impatiens glandulifera*'s stomata (red arrows) showing higher stomatal density on A. the abaxial compared to B. the adaxial leaf side. Pictures are from a plant grown in a greenhouse in Ghent (Belgium) from seed originating from Landskrona (south Sweden, cf. Table 1). ©Sarah Hertecant

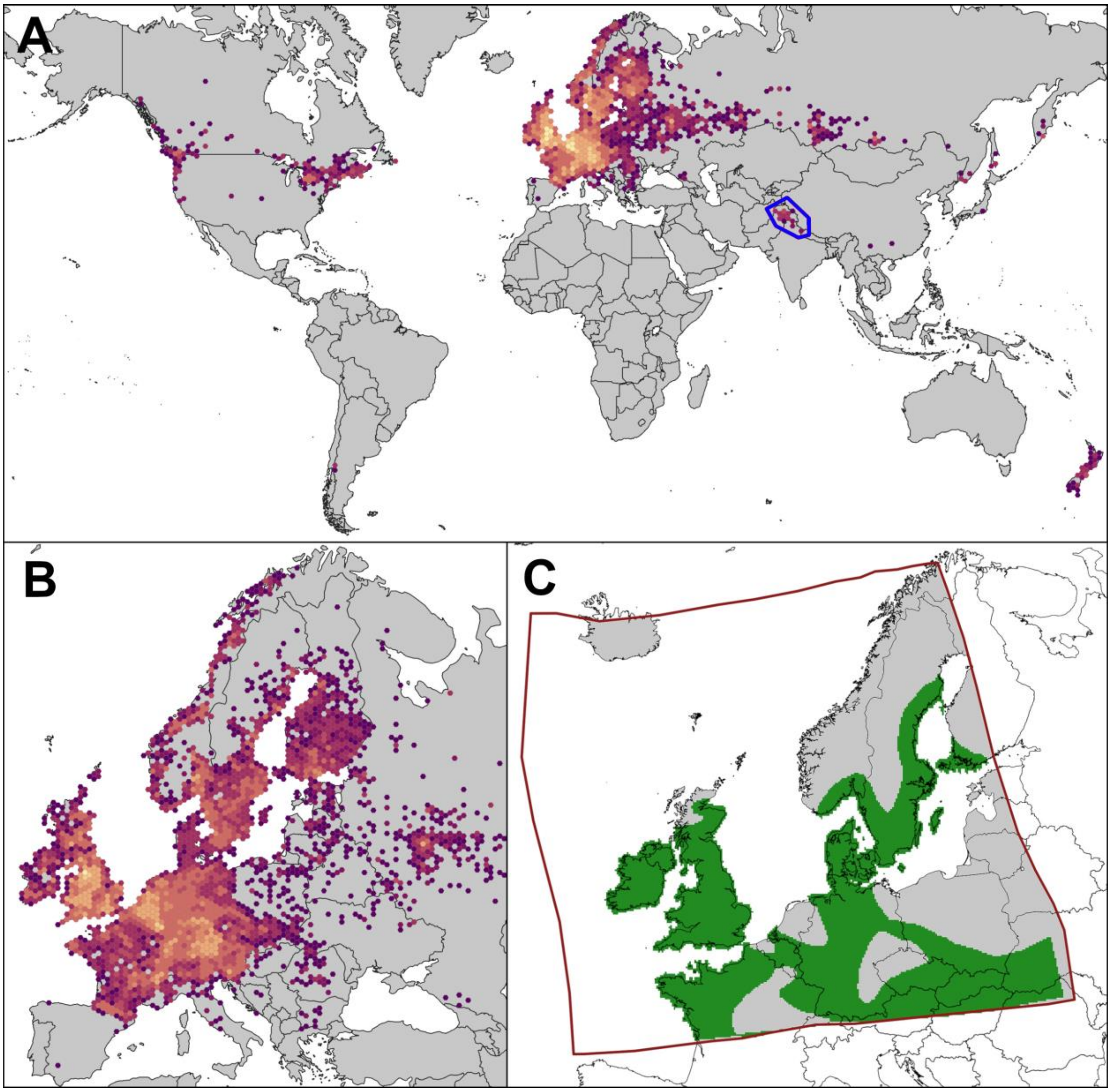

Figure 3. A. Current distribution range of *Impatiens glandulifera* in the world, based on GBIF presence data (GBIF Secretariat, 2019), showing both the native range in the Himalayas (blue polygon) and the invaded ranges across the temperate regions of the world. B. Detail map for present distribution in Europe based on GBIF presence data. Colour warmth relates to point density. C. The expert-based distribution range of *Impatiens glandulifera* (green) in Europe in 1978 (redrawn from Beerling (1993), the original source is Fitter (1978)). The baseline distribution range was only available inside the area depicted by the red polygon. The range expansion in B compared to C is remarkable.

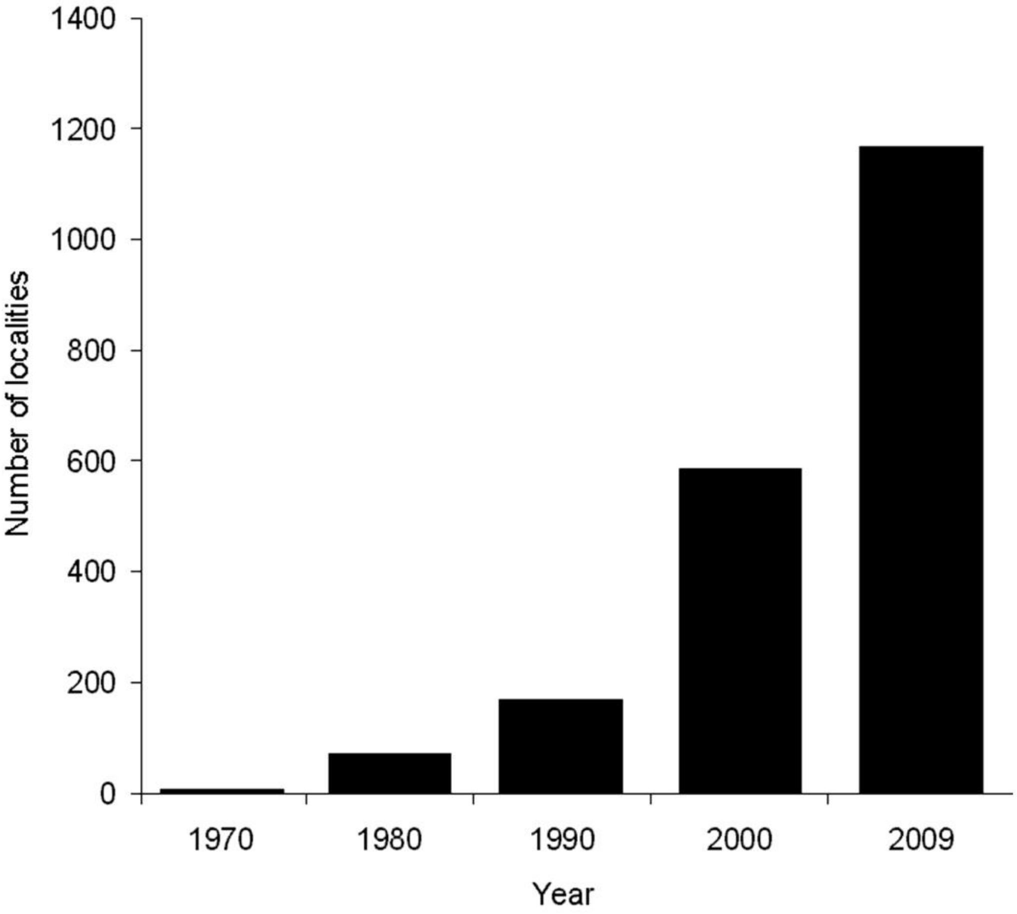

Figure 4. Number of identified populations of *Impatiens glandulifera* in the Polish Carpathians through time, showing a rapid increase. Figure reproduced with permission, from Zając et al. (2011).

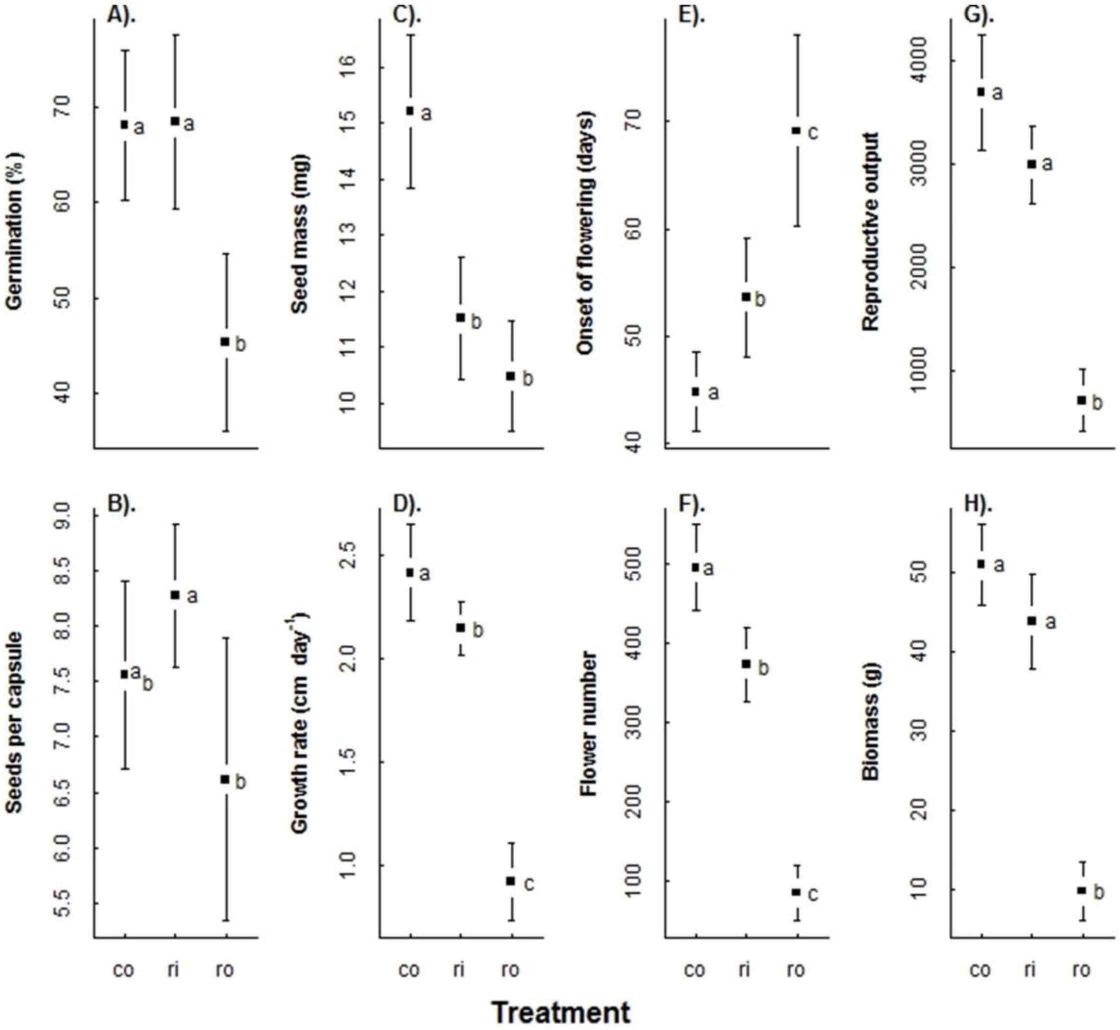

Figure 5. Variation in life history traits (means and 95% CIs) of *I. glandulifera* grown in greenhouse conditions. Co = control, plants grown in an individual pot without competition of other plants, ri = individual plant grown in a pot with competition of riparian herbaceous-dominated vegetation and ro = plant grown in a pot with competition of graminoid-dominated roadside vegetation. Different letters represent significant differences between treatments. Onsets of flowering are measured in days after sowing. Figure reproduced from Mujuni et al. (2015).

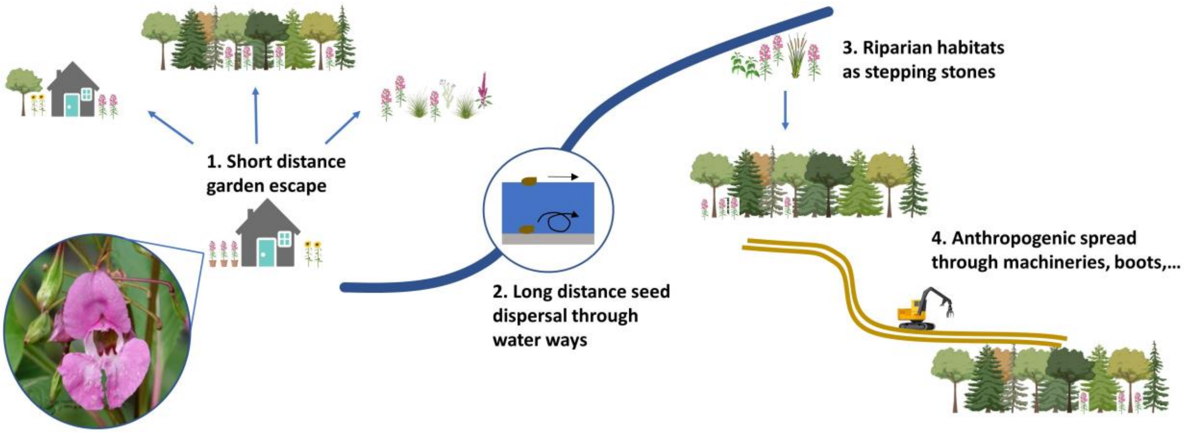

Figure 6. Schematic overview of pathways of post-introduction spread of *I. glandulifera*.