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Research Article

Sexual reproduction in invasive Japanese knotweed (*Reynoutria japonica*) in south Sweden

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To understand the potential for northward expansion of knotweeds into currently uninvaded regions, it is crucial to assess the potential for sexual reproduction alongside the ongoing vegetative spread. For that reason, we tested viability in *Reynoutria japonica* seeds in south Sweden, a region where viable seeds had not been previously reported. Knotweed in northernmost Europe has no genetic variation, indicating lack of fertile seeds, and northward colonization is considered limited by temperature and a short growing season. Observations of profuse flowering and seed production in recent years, however, prompted us to test seed germination. Seeds from seven localities in Scania and 20 localities in Halland, south Sweden, were collected in October and November 2021 and 2023 and germinated under laboratory conditions. In Scania, seeds from six out of seven stands germinated with an average germination of $57.7 \pm 32.1\%$. A second trial 10 months after seed collection showed $48.0 \pm 14.2\%$ germination on seeds from two of the sites. In Halland, seeds collected in November 2023 germinated with an average germination of $78.13 \pm 20.71\%$, and germination in soil was $15\% \pm 16.1$. Field inventories detected seedlings that were determined by metabarcoding to be *R. japonica* × *Fallopia baldschuanica* hybrids. Collected *Reynoutria* × *bohemica* × *F. baldschuanica* seeds from one site were fertile and the seedlings survived cool conditions for two winters. We established that *R. japonica* produces viable seed in south Sweden, which is further north than previously demonstrated in Europe. The observation that *F. baldschuanica* was a common pollen donor concurs with studies from other parts of Europe. Conclusion: the presence of fertile seeds and seedlings has implications for the northward dispersal of knotweeds in Europe. Russian vine *F. baldschuanica* was identified as the pollen donor for *R. japonica* stands and one putative *R.* × *bohemica* stand in south Sweden.

Keywords: *Fallopia baldschuanica*, hybridization, invasive alien species, Japanese knotweed, *Reynoutria japonica*, seed germination

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Introduction

Japanese knotweed *Reynoutria japonica* is one of the most troublesome invasive alien plants globally and has colonized large areas through its prolific rhizome growth (Forman and Kesseli 2003). The strong-growing rhizomes and ability to resprout from small rhizome fragments have resulted in widespread populations in the US, Canada, the UK, and central and western Europe (Conolly 1977, Beerling et al. 1994, Ellstrand and Schierenbeek 2000, Gillies et al. 2016, Rouleau et al. 2023). Japanese knotweed has no natural enemies in its invaded areas and, once established, forms dense stands that successfully out-compete native flora (Aguilera et al. 2010, Gillies et al. 2016). In addition to adverse effects on biodiversity, the strong-growing rhizomes can damage infrastructure and waterways (Barney et al. 2006, Smith et al. 2007). To limit damage from Japanese knotweed, management recommendations have focused on control of vegetative growth by glyphosate treatment, cutting, shoot pulling, excavation, shading, grazing, and heat treatment, and management costs are estimated to be the highest of all invasive alien plants (Barney et al. 2006, Jones et al. 2018, Martin et al. 2020, Bitarafan et al. 2021, Rouleau et al. 2023, Soto et al. 2025). However, complete eradication of *R. japonica* is unlikely and prevention of further spread is therefore a crucial step in its control (Townsend 1997, Hulme et al. 2018, Soto et al. 2025).

Compared to the successful invasions by rhizome fragments, seed dispersal has been regarded as less important in the invasion process of *R. japonica* (Brock 1995, Dusz et al. 2025). Dispersal by seed was regarded an unlikely event since male pollen donors were largely absent in the invasive range and, consequently, genetic variation in *R. japonica* was found to be low in invaded regions (Hollingsworth and Bailey 2000, Gillies et al. 2016). Molecular studies demonstrated that only a female clone was introduced to the UK, and that the same female clone occurred in mainland Europe and in the US (Hollingsworth and Bailey 2000, Mandák et al. 2004, Grimsby 2007, Bailey et al. 2009, Grimsby and Keseli 2010). However, *R. japonica* is compatible with *Reynoutria sachalinensis*, and in regions where both species co-occur, molecular studies detected hybrid knotweed *Reynoutria × bohemica* (Bailey et al. 2009, Bailey 2013, Gaskin et al. 2014). Fertile *R. × bohemica* has subsequently been found in several regions in the US and Canada (Bram and McNair 2004, Gaskin et al. 2014, Groeneveld et al. 2014). In the eastern US, hybrid *R. × bohemica* was found to be a common occurrence that contributed widely to seed production (Gaskin et al. 2014). In addition, Locandro (1973) reported viable seed in studies from New Jersey, USA, already in 1973, indicating that a pollen donor was available in the area. Evidence from molecular studies concluded that *R. japonica* and *R. sachalinensis* had spread predominantly by rhizome fragments in its invaded range, while *R. × bohemica* had spread both by rhizomes and by seeds (Gaskin et al. 2014). Viable and germinating *Reynoutria* seeds have presently been reported from invaded areas in the US and Canada as well as western and central Europe (Hruskova and Hofbauer 1999, Forman and

Kesseli 2003, Bram and McNair 2004, Tiébré et al. 2007, Engler et al. 2011, Strulg Kracek and Koce 2015, Gillies et al. 2016, Lamberti-Raverot et al. 2019, Dusz et al. 2025). Both hybrid *R. × bohemica* and *R. sachalinensis* can fertilize female *R. japonica* in invaded regions (Hollingsworth and Bailey 2000, Forman and Kesseli 2003, Bailey and Wisskirchen 2006, Grimsby et al. 2007, Engler et al. 2011, Gaskin et al. 2014, Dusz et al. 2025). While *R. japonica* has been shown to produce only 0–4 pollen grains per flower in Europe, the closely related *R. sachalinensis* produces thousands of pollen grains per flower, making it an important potential pollen donor (Tiébré et al. 2007). Another common pollen donor to *R. japonica* is the close relative *Fallopia baldschuanica* (Bailey 2013). Following multiple reports of the hybrid in the UK as well as continental Europe it was described to science as *Fallopia × conollyana* (Bailey 2001). Despite resulting in large seed production, *F. × conollyana* seedlings are considered rare and to be weak competitors, but have been reported from the UK, Norway, Germany, and Belgium (Bailey 2013, Hoste et al. 2017).

In contrast to the widespread evidence of seed germination in the invaded range of *R. japonica*, the Nordic region demonstrated no genetic variation in *R. japonica* and low genetic variation in *R. × bohemica* and *R. sachalinensis*, indicating that the taxa did not reproduce by seed (Holm et al. 2018). In general, the harsh conditions in the Nordic region do not eliminate biological invasions, as there is a high proportion of invasive compared to native species (Weidema 2000). However, the northern distribution of *R. japonica* is regarded to be limited by the length of the growing season and by minimum temperature, with early autumn frost that damages *R. japonica* flowers (Beerling 1993, Barney et al. 2006). Recently, more southern parts of the Nordic region have experienced milder winters that might change the conditions for seed set in autumn. The occurrence of several members of the knotweed species such as *R. japonica*, *R. sachalinensis*, hybrid *R. × bohemica*, *R. japonica* var. *compacta* and *F. baldschuanica* in the region provides potential for cross-fertilization. A similar situation occurs in Canada, where *R. × bohemica* hybrid knotweed was found to be a key component of the northwards expansion of *Reynoutria* species (Groeneveld et al. 2014, Gillies et al. 2016). In Canada, due to milder winters caused by climate change, the northern distribution limit was found to be extended 500 km northwards, with viable seeds produced in the city of Quebec (Groeneveld et al. 2014). Molecular studies demonstrated that seed dispersal in Canada was mediated by hybrid knotweed *R. × bohemica*, while dispersal of true *R. japonica* was vegetative (Groeneveld et al. 2014). This led to the conclusion that long-distance dispersal of knotweed was possible via seeds, and that the more diverse hybrid knotweed might disperse both further north and to higher elevations (Gillies et al. 2016). If seeds in the Nordic region are similarly fertile, this may have implications for the spread of knotweed in the Nordic regions, where previous predictions concluded that dispersal into the mountainous Nordic areas was prevented by low mean temperature and a short growing season (Beerling 1993).

Since male *R. japonica* are regarded to be absent in invaded areas, alternative pollen donors are necessary for seed production (Beerling et al. 1994, Bailey 2013, Gaskin et al. 2014). Molecular studies in mainland Europe and in the US demonstrated low genetic variation in *R. japonica* and *R. sachalinensis*, showing that regeneration was vegetative (Mandák et al. 2005, Grimsby 2007, Bailey et al. 2009, Grimsby and Keseli 2010, Gaskin et al. 2014). However, hybrid *R. × bohemica*, resulting from fertilization by *R. sachalinensis*, was detected in several regions (Hollingsworth and Bailey 2000, Forman and Kesseli 2003, Bailey and Wisskirchen 2006, Grimsby et al. 2007, Engler et al. 2011, Gaskin et al. 2014). Hybrid *R. × bohemica* can in turn act as a pollen donor to backcross with *R. japonica*, resulting in viable seed (Bailey 2013, Gaskin et al. 2014). An additional pollen donor is the ornamental plant *Fallopia baldshuanica* that forms the hybrid *Fallopia × conollyana* with *R. japonica* (Bailey 2001). Female *R. japonica* can therefore produce seeds with alternative pollen donors in the absence of male congeners, and *Reynoutria* seeds have been reported from invaded areas in the US and Canada as well as western and central Europe (Hruskova and Hofbauer 1999, Forman and Kesseli 2003, Bram and McNair 2004, Tiébré et al. 2007, Engler et al. 2011, Strulg Kracek and Koce 2015, Gillies et al. 2016, Bram and McNair 2017, Lamberti-Raverot et al. 2019).

The aim of the present study was to investigate if *R. japonica* in south Sweden produced viable seed and if seedlings occurred in the field. In addition, molecular analysis of potential hybrids was performed to determine their genetic background.

Material and methods

Sites for seed collection

Seeds were collected from seven *R. japonica* stands in Scania, south Sweden (October to December 2021) and 20 stands in Halland (November 2023) (Fig. 1) (Supporting information). The seeds were kept at 4°C for one to two months (Scania) or four months (Halland) before germination was tested.

In Halmstad municipality, 43 *Reynoutria japonica* stands obtained from the Species Observation System (2000–2023) were checked for seed production in autumn 2023, and 20 of those stands that produced seeds were included in this study (Species Observation System 2024) (Supporting information). The presence of giant and hybrid knotweed within a 2 km radius of each of the 20 *R. japonica* stands was compiled from the Species Observation System (Species Observation System 2024). Maps for the location of *R. japonica*, *R. sachalinensis*, and *R. × bohemica* in Halmstad were produced in ArcGIS Pro, and the nearest and furthest distance from each seed-producing *R. japonica* stand to a reported *R. sachalinensis* or *R. × bohemica* was determined.

Seed germination in Petri dish and in soil

Seeds without calyx and with calyx were used for germination tests. The seeds without calyx were prepared by removing the

calyx before they were placed on filter paper moistened with distilled water in Petri dishes (Ø10 cm) following the procedure in Groeneveld et al. (2014). The Petri dishes were kept at a controlled lab temperature with ambient light. The seeds were checked daily (Scania) or every other day (Halland) for signs of germination for 14 days. Development of cotyledons and/or a radicle was noted as germination. Distilled water was added when needed to keep the filter paper moist throughout the germination trial. For Scania 10 seeds per site were tested (except Björnstorp n = 3) in December 2021 and for Halland 40 seeds per site in March 2024 (Supporting information). Germination of seeds with calyx was tested for the stands Lund III (n = 4 × 25) and Flommen I (n = 25) following the same procedure as for the seeds without calyx.

The germination in soil was studied for all stands in Halmstad. Ten seeds with their calyx attached were sown in commercial potting compost in 9 cm square plastic pots. The seeds were covered with a 1–2 cm soil layer and watered with tap water as needed (Bram and McNair 2004, Tiébré et al. 2007). The pots were placed randomly in five rows with four pots per row at room temperature and ambient light. After 14 days the position of the pots was rotated, and after 28 days germination was noted as cotyledons that reached the soil surface. All pots were searched for roots when the trial was ended.

Seed viability was tested with Tetrazolium for seeds from sites Lund I–III and an additional stand near Lund I and II in November 2024. Two weeks after collection, 10 seeds without calyx from each stand were placed in Petri dishes following the same procedure as previously. Germinated seeds were removed and, after 14 days, the seed coat of non-germinated seeds was cut with a scalpel before placing them in 1% 2,3,5-triphenyl-tetrazolium-chloride (Sigma Tetrazolium) in Petri dishes at 30°C for 22 h (Tetrazolium Testing Handbook, <https://www.scribd.com/document/608140760/tetrazolium-testing-handbook>). Staining of the seed content was checked under stereo magnification and viability noted as red coloration of the seed content according to the Tetrazolium Testing Handbook (2000). If the radicle had a pink tip but the remaining seed was white this was noted as a dead seed as interpreted from the Tetrazolium Testing Handbook (2000).

Seed morphology

For the seeds from Halmstad, the width and length with or without calyx was measured with a digital caliper to ± 0.03 mm/mm accuracy, as described in Engler et al. (2011). Individual seeds with or without calyx were weighed. Seeds from Halmstad (n = 5 per site) and Flommen (n = 10), Lund I (n = 11) and Lund II (n = 3) were squeezed with tweezers to check if they were filled within one week after collection.

Metabarcoding analyses

Samples from nine sites with suspected hybrids were identified by the Centre for Genetic Identification at the Swedish Museum for Natural History (Report 356-2025). Entire young plants or entire leaves of young plants were sent for DNA-extraction, which was done using the OMEGA

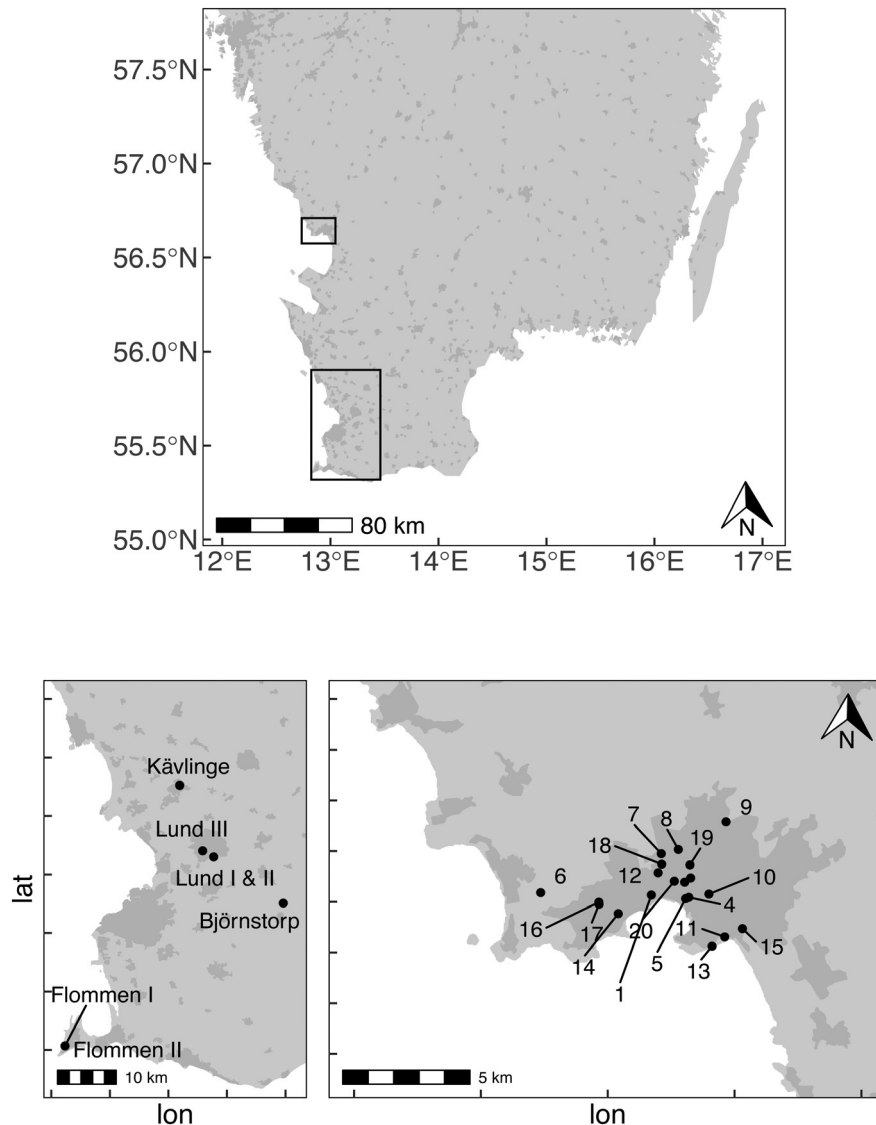


Figure 1. Top graph: Location of the two areas for seed collection of *Reynoutria* sp. in south Sweden: county Scania (bottom inserted rectangle) and Halmstad municipality in county Halland (top inserted rectangle). Bottom graphs: Enlarged cut-out maps showing location of the individual stands for seed collection in Scania (left) and Halland (right). The abbreviation lon is longitude and lat is latitude.

Mag-Bind® Plant DNA DS 96 kit and Kingfisher extraction robot according to the manufacturer's instructions. One nuclear marker (ITS) which is inherited biparentally and the plastid marker RbcL (which is maternally inherited) were used (Desjardins et al. 2023). Sequencing libraries were created according to Meyer and Kircher (2010) and run on a MinION instrument. The generated DNA sequences were analyzed using the blast tool (Altschul et al. 1990). Thereafter the DNA sequences were mapped first for the hybrid to *R. japonica* and then to *F. baldschuanica*. The data show the number of mutations of the ITS and RbcL genes. For the ITS gene, pure *R. japonica* would have a low number of mutations towards *R. japonica* ITS and a high number towards *F. baldschuanica* ITS. For the maternally inherited RbcL gene, a low number of mutations compared to *R. japonica* indicates this species as the maternal parent of the hybrid.

Statistical analyses

The effect of seed weight on percentage germination of seed with and without calyx and of seeds with calyx sown in soil was analyzed by linear regression. The percentage germination in relation to the weight to length ratio of seeds was also analyzed with linear regression. The effect of distance to the nearest potential pollen donor and the number of pollen donors within a 2 km radius was analyzed with linear regression. Probability plots were used to assess normal distribution of the data. Statistical analyses were performed in SPSS ver. 28.0.

Results

The *R. japonica* stands in Scania differed in the amount of seeds they produced. The *R. japonica* stands Lund II and III,

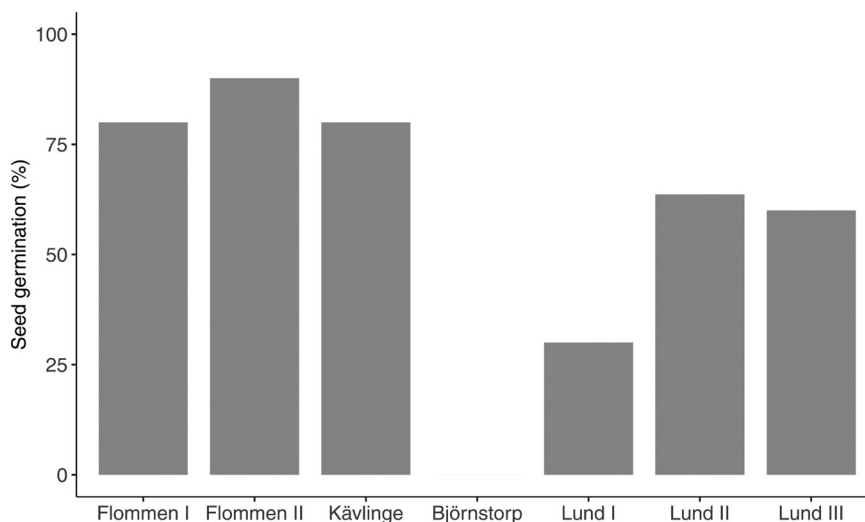


Figure 2. Seed germination from seven *Reynoutria japonica* stands in Scania, south Sweden. Coordinates for the sites are provided in Table 1. $n = 10$ except for Lund III ($n = 11$) and Björnstorp ($n = 3$).

Flommen I and II, and Kävlinge produced numerous seeds while Lund I and Björnstorp produced only a few seeds. All four *R. × bohemica* stands produced seeds. The seeds from Scania were fully filled except the few seeds from Björnstorp that were hollow. All *R. × bohemica* seeds were filled; however, these seeds were not tested for germination.

The seeds without calyx had an average germination of $57.7 \pm 32.1\%$, with only Björnstorp lacking germination (Fig. 2). The seeds from Björnstorp also became mouldy during the germination test. Seeds with calyx had on average $48.0 \pm 14.2\%$ germination for Lund III ($4 \times n = 25$) and 28% germination for Flommen I ($n = 25$). Germination with calyx was tested 11 months after collection.

The seeds collected in Lund in 2024 had $14.3\% (\pm 12.9)$ germination after 14 days (Lund I, IA, and II $n = 10$, Lund III $n = 8 \times 10$). A subsequent Tetrazolium test demonstrated $18.1\% (\pm 18.7)$ live seeds, $32.6\% (\pm 15.8)$ dead seeds, and $34.6\% (\pm 24.8)$ empty seeds.

In Halmstad an average of $31.25 (\pm 8.07)$ seeds out of 40 seeds per stand had germinated, equaling $78.13\% (\pm 20.71)$ germination (Fig. 3). Seven of the stands had over 90% germination (Fig. 3). There was a significant positive correlation between percentage seed germination and average seed weight for the sites in Halmstad ($r^2 = 0.413$; $df = 1, 18$; $p = 0.002$) (Fig. 4). Further, there was a positive relationship between germination and the W/L ratio without calyx ($r^2 = 0.420$, $F = 13$, $p = 0.002$) (Fig. 5). The mean ratio of width to length was $0.460 (\pm 0.037)$. In samples with a germination rate of over 90%, the W/L averaged 0.38, whereas for samples with less than 75% germination, the W/L was 0.27. Mean seed weight without calyx was $0.00101 \text{ g} (\pm 0.00024)$ ($n = 20$), mean seed width $1.39 (\pm 0.086)$ mm, and mean length $3.035 (\pm 0.239)$ mm.

The mean seed weight with calyx was $0.00187 \text{ g} (\pm 0.000315)$, width $4.53 \text{ mm} (\pm 0.466)$, and length $7.76 \text{ mm} (\pm 0.593)$. Germination in soil was on average $15\% (\pm 16.1)$,

with higher germination for seeds with higher seed weight (linear regression $r^2 = 0.251$; $df = 1, 18$; $p = 0.025$) (Fig. 6). Cotyledons appeared 8 days after sowing and levelled off after 17 days. When the experiment was terminated after 28 days, additional cotyledons below the soil surface were noted, resulting in 17.5% germination. Six of the *R. japonica* stands showed no germination in soil, independent of seed weight

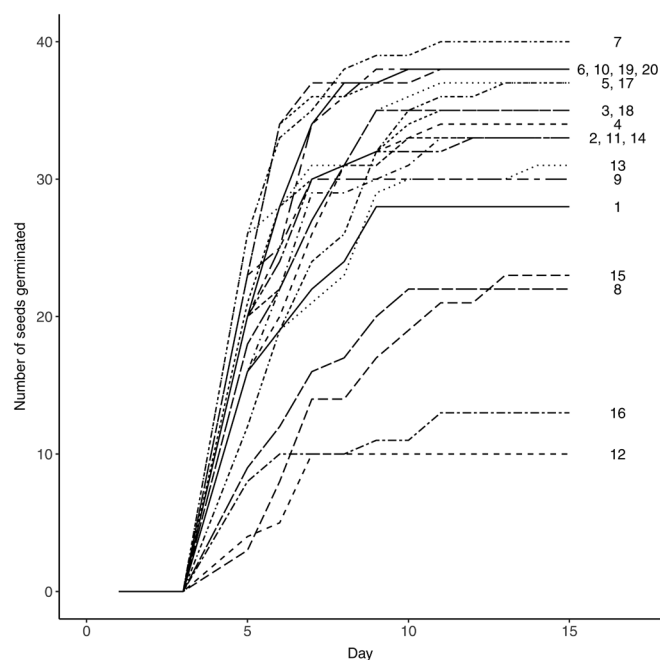


Figure 3. Germination for the 20 *Reynoutria japonica* stands in Halmstad municipality plotted as number of germinated seeds. The numbers to the right of each germination curve denote stand numbers (stand locations in Fig. 1). $n = 40$ for each stand. Seeds were germinated without calyx.

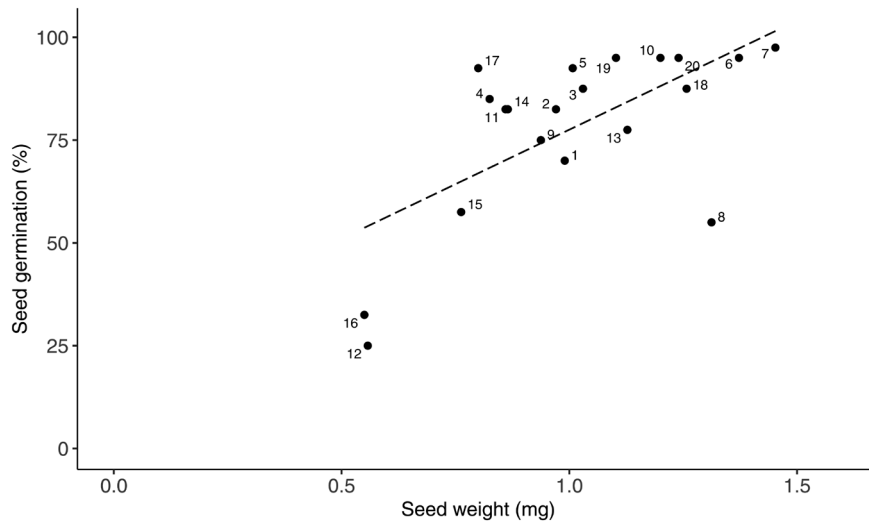


Figure 4. The relation between percentage seed germination and mean seed weight of seeds without calyx for *R. japonica* in Halmstad. Labels indicate stand number (coordinates in Appendix 1).

(Fig. 6). The width/length ratio of the seeds (with calyx) did not affect germination (linear regression ns).

Each of the *R. japonica* stands in Halmstad included in this study had on average $6.15 (\pm 2.65)$ *R. sachalinensis* and/or *R. × bohémica* stands within a 2 km radius (Supporting information). The average distance to the nearest *R. sachalinensis* or *R. × bohémica* was $530 (\pm 334)$ m. There was a positive correlation between seed germination and distance to the nearest *R. sachalinensis* and/or *R. × bohémica* ($r^2=0.475$, $p=0.034$) (Fig. 7). However, when one stand with low germination (ID12) was excluded the trend was lost ($r^2=0.117$; $p=0.151$, $df=1.17$). The distance to the nearest *Reynoutria* sp. did not affect seed weight ($r^2=0.043$; $df=1.18$; $p=0.378$). Seed germination (without calyx) was not affected by the number of *R. sachalinensis* or *R. × bohémica* within a 2 km radius ($r^2=0.000$, $df=1$; 18 ; $P=0.979$).

Further, *F. baldschuanica* is reported from Halmstad municipality (Species Observation System).

Metabarcoding

The results from the metabarcoding analyses for the suspected hybrids performed by the Centre for Genetic Identification showed that all nine samples were *R. japonica* × *F. baldschuanica* hybrids (Table 1) (Fig. 8).

Discussion

Japanese knotweed in Scania and Halmstad produced numerous seeds, but germination under laboratory conditions varied between sites. In Scania the stands produced hundreds to very few seeds, and seed germination varied from 0 to 90%

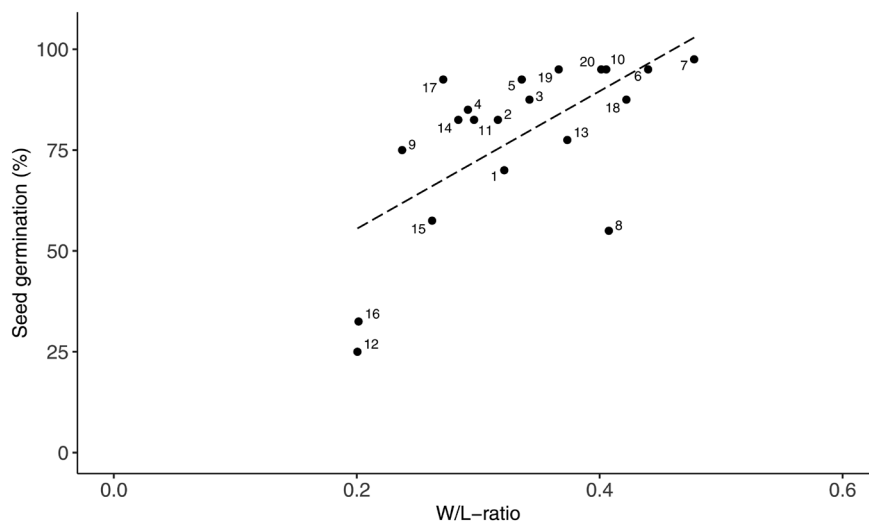


Figure 5. The relation between germination and seed weight to length ratio (W/L) for 20 *R. japonica* stands in Halmstad. Labels indicate stand numbers (coordinates in Appendix 1).

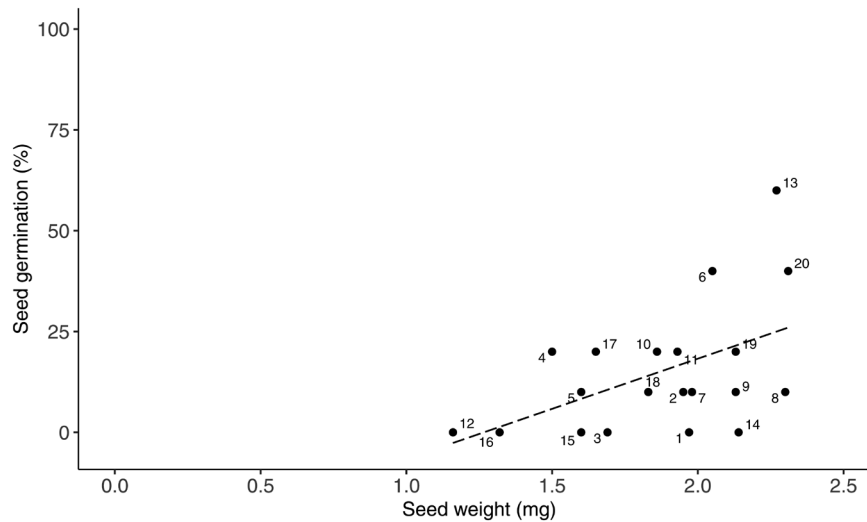


Figure 6. Seed germination in soil related to mean seed weight (with calyx) for the 20 stands in Halmstad. Labels indicate stand numbers (coordinates in Appendix 1). $n = 40$ seeds for each stand.

germination. The stands in Halmstad all produced seeds but germination varied substantially from 20.0 to 97.5% germination. Results from previous germination studies in Europe and North America similarly showed varying germination from 0 to 100% germinating seeds (Forman and Kesseli 2003, Bram and McNair 2004, Tiébré et al. 2007, Engler et al. 2011, Groeneveld et al. 2014). Collection time has been found to affect germination, as seeds that were collected in October in North America had higher germination than seeds collected in September, which was attributed to the longer time for seeds to develop fully (Bram and McNair 2004). Conditions during germination were, however, not found to affect germination, and high germination was found irrespective of whether seeds had been covered with soil, were germinated in autumn or the following spring, or were left attached to the parent plant prior to seed collection (Forman

and Keseli 2003). The seeds in our study were collected at similar times in October and November, and collection time was unlikely to affect germination (Bram and McNair 2004). However, the considerably lower germination in soil than in Petri dishes suggests that the soil conditions affected germination negatively. The production of viable seeds at northern latitudes has previously been attributed to the urban heat island effect (Groeneveld et al. 2014), which may fit germination in seeds from Lund and Halmstad. The occurrence of hollow seeds found both in the squeeze test and when bisecting seeds after the Tetrazolium test demonstrated that not all seeds from Scania and Halmstad were viable.

The results suggested that seed size positively affected germination, as seeds with a higher seed weight and weight to length (W/L) ratio had higher germination. The results of seed weight agree with general findings that higher seed

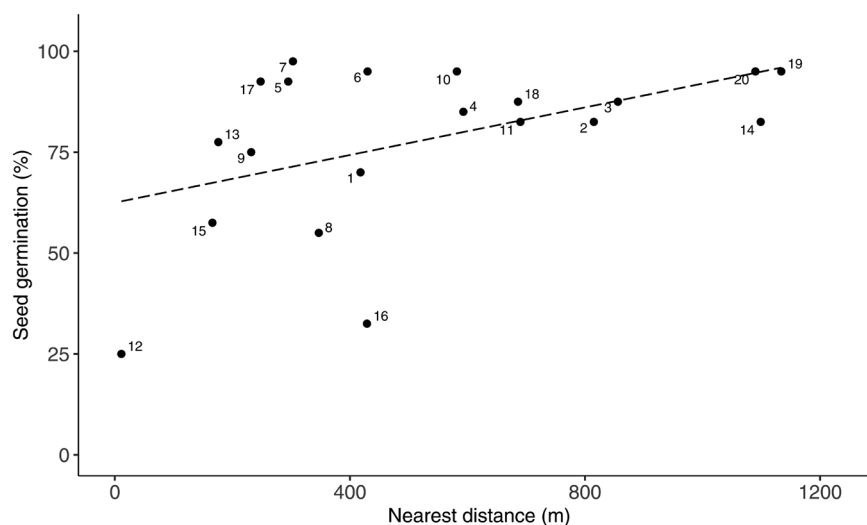


Figure 7. Seed germination (without calyx and in petri dishes) in relation to distance to the nearest *R. sachalinensis* or *R. x bohemica* in Halmstad.

Table 1. DNA barcoding analysis of knotweeds from south Sweden. The data shown in the column 'Gene' are the counts for mutations for the ITS and RbcL (maternal plastid) marker genes, respectively. Sample Backa was provided by Stefan Borgström and Onsala 2 and 3 by Alexander Zimmermann, Invaterm AB and Halmstad 2 and 3 from Mats Lindqvist, the Swedish Traffic Administration. Metabarcoding analyses were performed by the Centre for Genetic Identification at the Swedish Museum for Natural History and are available there as Open Access (Report 356-2025): <https://invaterm.com/kunskapsbank/naturhistoriska-riksmuseet-dna-analysis-a-v-parkslide-reynoutria-japonica/>.

Site		Gene	
		ITS	RbcL
Backa	<i>Reynoutria japonica</i>	168	6
	<i>Fallopia baldschuanica</i>	112	12
Halmstad 2	<i>R. japonica</i>	153	7
	<i>F. baldschuanica</i>	120	13
Halmstad 3	<i>R. japonica</i>	163	7
	<i>F. baldschuanica</i>	88	14
Glumslöv	<i>R. japonica</i>	162	6
	<i>F. baldschuanica</i>	93	12
Onsala 1	<i>R. japonica</i>	145	6
	<i>F. baldschuanica</i>	140	14
Onsala 2	<i>R. japonica</i>	148	7
	<i>F. baldschuanica</i>	135	17
Onsala 3	<i>R. japonica</i>	151	7
	<i>F. baldschuanica</i>	149	13
Lund	<i>R. japonica</i>	141	6
	<i>F. baldschuanica</i>	125	14
Ljungskile	<i>R. japonica</i>	90	6
	<i>F. baldschuanica</i>	84	11

weight is positive for germination (Seltmann et al. 2007). Further, non-germinated *R. japonica* seeds were previously found to have low W/L ratios (Engler et al. 2011). Although the W/L ratio is a reliable predictor of seed maturity, it has

been suggested to be less important as a predictor for successful germination in *R. japonica* (Ramaswamy et al. 1980, Engler et al. 2011). However, the results of the present study support that the W/L ratio could be useful as an indicator of seed quality in knotweeds.

Two factors that commonly affect seed viability are climate and pollination, which are also likely to have affected seed development in the present study (Jaganathan et al. 2020, Walker 2020). Over 30 years ago, climate was predicted to control the northern distribution limit of *R. japonica* through the length of the growing season (with a suggested threshold of 2500 day-degrees) and minimum temperature (Beerling 1993). This was substantiated by Groeneveld et al. (2014) who reported viable seed from Quebec city (with approximately 2750 day degrees) but non-viable seeds from two sites with less than 2500 day degrees. Further, Negrea et al. (2022) in an extensive land cover study concluded that cool microclimates would not be invaded in the Romanian mountains. In northern Europe, Holm et al. (2018) demonstrated that there was no genetic variation in *R. japonica* at the northern distribution limit, and concluded that no sexual reproduction occurred in the area. Since our stands grew approximately 500 km further south than the most southern stands investigated by Holm et al. (2018), the milder climate may be the reason that *R. japonica* produced fertile seed in Scania, similar to the differences between regions reported by Groeneveld et al. (2014). In addition, the first frost starts to arrive later in northern Europe, likely improving the conditions for seed production. This corresponds to the development in the UK, where seed production went from being a rare event in 1977 to more common approximately 30 years later (Bailey et al. 2009). Although climate is arguably a limiting factor for knotweed distribution, ongoing climate change is likely to



Figure 8. Morphology of *R. japonica* × *F. baldschuanica* hybrids. Left: Putative *R. x bohémica* × *F. baldschuanica* after two winters (collected by Mattias West, cultivated by Henrik Morin, photo Bibbi Bonorden). Center: Seedling, Glumslöv. Right: Seedling from Halmstad, grown in greenhouse (collected by Mats Lindqvist).

provide improved conditions for seed production and potentially seedling establishment.

In addition to climate, pollination is an important factor for viable seed production in outcrossing species (Walker 2020). In female plants of *R. japonica* seed production is, however, limited by the absence of male *R. japonica* in its invaded range (Hollingsworth and Bailey 2000). Despite the absence of male *R. japonica* pollen donors, seed production has increased in Europe due to availability of alternative pollen donors, lower risk for frost in late autumn, and changes in pollinator behavior (Bailey et al. 2009). It is well documented that *R. sachalinensis*, *R. × bohemica*, and *F. baldschuanica* function as pollen donors to female *R. japonica* in central and western Europe, North America, and the UK (Tiébré et al. 2007, Bailey et al. 2009, Bailey 2013, Parepa et al. 2013, Gaskin et al. 2014, Groeneveld et al. 2014, Hoste et al. 2017). At the south Swedish sites, *R. × bohemica* and/or *R. sachalinensis* co-occur with *R. japonica* at the sites Kävlinge, Lund I, and II, and in Halmstad municipality. All *R. japonica* stands were on average within 550 m of a *Reynoutria sachalinensis* or *R. × bohemica* stand, which is well within the 2–3 km distance that was previously found to result in successful seed set (Engler et al. 2011). In addition, *F. baldschuanica* is a common ornamental plant in the area. The positive effect of distance on germination in Halmstad municipality suggests no shortage of pollen donors, and ready access to pollen donors has repeatedly been found in Europe (Mandák et al. 2004, Bailey et al. 2009, Engler et al. 2011). The metabarcoding analyses identified *F. baldschuanica* as the pollen donor in all nine analyzed samples. Although some of the proportions were skewed, this was a relatively small study, and further analyses are needed to evaluate the possibility that some samples were back crosses. In addition, a wider analysis including markers for *R. sachalinensis* is needed. The results support studies from the UK, Belgium, and Germany that identified *F. baldschuanica* as a common pollen donor to *R. japonica* (Bailey and Conolly 2000, Bailey et al. 2009, Engler et al. 2011, Hoste et al. 2017).

Although seed set has been commonly reported in the invaded range of *R. japonica*, seedlings are rare in Europe (Engler et al. 2011, Hoste et al. 2017). Bailey (2001) stated that *F. × conollyana* seedlings required a warm, wet autumn followed by a cold winter and a subsequent warm winter, conditions that were considered rare. The *R. japonica* × *F. baldschuanica* seedlings reported in the present study were the first reports of *Reynoutria* seedlings in Sweden and indicate that appropriate conditions for germination can occasionally be found in the field. Our potted plants survived the winter in a cool greenhouse and others were reported to survive in an unheated greenhouse and in a cold frame (Morin, H. and West, M., pers. comm.). These observations suggest that knotweed seedlings may overwinter in south Sweden. However, *R. japonica* × *F. baldschuanica* seedlings appeared to have relatively weak growth, supporting the conclusion by previous authors that they would not provide a high risk for invasion (Bailey 2001, Hoste et al. 2017). One reason for increased invasive ability is that hybrids in general are considered to

have higher plasticity and be more tolerant to environmental conditions than the parent species (Weber and D'Antonio 1999, Buhk and Thielsch 2015). Knotweed hybrids have been concluded to increase invasiveness, and in interspecific competition, *R. japonica* × *R. sachalinensis* hybrids were found to be more competitive than the parent species (Mandák et al. 2004, Parepa et al. 2013, Buhk and Thielsch 2015). Given the high trait variation among different knotweed hybrids, even low occurrence of hybrid seedlings is considered to boost invasive potential (Pysek et al. 2003).

Although seedlings are reported to be rare in Europe, seedlings appear to be more common in the US (Hruskova and Hofbauer 1999, Forman and Keselli 2003, Bram and McNair 2004, Funkenberg et al. 2012, Hoste et al. 2017). They are negatively affected by drought and frost, but these factors were not considered to explain the low numbers in Europe, where seedlings are found in mountainous areas with a cool climate (Funkenberg et al. 2012, Martin et al. 2019, Mereda et al. 2019, Negrea et al. 2022). Expansion of *R. × bohemica* is reported to increase the northward knotweed dispersal in Canada and it has therefore been suggested to also be a factor in northward expansion in Europe (Mandák et al. 2004, Groeneveld et al. 2014). Further, Dusz et al. (2025) stated that the possibility of sexual reproduction of Asian knotweeds (*Reynoutria* spp.) in its invaded range is often overlooked, and suggested adapting knotweed management to include interventions that limit seed set and seed germination. To date, *R. japonica* is not reported from the northwestern mountainous regions (500–2000 a.s.l.) in Sweden, which is in accordance with the Nordic distribution modelled by Beerling (1993) (Species Observation Site). The present study shows that co-occurrence of interbreeding knotweeds and a changing climate in the Nordic region have provided conditions for seed set and germination of knotweeds at their northern distribution range.

Conclusions

The germination studies confirmed that *R. japonica* produces viable seed in south Sweden, which is further north than previously demonstrated in Europe. This study demonstrated that *F. baldschuanica* was a common pollen donor, and that knotweed seedlings occurred in south Sweden. How common different hybrid knotweeds are in the Nordic region, and their potential contribution to northward expansion, remain to be determined.

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Author contributions

Tina D'Hertefeldt: Conceptualization (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead). **Annette Andersson**: Investigation (equal); Writing – original draft (equal). **Ellen Andersson**: Investigation (equal); Writing – original draft (equal). **Bea Nerer**: Investigation (equal); Writing – original draft (equal). **Mattias West**: Investigation (supporting). **Alexander Zimmerman**: Investigation (supporting).

Data availability statement

Data are provided as supplementary material and will be uploaded to a data repository if required. Molecular data and DNA extracts are available as Open access Report 356-2025 at the Center for Genetic Identification at the National History Museum, Stockholm, Sweden (nrm.se).

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.79cnp5j9k> (D'Hertefeldt et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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