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Authors: Drazan, Dallas, Smith, Alan G., Anderson, Neil O., Becker,

Roger, and Clark, Matthew

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Review

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Author for correspondence:

Alan G. Smith, Department of Horticultural Science, University of Minnesota, 305 Alderman Hall, 1970 Folwell Avenue, St. Paul, MN 55108. (Email: smith022@umn.edu)

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History of knotweed (Fallopia spp.) invasiveness

Dallas Drazan¹, Alan G. Smith², Neil O. Anderson², Roger Becker³ and Matthew Clark⁴

¹Graduate Research Assistant, Department of Horticultural Science, University of Minnesota, St. Paul, MN, USA; ²Professor, Department of Horticultural Science, University of Minnesota, St. Paul, MN, USA; ³Professor and Extension Agronomist, Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN, USA and ⁴Assistant Professor, Department of Horticultural Science, University of Minnesota, St. Paul, MN, USA

Abstract

Knotweed (Fallopia spp.) is an herbaceous perennial from East Asia that was brought to Europe and North America and, despite control efforts, subsequently spread aggressively on both continents. Data are available on knotweed's modes of sexual and asexual spread, historical spread, preferred habitat, and ploidy levels. Incomplete information is available on knotweed's current global geographic distribution and genetic diversity. The chemical composition of knotweed leaves and rhizomes has been partially discovered as related to its ability to inhibit growth and germination of neighboring plant communities via phytochemicals. There is still critical information missing. There are currently no studies detailing knotweed male and female fertility. Specifically, information on pollen viability would be important for further understanding sexual reproduction as a vector of spread in knotweed. This information would help managers determine the potential magnitude of knotweed sexual reproduction and the continued spread of diverse hybrid swarms. The potential range of knotweed and its ability to spread into diverse habitats makes studies on knotweed seed and rhizome cold tolerance of utmost importance, yet to date no such studies have been conducted. There is also a lack of genetic information available on knotweed in the upper Midwest. Detailed genetic information, such as ploidy levels and levels of genetic diversity, would answer many questions about knotweed in Minnesota, including understanding its means of spread, what species are present in what densities, and current levels of hybridization. This literature review summarizes current literature on knotweed to better understand its invasiveness and to highlight necessary future research that would benefit and inform knotweed management in the upper Midwest.

Introduction

Knotweed (Fallopia spp.) is a highly competitive, invasive, herbaceous perennial that has spread from its native range in Japan, China, and Korea to Europe and then to North America. It was first introduced to the United States in 1873 (Barney 2006) and has since been widely distributed by humans as an ornamental plant. The knotweed complex includes Japanese knotweed [Fallopia japonica (Houtt.) Ronse Decr.; syn.: Polygonum cuspidatum Siebold & Zucc.], a dwarf-type Japanese knotweed [Fallopia japonica var. compacta (Hook.f.) J.P. Bailey], giant knotweed [Fallopia sachalinensis (F. Schmidt) Ronse Decr.; syn.: Polygonum sachalinense F. Schmidt ex Maxim.], and their hybrid, Bohemian knotweed [Fallopia × bohemica (Chrtek and Chrtková) J.P. Bailey; syn.: Polygonum× bohemica (J. Chrtek & Chrtková) Zika & Jacobson [cuspidatum× sachalinense]. The use of the term "knotweed" throughout this paper will refer only to these two species and their hybrid. Knotweed can spread prolifically via both asexual propagation (rhizomes and adventitious rooting) and sexual reproduction (seeds) (Bailey et al. 2008). Knotweed spread is also greatly facilitated by its propensity to inhabit riparian areas (Bímová et al. 2001). Knotweed seeds are highly buoyant in water, allowing them to travel away from the mother plant to establish new knotweed populations (Lamberti-Raverot et al. 2017). A study also found that even though most seeds fall close to the maternal clone, seeds can disperse via wind up to 16 m (Tiébré et al. 2007). Additionally, rhizome fragments as small as 1 cm (0.7 g) can give rise to new plants (Bailey et al. 2008). The large number of wetlands, lakes, streams, and rivers in Minnesota makes the state particularly susceptible to the effects of a knotweed invasion. However, little research has been conducted on the spread of knotweed in Minnesota and other northern Midwest states. The primary goal of this literature review is to discuss research on the mechanisms of dispersal, genetics, and growth habit of knotweed to better understand its invasiveness with a secondary goal of proposing necessary future research specifically for the state of Minnesota.

It is important to note at the onset of this literature review that a great deal of research on the knotweed complex has been reported on European populations. Thus, much of our

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Table 1. Summary of change in nomenclature of *Fallopia japonica* since its first classification in 1777.

Past taxonomic classification of <i>F. japonica</i>	Authority	Year
Reynoutria japonica	Houttuyn ^{a,b}	1777
Polygonum sieboldii	Reinw. ^a	1848
Polygonum cuspidatum	Sieb. & Zucc. ^a	1846
Polygonum reynoutria	Makino ^a	1901
Classified as Fallopia	Decraene & Akeroyd ^{c,d}	1988

^aBailey and Conolly 2000.

understanding of knotweeds is specific to Europe, which is even more reason to conduct research in Minnesota to have the geographic specificity necessary to make accurate management decisions.

Classification

The taxonomic classification of knotweed has changed numerous times since its initial classification. Fallopia japonica was originally classified as Reynoutria japonica by Houttuyn in 1777 (Bailey and Conolly 2000; Beerling et al. 1994; Table 1). In 1848 it was reclassified as Polygonum sieboldii Reinw. (= Polygonum cuspidatum Sieb. & Zucc.) in reference to Phillipe von Siebold, who originally brought specimens to the Netherlands from his sojourn in Japan (Bailey and Conolly 2000). These two names were combined by Makino in 1901 to create the new nomenclature *Polygonum rey*noutria Makino (Bailey and Conolly 2000). The knotweed complex was first classified in the genus Fallopia by Decraene and Akeroyd in 1988 (Bailey and Stace 1992; Decraene and Akeroyd 1988). Throughout the literature, authors use the Polygonum, Reynoutria, and Fallopia genera. Confusion with the nomenclature of knotweed continues due to the use of multiple specific epithets. Different countries also have different preferences on the nomenclature they use (Bailey and Wisskirchen 2006).

Distribution and Spread

Fallopia japonica was commercially available in Europe in 1848 (Bailey and Conolly 2000). In England, the first record of *F. japonica* dates to the late 1840s (Bailey 1994). The initial introduction of *F. japonica* to England was a single male-sterile clone that successfully spread and created a massive knotweed infestation that exists across the United Kingdom today (Bailey et al. 2008; Hollingsworth and Bailey 2000). The earliest herbarium record of *F. japonica* in the United States is from 1873 (Barney 2006). Knotweed (*F. japonica*) was being sold in Minnesota as early as 1908 (Figure 1) (The Jewell Nursery Co. 1908), but residents could have purchased knotweed earlier from nurseries on the East Coast of the United States (Maule's Seed Catalogue 1895; James Vick's Sons 1898).

Fallopia sachalinensis arrived in Europe in 1864 at the botanic gardens of St. Petersburg, Russia (Bailey and Wisskirchen 2006). Fallopia × bohemica was not recorded in Europe until the 1980s, when it was first described by Chrtek and Chrtková, although it is now known to have occurred earlier, as early as 1872, and spread undetected (Bailey and Wisskirchen 2006).

The undetected spread is primarily due to the difficulty in visually identifying the hybrid (Bailey and Wisskirchen 2006). Morphological traits of F. \times bohemica are variable and can exhibit traits of F. japonica or F. sachalinensis. Fallopia \times bohemica was confirmed in the United States in 2001 (Bailey and Wisskirchen 2006). Interestingly, F. \times bohemica was not described in its native range in Japan until 1997 because the parental species were not sympatric in Japan until that time (Bailey 2003).

A total of 47% of 92 knotweed populations sampled in the first transcontinental genetic study of knotweed in the United States were identical to the British male-sterile clone of F. japonica (Grimsby and Kesseli 2009); this included one population sampled from Duluth, MN (Grimsby and Kesseli 2009; see supplemental information here: http://www.genetics.umb.edu). As many as 54% of samples in this study were found to be F. japonica (50 samples), 3% F. sachalinensis (3 samples), and 42% F. × bohemica (39 samples). This contrasts with a study of knotweed in the western United States that found F. \times *bohemica* to be more common than F. japonica with a ratio of 5:1 (Gaskin et al. 2014). The difference between these two studies could potentially be attributed to the fact that the Grimsby and Kesseli study specifically requested collaborators to collect "Japanese knotweed," which may have dissuaded collectors from sending in samples of other taxa. There is potential that the composition of knotweed taxa in Minnesota is similar to that seen in other areas across the United States, but without a thorough sampling and genetic testing, it is impossible to know which species is most prevalent.

Invasiveness

It is necessary to first understand what unique characteristics make knotweed such a strong invader in order to ultimately control it. Invasive nonnative plant species have many effects on environments in their adventive ranges. Invasive alien plants reduce the overall fitness and growth of local plant species, decrease plant species abundance and diversity, and decrease animal species' fitness and abundance (Vilà et al. 2011). Knotweeds have been shown to reduce the overall biomass of macroinvertebrates in their stands by up to 60% and also negatively impact the biomass, cover, and species richness of native plants (Lavoie 2017). It has been found that 1.6 to 10 times as many species grow outside knotweed stands as compared to within (Aguilera et al. 2010). Knotweeds also negatively impact riparian areas by changing leaf litter nitrogen composition (Urgenson 2006) and reducing ecosystem services such as access to riverbanks (Kidd 2000). Knotweeds are also often considered aesthetically displeasing (Kidd 2000).

Managing and eradicating invasive plants can also be extremely costly. An estimated US\$500 million is spent yearly on the management of nonnative plant species just on residential properties alone in the United States (Pimentel et al. 2005). It would cost an estimated $\mbox{\ensuremath{\mathfrak{G}}32.3}$ million (US\$38 million) annually to control all the knotweed populations in Germany (Reinhardt et al. 2003).

Reproduction

Knotweed can spread asexually by both rhizomes and adventitious rooting of stem fragments (Bailey et al. 2008). Knotweed primarily spreads via rhizome dispersal occurring from floods or human activity in the adventive range (Bailey et al. 2008). Reproduction via adventitious rooting of stem fragments results in lower levels of regeneration for F. japonica and F. \times bohemica as compared with regeneration from rhizomes. However, F. sachalinensis has

^bBeerling et al. 1994.

cBailey and Stace 1992.

dDecraene and Akeroyd 1988.

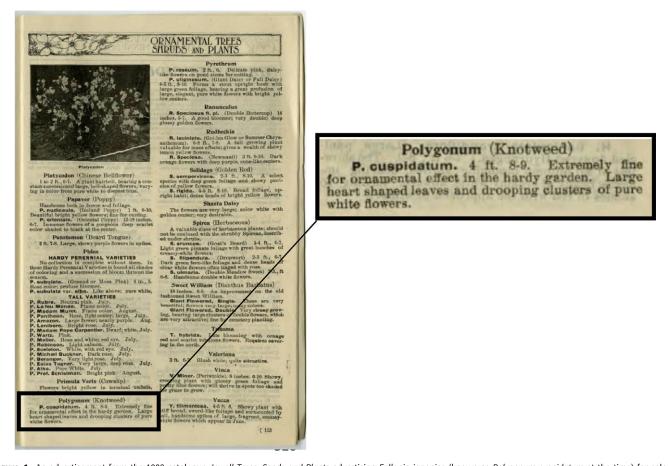


Figure 1. An advertisement from the 1908 catalogue Jewell Trees, Seeds and Plants advertising Fallopia japonica (known as Polygonum cuspidatum at the time) for sale in Minnesota. https://umedia.lib.umn.edu/item/p16022coll265:2855?q=polygonum+cuspidatum.

higher levels of regeneration from adventitious rooting of stem fragments and only low levels of regeneration when grown from rhizomes (Bímová et al. 2003). Overall, vegetative regeneration is highest in F. × bohemica (Bímová et al. 2003). Knotweeds form shoot clumps or crowns composed of dead shoots from previous growth years and underground wintering buds that give rise to new aerial shoots in the spring (Bailey et al. 2008; Dauer and Jongejans 2013). Size of crowns varies between species, with F. japonica having larger crowns than F. sachalinensis, while the hybrid, F. × bohemica, has an intermediate crown size (Bailey et al. 2008).

Fallopia japonica frequently reproduces via seed in its native range (Bailey 2003; Bram and Mcnair 2004) and has been reported to reproduce via seed in the adventive range (Bram and Mcnair 2004; Forman and Kesseli 2003), although this is thought to be less common than asexual reproduction (Bailey et al. 2008). Knotweed produces prolific seed, with a study of F. japonica and F. sachalinensis in Pennsylvania reporting 50,000 to 150,000 seeds annually per stem (Niewinski 1998). Knotweeds have high germination rates of up to 92% (field germinations) (Bram and Mcnair 2004), 93% (dried seed) (Groeneveld et al. 2014), and even up to 100% (overwintered seed) (Forman and Kesseli 2003). Germination has been shown to rely on seed maturity levels (Bram and Mcnair 2004). Knotweeds are dioecious, but there are known cases of gynodioecious plants in each taxa (Bailey et al. 2008; Beerling et al. 1994; Holm et al. 2018; Karaer et al. 2020; Niewinski 1998). There are also reports of androdioecious knotweed from the Amami Islands of Japan (Mitsuru Hotta, personal communication, in Bailey 2003). There is currently no research on knotweed pollen viability reported in the literature. Sexual reproduction may not be an important management concern if there is no pollen donor present. On the other hand, if many viable pollen donors are present, then sexual reproduction is a major concern and a priority for management decisions. That is why it is critical that research be conducted on male and female fertility of knotweed.

Structure of Growth

A study in the Czech Republic found that, on average, invasive species as a whole were 1.2 m taller than native species across all habitat types (Divíšek et al. 2018). Knotweeds are incredibly tall and range in height from 2 to 4 m thus shading out other plants (Bailey et al. 2008; Bímová et al. 2001). Fallopia japonica has a smaller overall stature ranging from 2 to 3 m in height; F. sachalinensis is the tallest of the species and reaches 4 m in height; while the hybrid F. \times *bohemica* has the greatest range in height of 2.5 to 4 m (Bailey et al. 2008). Knotweeds create a monoculture (Figure 2) with large leaves that form an extremely dense canopy, shading other plants throughout the majority of the growing season, making it difficult for smaller plants to grow in the same area (Bailey et al. 2008; Siemens and Blossey 2007). This is especially true of *F*. sachalinensis, whose leaves can reach 40 cm in length (Bailey and Stace 1992). However, it is worth noting that Moravcová et al. (2011) concluded that shading is unlikely the primary invasive 620 Drazan et al.: Knotweed review



Figure 2. Example of a knotweed monoculture growing in Minnesota. Photograph shows a $Fallopia \times bohemica$ population from Brooklyn Center, MN, on August 16, 2019.

mechanism of knotweeds, as light treatment studies yielded inconclusive results.

It is generally accepted that knotweed rhizomes can grow up to 7 m from the crown of origin, but recent research has shown that *F. japonica* rhizomes typically extend no more than 4 m (Fennell et al. 2018). Still, knotweed rhizomes are a formidable opponent, as they can grow up through asphalt (Wade et al. 1996). They can also cause bank destabilization when growing alongside water bodies, as the rhizomes are less able to bind soil together compared with some native riparian plants (Reinhardt et al. 2003).

Soil Conditions

Knotweed is an early successional species growing on volcanic ash and recent lava flows in its native habitat in Japan (Bailey et al. 2008; Barney et al. 2006). The range of habitats and soil types it is known to grow in is extremely diverse. It can be found across 35 latitudinal degrees and grows from sea level to 3,500 m above sea level (Bailey 2003). It often grows in riparian and ruderal areas, areas experiencing human disturbances, forest margins, urban landscapes, and gardens (Bailey et al. 2008; Clements et al. 2016; Mandák et al. 2004). It grows on a variety of terrains, including sandy soils, swamps, rocky banks, and alluvial floodplains (Barney et al. 2006). Knotweeds have highly plastic salt-tolerance traits and are now known to grow in salt marsh habitats in the eastern United States (Richards et al. 2008). Furthermore, knotweeds are known to grow in soils with high concentrations of metal pollutants (Michalet et al. 2017). Indeed, knotweed growth rates are greater in soils with average concentrations of metallic pollutants (2 mg kg⁻¹ Cd, 150 mg kg⁻¹ Cr, 100 mg kg⁻¹ Pb, and 300 mg kg⁻¹ Zn) compared with unpolluted soil (Michalet et al. 2017). Fallopia × bohemica accumulated the greatest concentration of metals relative to either F. japonica or F. sachalinensis (Michalet et al. 2017).

Allelopathy

Fallopia japonica contains chemicals with the potential to cause allelopathic effects; these chemicals include resveratrol, resveratroloside, piceid, piceatannol glucoside, polydatin, emodin, and catechins (Serniak 2016; Vastano et al. 2000). *Fallopia* × *bohemica* has

also been found to have allelopathic effects on nearby plants, particularly affecting seed germination and seedling growth (Siemens and Blossey 2007). One study found that mechanical control of F. \times bohemica via stem cutting causes an overall reduction in production of allelochemicals (Murrell et al. 2011). Fallopia sachalinensis also has allelopathic capabilities and has been shown to have the greatest phytotoxic effects on other plants (Moravcová et al. 2011).

The highest level of phenolic compounds is found in the rhizomes (Vaher and Koel 2003). However, the decomposition of knotweed litter from each of the taxa also has phytotoxic effects on other plants (Moravcová et al. 2011). These allelopathic chemicals are significant, because they greatly increase knotweed's invasive and competitive ability.

Genetic Diversity

Knotweed has higher levels of genetic diversity in its native range than its invasive range (Bailey 2003). There are also many more subspecies and varieties of knotweed in the native range compared with the adventive range (Bailey 2003; Inamura et al. 2000). Hybridization of knotweed in Japan is limited, which differs from the knotweed found in Europe and North America, where hybridization is common (Bailey 2003; Grimsby et al. 2007). Clonal invasive species that reproduce asexually typically have lower genetic variation (Bailey 2003), so it would follow that invasive knotweed would have low genetic variability; however, the ability of an invasive to hybridize can increase its invasive success (Ellstrand and Schierenbeck 2006). Indeed, $F. \times bohemica$ shows heterosis in that it is more invasive than its parents (Parepa et al. 2014), spreads faster than both parents (Mandák et al. 2004), and has a higher regenerative ability than its parents (Bímová et al. 2003).

Knotweed in the United Kingdom shows interspecific diversity, with F. japonica, F. \times bohemica, and F. sachalinensis all clustering separately in diversity analyses and F. \times bohemica clustering two-thirds closer to F. japonica than F. sachalinensis (Hollingsworth et al. 1998). This could potentially be due to multiple backcrossing events. It was found that F. japonica and F. \times bohemica are most genetically similar, whereas F. japonica and F. sachalinensis are the least similar (Holm et al. 2018). It has also been found that F. \times bohemica shows higher diversity compared with either parent, which could be explained by spread via sexual reproduction (Hollingsworth et al. 1998).

Low genetic diversity was found for all three of the knotweed taxa across Norway (Holm et al. 2018). Due to these low levels of genetic variation, it was concluded that knotweed likely has not reproduced sexually in Norway (Holm et al. 2018).

Within-species genetic diversity was found to be low across all taxa in a study of knotweeds in Poland and Japan (Bzdega et al. 2016), with *F. japonica* and *F. sachalinensis* showing the lowest levels of polymorphism. *Fallopia japonica* populations in this study were not found to be a single clone.

Fallopia japonica spreads exclusively by vegetative reproduction, and the clones are monotypic in the western United States (Gaskin et al. 2014). The Gaskin et al. (2014) study used amplified fragment length polymorphisms (AFLPs) to compare F. japonica with multiple samples of the clone that invaded the United Kingdom and found them to be genetically identical. Fallopia sachalinensis was also found to spread primarily by vegetative means and was mostly monotypic in the western United States (Gaskin et al. 2014). However, F. \times bohemica differed from its parents, in that it was found to spread by both asexual and sexual mechanisms, had the lowest number of monotypic populations,

the highest proportion of loci that are polymorphic, and the highest genetic diversity (Gaskin et al. 2014).

A study in Massachusetts that used simple sequence repeat (SSR) markers also found the UK clone of *F. japonica* in all three of the populations surveyed (Grimsby et al. 2007). This study found 26 genotypes from 66 samples across three distinct *F. japonica* populations. They also found evidence for sexual spread of knotweed in Massachusetts, as most knotweed patches were composed of unique genets that were not found in other patches.

A transcontinental study of knotweed analyzed 92 locations across the United States and, using SSR markers, identified 36 genotypes (Grimsby and Kesseli 2009). *Fallopia* × *bohemica* had the most diversity, as it was composed of 26 genotypes, while *F. japonica* samples were made up of 8 genotypes, and *F. sachalinensis* had only 2 genotypes. The UK clone of *F. japonica* was also detected in this study.

Another study used random amplified polymorphic DNA analysis to study the genetic diversity of *F. japonica* along two creeks in Kentucky (Wymer et al. 2007). The authors found no evidence of asexual spread and concluded that the genetic diversity that did exist resulted from multiple introductions.

Populations of *F. japonica* and $F. \times bohemica$ have been shown to have a large amount of epigenetic diversity. Epigenetic diversity occurs through processes such as DNA methylation or histone modification instead of DNA base pair changes. One study used AFLP genetic diversity markers to measure genetic diversity, which were then compared with epigenetic diversity levels found using methylation-sensitive AFLP epigenetic diversity markers that could identify methylated cytosine (Richards et al. 2012). The authors found that a single clone of F. japonica contained 129 epigenotypes, even though it was only composed of one genotype and had no genetic variation (Richards et al. 2012). This study also analyzed F. × bohemica and found 85 epigenotypes, but only 7 genotypes, across 155 individuals. Both F. japonica and F. \times bohemica showed higher levels of epigenetic variation than genetic variation, with the epigenetic variation for F. \times bohemica being 10 times higher than its genetic variation. This is important, because epigenetic variation is one explanation for the phenotypic diversity and successful establishment of clonally spread F. japonica in diverse environments with invasive populations that have low genetic variation. (Banerjee et al. 2019).

In a study of central European *F. japonica*, a single genotype of *F. japonica* contained 27 different epigenotypes (Zhang et al. 2016). The authors also found that the epigenetic variation was a full order of magnitude higher than the genetic variation. Their study was able to correlate epigenetic diversity with both phenotypic diversity and the climate from which the *F. japonica* population originated. Notably, *F. japonica* varied in some key phenotypic traits associated with invasiveness, such as specific leaf area. They concluded this correlation could potentially lead to habitat adaptation, which could explain how a single clone of *F. japonica* was able to become such a strong invader across much of Europe.

It is important that a genetic diversity study be conducted in Minnesota, because it has been shown that each congener can react differently to different control methods (Bímová et al. 2001). It has also been shown that F. japonica, F. sachalinensis, and F. \times bohemica all react differently to biological control with the psyllid $Aphalara\ itadori\ Shinji\ (Grevstad\ et\ al.\ 2013)$. Thus, it is imperative that land managers and homeowners know exactly which taxa is invading an area so that they can choose the most effective control method.

Ploidy and Cytogenetics

Knotweed has a base chromosome number of x = 11 (Bailey and Stace 1992). In Japan, high-altitude dwarf F. japonica has been found as a tetraploid (2n = 4x = 44), and tall lowland F. japonica has been found as tetraploid and octoploid (2n = 8x = 88; Bailey 2003). Limited sampling found F. japonica from China to be octoploid and decaploid (Bailey 2003). Fallopia sachalinensis is tetraploid in its native range (Bailey 2003) with the exception of Korean F. f sachalinensis being dodecaploid (Kim and Park 2000).

In the adventive range, F. japonica var. japonica has been found to be octaploid, and F. japonica 'Compacta' has been found as a tetraploid (Mandák et al. 2003). There have been no reports of F. japonica as a diploid. Fallopia sachalinensis has been found as a mixture of tetraploid, hexaploid, and octoploid, and F. \times bohemica is primarily hexaploid with evidence for tetraploids and octoploids as well (Mandák et al. 2003). The hybrid created between F. sachalinensis and Compacta has also been found as a tetraploid (Bailey and Stace 1992). Even though F. \times bohemica can be crossed with itself or either parent, resulting in a range of euploid and aneuploid progeny, it is primarily found in nature in a euploid state as a tetraploid, hexaploid, octoploid, or infrequently a decaploid (Bailey and Wisskirchen 2006).

Tetraploid knotweed shows normal bivalent pairing in meiosis and a low level of chiasma (Bailey and Stace 1992). Tetraploid and octoploid *F.* × *bohemica* have a more normal meiosis than the hexaploid *F.* × *bohemica* (Bailey and Stace 1992). The hexaploid *F.* × *bohemica* shows irregular meiosis that consists of numerous univalents and multivalents not surpassing quadrivalents (Bailey and Stace 1992). The DNA 2C-values per 2x genome of the taxa ranged from 1.23 to 1.62 pg, with *F. sachalinensis* at 1.33 pg, Compacta at 1.29 pg, *F. japonica* ranging from 1.30 to 1.62 pg, and *F.* × *bohemica* ranging from 1.23 to 1.59 pg (Bailey and Stace 1992). This paper also posits that the tetraploids are much older than the octoploids, because the tetra-haploid genome of *F. japonica* var. *japonica* can form bivalents, yet the di-haploid genome of *F. sachalinensis* cannot.

Ploidy levels of knotweed are important, because they can impart reproductive barriers or reduce fertility, which determine the taxa that can successfully reproduce sexually together. For example, *F. japonica* can produce seed after pollination by the related species Bukhara fleeceflower (*Fallopia baldschuanica* Regel; syn.: *Polygonum baldschuanicum* Regel), but this hybrid seed is infertile and rarely becomes established (Bailey et al. 2008).

Conclusion

The depth of research on knotweeds is impressive, but it would be poor practice to assume knotweeds will operate similarly in a different environment such as Minnesota or that we have sufficient knowledge to efficiently control it. Research on the genetic diversity of knotweed has been conducted elsewhere in the United States (Gaskin et al. 2014; Grimsby and Kesseli 2009; Grimsby et al. 2007; Richards et al. 2012; Wymer et al. 2007), but to date no such research has taken place in the Midwest or Minnesota. This is especially worrisome, given that knotweed has been reported in every midwestern state (EDDMapS 2021; https://www.eddmaps.org/) and all three taxa are listed as noxious in Minnesota (Midwest Invasive Plant Network 2018). The density of knotweed varies across the state, with the highest number of knotweed populations being reported in Duluth and the Twin Cities (EDDMapS 2021). For example, there are currently 264 confirmed reports of knotweed just in Duluth alone (EDDMapS 2021), meaning there is a 622 Drazan et al.: Knotweed review

knotweed population every 0.78 km². With varied mechanisms of dispersal, including intentional human spread, it is extremely important to know which species are present in Minnesota and the primary means by which each taxa is spreading, either by sexual or asexual means, so that their spread can be better combated to inform and improve management outcomes. Each taxa responds differently to mechanical, chemical, and biological control (Bímová et al. 2001; Grevstad et al. 2013). Thus, it is essential to know exactly which type of knotweed is going to be treated before a control measure is selected. Because it can be difficult to visually distinguish the taxa from one another, genetic testing is essential to provide accurate identification information. Measuring fertility and sexual reproduction of invasive knotweeds will foretell increasing genetic diversity and the potential for evolution of resistance to management.

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References

- Aguilera AG, Alpert P, Dukes JS, Harrington R (2010) Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem processes. Biol Invasions 12:1243–1252
- Bailey JP (1994) The reproductive biology and fertility of *Fallopia japonica* (Japanese knotweed) and its hybrids in the British Isles. Pages 141–158 *in* de Waal LC, Child LE, Wade PM, Brock JH, eds. Ecology and Management of Invasive Riparian Plants. Chichester: John Wiley and Sons
- Bailey JP (2003) Japanese knotweed s.l. at home and abroad. Pages 183–196 in Child L, Brock J, Brundu G, Prach K, Pyšek P, Wade P, Williamson M, eds. Plant Invasions: Ecological Threats and Management Solutions. Leiden: Backhuys
- Bailey JP, Bímová K, Mandák B (2008) Asexual spread versus sexual reproduction and evolution in Japanese knotweed s.l. sets the stage for the "battle of the clones." Biol Invasions 11:1189–1203
- Bailey JP, Conolly AP (2000) Prize-winners to pariahs—a history of Japanese knotweed s.l. (*Polygonaceae*) in the British Isles. Watsonia 23:93–110
- Bailey JP, Stace CA (1992) Chromosome number, morphology, pairing, and DNA values of species and hybrids in the genus *Fallopia* (Polygonaceae). Plant Syst Evol 180:29–52
- Bailey JP, Wisskirchen R (2006) The distribution and origins of *Fallopia* × *bohemica* (*Polygonaceae*) in Europe. Nord J Bot 24:173–199
- Banerjee AK, Guo W, Huang Y (2019) Genetic and epigenetic regulation of phenotypic variation in invasive plants—linking research trends towards a unified framework. NeoBiota 103:77–103
- Barney JN (2006) North American history of two invasive plant species: phytogeographic distribution, dispersal vectors, and multiple introductions. Biol Invasions 8:703–717
- Barney JN, Tharayil N, Ditommaso A, Bhowmik PC (2006) The biology of invasive alien plants in Canada. 5. *Polygonum cuspidatum* Sieb. & Zucc. [= *Fallopia japonica* (Houtt.) Ronse Decr.]. Can J Plant Sci 86:887–905
- Beerling DJ, Bailey JP, Conolly AP (1994) Fallopia japonica (Houtt.) Ronse Decraene. J Ecol 82:959–979
- Bímová K, Mandák B, Pyšek P (2001) Experimental control of *Reynoutria* congeners: a comparative study of a hybrid and its parents. Pages 283–290 *in* Brundu G, Brock J, Camarda I, Child L, Wade M, eds. Plant Invasions: Species Ecology and Ecosystem Management. Leiden: Backhuys
- Bímová K, Mandák B, Pyšek P (2003) experimental study of vegetative regeneration in four invasive *Reynoutria* taxa (*Polygonaceae*). Plant Ecol 166:1–11
- Bram MR, Mcnair JN (2004) Seed germinability and its seasonal onset of Japanese knotweed (*Polygonum cuspidatum*). Weed Sci 52:759–767
- Bzdega K, Janiak A, Książczyk T, Lewandowska A, Gancarek M, Sliwinska E, Tokarska-Guzik B (2016) A survey of genetic variation and genome evolution within the invasive *Fallopia* complex. PLoS ONE 11:1–23

- Clements DR, Larsen T, Grenz J (2016) Knotweed management strategies in North America with the advent of widespread hybrid bohemian knotweed, regional differences, and the potential for biocontrol via the psyllid *Aphalara itadori* Shinji. Invasive Plant Sci Manag 9:60–70
- Dauer JT, Jongejans E (2013) Elucidating the population dynamics of Japanese knotweed using integral projection models. PLoS ONE 8:1–11
- Decraene LR, Akeroyd JR (1988) Generic limits in *Polygonum* and related genera (*Polygonaceae*) on the basis of floral characters. Bot J Linn Soc 98:321–371
- Divíšek J, Chytrý M, Beckage B, Gotelli NJ, Lososová Z, Pyšek P, Molofsky J (2018) Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat Commun 9:1–10
- EDDMapS (2021) Early Detection & Distribution Mapping System. University of Georgia–Center for Invasive Species and Ecosystem Health. http://www.eddmaps.org. Accessed: August 20, 2021
- Ellstrand NC, Schierenbeck KA (2006) Hybridization as a stimulus for the evolution of invasiveness in plants? Euphytica 148:35–46
- Fennell M, Wade M, Bacon KL (2018) Japanese knotweed (*Fallopia japonica*): an analysis of capacity to cause structural damage (compared to other plants) and typical rhizome extension. PeerJ 6:e5246
- Forman J, Kesseli RV (2003) Sexual reproduction in the invasive species Fallopia japonica (Polygonaceae). Am J Bot 90:586–592
- Gaskin JF, Schwarzländer M, Grevstad FS, Haverhals MA, Bourchier RS, Miller TW (2014) Extreme differences in population structure and genetic diversity for three invasive congeners: knotweeds in western North America. Biol Invasions 16:2127–2136
- Grevstad F, Shaw R, Bourchier R, Sanguankeo P, Cortat G, Reardon RC (2013) Efficacy and host specificity compared between two populations of the psyllid *Aphalara itadori*, candidates for biological control of invasive knotweeds in North America. Biol Control 65:53–62
- Grimsby JL, Kesseli R (2009) Genetic composition of invasive Japanese knotweed s.l. in the United States. Biol Invasions 12:1943–1946
- Grimsby JL, Tsirelson D, Gammon MA, Kesseli R (2007) Genetic diversity and clonal vs. sexual reproduction in *Fallopia* spp. (*Polygonaceae*). Am J Bot 94:957–964
- Groeneveld E, Belzile FÇ, Lavoie C (2014) Sexual reproduction of Japanese knotweed (*Fallopia japonica* s.l.) at its northern distribution limit: new evidence of the effect of climate warming on an invasive species. Am J Bot 101:459–466
- Hollingsworth ML, Bailey JP (2000) Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese knotweed). Bot J Linn Soc 133:463–472
- Hollingsworth ML, Hollingsworth PM, Jenkins GI, Bailey JP, Ferris C (1998) The use of molecular markers to study patterns of genotypic diversity in some invasive alien *Fallopia* spp. (*Polygonaceae*). Mol Ecol 7:1681–1691
- Holm AK, Elameen A, Oliver BW, Brandsæter LO, Fløistad IS, Brurberg MB (2018) Low genetic variation of invasive *Fallopia* spp. in their northernmost European distribution range. Ecol Evol 8:755–764
- Inamura A, Ohashi Y, Sato E, Yoda Y, Masuzawa T, Ito M, Yoshinaga K (2000) Intraspecific sequence variation of chloroplast DNA reflecting variety and geographical distribution of *Polygonum cuspidatum* (*Polygonaceae*) in Japan. J Plant Res 113:419–426
- James Vick's Sons (1898) Vick's Garden and Floral Guide. 104 p
- Karaer F, Terzioğlu S, Kutbay HG (2020) A new genus record for the flora of Turkey: Reynoutria (*Polygonaceae*). Kahramanmaraş Sütçü İmam Üniversitesi Tarım ve Doğa Dergisi 23:606–610
- Kidd H (2000) Japanese knotweed—the world's largest female! Pestic Outlook 11:99–100
- Kim JY, Park C (2000) Morphological and chromosomal variation in Fallopia section Reynoutria (Polygonaceae) in Korea. Brittonia 52:34–48
- Lamberti-Raverot B, Piola F, Thiébaut M, Guillard L, Vallier F, Puijalon S (2017) Water dispersal of the invasive complex *Fallopia*: the role of achene morphology. Flora 234:150–157
- Lavoie C (2017) The impact of invasive knotweed species (*Reynoutria* spp.) on the environment: review and research perspectives. Biol Invasions 19: 2319–2337

Mandák B, Pyšek P, Bímová K (2004) History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: a hybrid spreading faster than its parents. Preslia 76:15–64

- Mandák B, Pyšek P, Lysák M, Suda J, Krahulcová A, Bímová K (2003) Variation in DNA-ploidy levels of *Reynoutria* taxa in the Czech Republic. Ann Bot 92:265–272
- Maule WH (1895) Maule's Seed Catalogue. 65 p
- Michalet S, Rouifed S, Pellassa-Simon T, Fusade-Boyer M, Meiffren G, Nazaret S, Piola F (2017) Tolerance of Japanese knotweed s.l. to soil artificial polymetallic pollution: early metabolic responses and performance during vegetative multiplication. Environ Sci Pollut Res 24:20897–20907
- Midwest Invasive Plant Network (2018) Midwest Invasive Plant List. https://www.mipn.org/plantlist. Accessed: August 20, 2021
- Moravcová L, Pyšek P, Jarošik V, Zákravský P (2011) Potential phytotoxic and shading effects of invasive Fallopia (Polygonaceae) taxa on the germination of native dominant species. NeoBiota 9:31–47
- Murrell C, Gerber E, Krebs C, Parepa M, Schaffner U, Bossdorf O (2011) Invasive knotweed affects native plants through allelopathy. Am J Bot 98:38–43
- Niewinski AT (1998) The Reproductive Ecology of Japanese Knotweed (*Polygonum cuspidatum*) and Giant Knotweed (*Polygonum sachalinensis*) Seed. MS thesis. University Park, PA: Pennsylvania State University. 49 p
- Parepa M, Fischer M, Krebs C, Bossdorf O (2014) Hybridization increases invasive knotweed success. Evol Appl 7:413–420
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52:273–288
- Reinhardt F, Herle M, Bastiansen F, Streit B (2003) Economic Impact of the Spread of Alien Species in Germany. Berlin: Federal Environmental Agency of Germany. 83 p
- Richards CL, Walls RL, Bailey JP, Parameswaran R, George T, Pigliucci M (2008) Plasticity in salt tolerance traits allows for invasion of novel habitat by Japanese knotweed s. l. (*Fallopia japonica* and *F.* × *bohemica*, Polygonaceae). Am J Bot 95:931–942

- Richards CL, Schrey AW, Pigliucci M (2012) Invasion of diverse habitats by few Japanese knotweed genotypes is correlated with epigenetic differentiation. Ecol Lett 15:1016–1025
- Serniak L (2016) Comparison of the allelopathic effects and uptake of Fallopia japonica phytochemicals by Raphanus sativus. Weed Res 56:97–101
- Siemens TJ, Blossey B (2007) An evaluation of mechanisms preventing growth and survival of two native species in invasive Bohemian knotweed (*Fallopia* × bohemica, Polygonaceae). Am J Bot 94:776–783
- The Jewell Nursery Co. (1908) Jewell Trees, Seeds and Plants. University of Minnesota Libraries, Andersen Horticultural Library. https://umedia.lib.umn.edu/item/p16022coll265:2855. Accessed: September 30, 2021
- Tiébré M, Vanderhoeven S, Saad L, Mahy G (2007) Hybridization and sexual reproduction in the invasive alien *Fallopia (Polygonaceae)* complex in Belgium. Am J Bot 94:1900–1910
- Urgenson LS (2006) The Ecological Consequences of Knotweed Invasion into Riparian Forests. MS thesis. Seattle, WA: University of Washington. 65 p
- Vaher M, Koel M (2003) Separation of polyphenolic compounds extracted from plant matrices using capillary electrophoresis. J. Chromatogr A 990:225–230
- Vastano BC, Chen Y, Zhu N, Ho CT, Zhou Z, Rosen RT (2000) Isolation and identification of stilbenes in two varieties of *Polygonum cuspidatum*. J Agric Food Chem 48:253–256
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a metaanalysis of their effects on species, communities and ecosystems. Ecol Lett 14:702-708
- Wade M, Child L, Adachi N (1996) Japanese knotweed a cultivated colonizer. Biological Sciences Review 8:31–33
- Wymer CL, Gardner J, Steinberger Z, Peyton DK (2007) Polygonum cuspidatum (Polygonaceae) genetic diversity in a small region of eastern Kentucky. J Ky Acad Sci 68:89–95
- Zhang Y, Parepa M, Fischer M, Bossdorf O (2016) Epigenetics of colonizing species? A study of Japanese knotweed in Central Europe. Pages 328–340
 in Barrett SCH, Colautti R, Dlugosch KM, Rieseberg LH, eds. Invasion Genetics: The Baker and Stebbins Legacy. Hoboken, NJ: Wiley