Knotweed (*Fallopia* spp.) Invasion of North America Utilizes Hybridization, Epigenetics, Seed Dispersal (Unexpectedly), and an Arsenal of Physiological Tactics

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More than 100 years ago, Japanese knotweed was introduced to North America. Given its vigorous rhizome system and capability to grow from rhizome and stem fragments, it persists and spreads locally, forming monotypic stands. The Japanese knotweed clone originally introduced was a male sterile female clone; thus, early in the invasion, reproduction from seed was not an issue. The implication was that long-distance dispersal was relatively rare. However, recently, widespread hybridization between Japanese knotweed and Sakhalin (giant) knotweed has been reported, with the hybrid species, Bohemian knotweed, forming the majority of knotweed plants in many areas and possessing higher variability than the parent species. The hybrids produce large numbers of wind-dispersed viable seeds that germinate at rates approaching 100% in some populations. As temperatures increase, knotweed is predicted to expand its range farther north and to higher elevations. With the ability to regenerate from vegetative fragments and disperse via seeds, invasive knotweed species are on the move. An arsenal of chemical weapons, the ability to shade out competitors, and the ability to adapt rapidly through epigenetic change makes knotweed a formidable invader. We observed that knotweed species clearly possess 8 of the 12 ideal weed characteristics, with Bohemian knotweed likely exhibiting still more because of prolific seed production. More research is needed to answer pressing questions. How does hybridization affect knotweed epigenetics? Under what conditions might seed production become more frequent? What kind of niche expansion is possible with the increased variability? Given the considerable challenges posed by knotweed species that promise to become even greater with the proliferation and spread of Bohemian ecotypes, only a thoroughly researched, well-informed approach to knotweed management across North America can be successful.

Nomenclature: Japanese knotweed, *Fallopia japonica* (Houtt.) Dcne. syn. *Polygonum cuspidatum* Sieb. & Zucc.; Sakhalin knotweed, *Fallopia sachalinensis* (F. Schmidt ex Maxim.) Dcne.; Bohemian knotweed, Fallopia × *bohemica* Chrtek & Chrtkova.

Key words: Allelopathy, clonal reproduction, epigenetics, hybridization, ideal weed characteristics, invasive species.

Japanese knotweed [*Fallopia japonica* (Houtt.) Dcne., formerly *Polygonum cuspidatum* Sieb. & Zucc.] was introduced to North America and Europe more than 100 yr ago; the earliest recorded presence of the plant in North America was as a cultivated specimen in Yorkville, NY, in 1873 (Barney 2006). The earliest recorded specimens in Canada were in 1901 for three provinces: British Columbia, Ontario, and Quebec (Barney 2006). Since that time, it has gone from being a prize-winning horticultural species to one of the world's top 100 most invasive species (Bailey and Conolly 2000; Lowe et al. 2000). Only the female clone of Japanese knotweed ($2n = 8x = 88$) was brought to North America and parts of Europe (Bailey 1994; Hollingsworth and Bailey 2000) and is genetically identical to the female clone found in Great Britain (Grimsby et al. 2007). Originally from Japan, Korea, China, and Taiwan, Japanese knotweed is found on volcanic slopes as an early seral species suitable for colonizing disturbed areas (Seiger 1984). It is

also known to tolerate poor soil conditions (Adachi et al. 1996), growing under a wide range of soil pH and even soils with heavy metals that accumulate in its leaves (Berchová-Bímová et al. 2014; Rahmonov et al. 2014). In most areas, knotweed preferentially colonizes disturbed areas (Tiébré et al. 2008). As of January 2015, invasive knotweed is present in 40 states in the United States and 8 provinces in Canada (USDA-NRS 2015). Although its North American range has historically extended only north to southern Canada, there is evidence that it is advancing northward in Canada (Bourchier and Van Hezewijk 2010) and is also found in Alaska (USDA-NRS 2015). Evolutionary change may facilitate such northward range expansion (Clements and DiTommaso 2012; Clements et al. 2014).

The limitation of the spread of knotweed in Canada was identified by Bourchier and Van Hezewijk (2010) utilizing published thresholds [2,505 degree days (DD), minimum temperature $= -30.2$ C, base temperature $= 0$ C]. Their study indicated that just over 50% of the suitable areas of British Columbia was occupied by knotweed species, noting many areas still have not yet been invaded. From the current distribution of knotweed in British Columbia, they were able to determine an annual precipitation threshold of 735 mm yr^{-1}. They found that warmer temperatures from 2000 to 2008 resulted in an increase to 53% of the habitat being suitable for knotweed in southern Ontario, compared with 35% when 1971 to 2000 weather data were used. Temperature increases as a result of climate change could increase the range of knotweed.

Hardy and herbaceous, Japanese knotweed has extensive underground rhizomes. Stem apices emerge in the spring. Shoots can grow more than 4 cm d^{-1} (Ainsworth et al. 2002) and up to 8 cm d^{-1} in full sunlight (Siemens and Blossey 2007). The fast-growing shoots reach 3 m in height in less than 2 mo (Herpigny et al. 2012) to create vast, dense stands with large leaves, forming a closed canopy that reduces or eliminates competition (Siemens and Blossey 2007).

Because introduced Japanese knotweed is male sterile, reproduction was considered to be clonal, and spread was by fragmentation and rhizomes (Brock et al. 1995). Japanese knotweed is considered one of the world's largest vascular plants owing to extensive clonal growth observed and quantified in Britain (Hollingsworth and Bailey 2000). In Europe, Japanese knotweed shows high herbivore resistance compared with two native plant species, suggesting *Fallopia* taxa are resistant to herbivory in Europe (Krebs et al. 2011). Without the diseases and herbivores found in its native range, knotweed is free to produce rampant clones forming monotypic colonies that compete against native vegetation (Hollingsworth and Bailey 2000). Many aspects of Japanese knotweed make it a successful invader. For a recent review, see Sołtysiak and Brej (2012).

A related species, Sakhalin (giant) knotweed [*Fallopia sachalinensis* (F. Schmidt ex Maxim.) Dcne.], native to northern Japan (Sukopp et al. 1995) was also introduced to North America and Europe in the late 1850s (Bailey and Conolly 2000). Giant knotweed is tetraploid, and in Europe, varying levels of genetic diversity have been found: from low (Tiébré et al. 2007) to high (Krebs et al. 2010); little information is available about its genetic diversity in North America. Less invasive than Japanese knotweed, giant knotweed produces copious amounts of viable pollen; Tiébré et al. (2007) recorded pollen production of 7,306 to 8,072 pollen grains per flower for giant knotweed, compared with just zero to four pollen grains per flower for Japanese knotweed clones. In the absence of male Japanese knotweed plants, the female Japanese knotweed can produce seeds utilizing pollen from related knotweed species such as giant knotweed. Comparing the genetic variability of the three *Fallopia* species in western North America, Gaskin et al. (2014) found that giant knotweed was the second most variable after the hybrid species, with 27 of the 116 populations representing the three most common giant knotweed genotypes. However, Gaskin et al. (2014) also identified nine genotypes among just 10 plants sampled in one population.

In this review, we detail what is known of the arsenal of tactics that knotweed species invading North America have at their disposal. This paper is one of two papers presented on knotweed at a symposium at the Weed Science Society of America annual meeting in Vancouver, BC, in February 2014 on the vulnerability of the Pacific Northwest to plant invasions. The related paper (Clements et al. 2016) details how management approaches are being developed to attempt to grapple with the complex challenges posed by knotweed infestations.

Extent of Hybridization. In many areas of North American and Europe a hybrid of Japanese and giant knotweed known as Bohemian knotweed (*Fallopia × bohemica* Chrtek & Chrtkova) has become very common. For many years researchers assumed that such hybridization was insignificant. This appears to be the case in Great Britain, where hybridization is rare and mostly occurs between Japanese knotweed and fleeceflower, *Fallopia baldschuanica* (Regel) Holub (Bailey et al. 2009). As early as 2007, however, studies in North America indicated that the incidence of hybridization of Japanese knotweed and giant knotweed was far more prevalent than previously suspected. Genetic analysis in three Massachusetts knotweed populations by Grimsby et al. (2007) identified 26 genotypes, which was compelling evidence for the occurrence of sexual reproduction. Their analysis also showed that all the genotypes were likely descended from a British Japanese knotweed clone (Grimsby et al. 2007). Gammon et al. (2007) also found evidence of hybridization in New England knotweed populations. However, the lack of consistent methods for determining hybridization makes it difficult to evaluate and compare

these studies; the addition of cytological information would help clarify the issue but was not examined in these studies.

Recently, several large studies have been conducted in North America on the diversity of invasive knotweed. A survey by Grimsby and Kesseli (2010) examined genetic variability of knotweed at 92 locations throughout the United States, from Alaska through parts of Canada to the eastern United States (but including relatively few samples from the Pacific Northwest). They found 47% of their samples were identical to the female "British clone," but hybridization and introgression likely accounted for the large genetic diversity they found in the remaining 53%. In a recent study by Gaskin et al. (2014) of populations in western North America, the hybrid Bohemian knotweed comprised a staggering 71% of plants sampled. The sample of 833 knotweed plants incorporated 131 populations from the western United States and southwestern Canada. They found evidence to suggest both seed and clonal propagation of Bohemian knotweed is taking place, with 46 of 77 populations containing the most common genotype, and some riverine systems being monotypic for this genotype, in contrast to other areas where populations were more diverse genetically (Gaskin et al. 2014).

The amount of genetic diversity resulting from hybridization seems to vary considerably, with the population genetics likely varying as a result of the degree of clonal growth, habitat influences, and invasion history. Duquette et al. (2015) observed relatively low genetic diversity in both Japanese and Bohemian knotweed populations growing along the Chaudière River in Québec. Yet near Québec City (Groeneveld et al. 2014), 10 different genotypes were identified among 13 tested individuals. The number of genotypes identified by Gaskin et al. (2014) in northwestern North America was 122 among the 612 samples they tested. Duquette et al. (2015) concluded that in their region, propagation was occurring almost entirely by fragments of stems or rhizomes.

Since 2010, we have been tracking knotweed populations in the Fraser Valley in British Columbia. As in other recent North American studies, we have been identifying many populations that are largely composed of Bohemian knotweed, based on leaf morphology, seed viability and the use of molecular markers (S. Gillies, unpublished data). For example, among samples collected in 2010 to 2011, 69% were estimated to be Bohemian knotweed (S. Gillies, unpublished data). As has been found throughout the Pacific Northwest (Gaskin et al. 2014), giant knotweed is relatively uncommon but abundant enough to act as a pollen donor for infertile Japanese knotweed, leading to the widespread occurrence of Bohemian knotweed, presumably because the hybrid spreads from the initial stands where hybridization occurs.

Also in contrast to Great Britain, hybridization between Japanese knotweed and giant knotweed may be quite common in Central Europe. Bzdęga et al. (2012) found evidence of genetic diversity in Japanese knotweed that may have been the result of multiple introductions of Japanese knotweed into this region or the result of sexual reproduction. They also found evidence hybridization was occurring. Bohemian knotweed was most genetically diverse when found in the same location as Japanese and giant knotweed, although again, cytology was not examined in this study.

Seed production and germination of knotweed is now commonly observed in North America. Gammon et al. (2010) conducted several studies in Massachusetts looking at knotweed crosses, both natural and in a garden. They found a remarkable variety of ploidy levels, many with the previously documented $4x$ and $8x$ for parental species and $6x$ for hybrids. They also found other cytotypes established in their garden ($5x$, $7x$, $9x$, $10x$, $11x$, and $12x$) and possibly $14x$ ploidy levels in progeny from garden seed parents. Their data suggest both significant introgression and possible introduction of multiple cytotypes from Asia. More importantly, they found most cytotypes were capable of strong vegetative growth, seed set, and the production of viable pollen. The male-sterile Japanese knotweed is now no longer limited to pollen from the less numerous giant knotweed because introgression has produced a diverse hybrid swarm of invasive cytotypes of $F. \times bohemica$, most of which can produce viable pollen.

Seed Production and Significance of Hybrid Knotweed Species. Japanese knotweed in its home range frequently reproduces sexually (e.g., most recruits found on Mount Fuji originated from seed) (Maruta 1983). As early as 2000, Bram and McNair (2004) and Forman and Kesseli (2003) showed that Japanese knotweed seed collected in the field in the eastern United States successfully germinated in both the laboratory and the field, with germination rates varying from 10-100%. The identity of the Japanese knotweed in these reports is not clear, with Bram and McNair (2004) allowing for the possibility that the seeds they tested may have come from hybrids and Forman and Kesseli (2003) likewise acknowledging that further studies were needed to determine the role of hybridization in the breeding system of knotweed species in North America. Flower counts for several individual Japanese knotweed stems in the United Kingdom indicate that a single stem hypothetically is capable of producing as many as 191,892 seeds (Bailey 1994); therefore, even a low germination rate of 10% could result in more than 19,000 viable seeds per stem. Further studies on seed set and germination rates on different cytotypes would be helpful. In a study by Engler et al. (2011), knotweed seeds of different ages, quality, and storage conditions collected in Germany successfully germinated (48 to 79%), even after natural overwintering in the soil. Several studies have shown that neither cold treatment nor dormancy are required for high germination of seeds collected in the wild (Bram

and McNair 2004; Engler et al. 2011; Forman and Kesseli 2003).

Toews (2012) found Bohemian knotweed can also become a prominent part of seed banks, with 786 seeds m^{-2} of Bohemian knotweed found in invaded sites. He also found that the presence of knotweed had an effect on the total seed bank, with significantly fewer seedlings per square meter in soil samples collected from knotweed patches than from soil collected in noninvaded sites; 3,380 seedlings m^{-2} emerged in invaded site soil compared with 5,801 seedlings m^{-2} in noninvaded site soils. Toews (2012) surmised that the difference could potentially be due to the ability of knotweed to grow rapidly from rhizomes early in the spring, inhibiting all seedlings, including its own. Research in the Fraser Valley of British Columbia in 2015 found that few or no seedlings emerged in dense knotweed patches, even when soil from the same patches yielded knotweed germinants (S. Balzer, unpublished data).

The northern limit for seed production was formerly reported to be Boston, MA; however, a recent study in Quebec by Groeneveld et al. (2014) found substantial seed germination from Japanese and Bohemian knotweed (65 and 53%, respectively) and suggest that the current northern limit to seed production is Quebec City, about 500 km farther north of Boston. Bourchier and Van Hezewijk (2010) suggested that different invasive Japanese knotweed genotypes might be selected for in different Canadian regions; Bohemian knotweed likely has a greater propensity to respond to climate change with its potential for greater genetic variation (Clements et al. 2014).

Sexually reproducing knotweed in North America have the potential to spread through the movement of seed, in addition to the well-known clonal growth pattern. Seeds tend to travel farther than rhizomes and are a source of new genetic combinations; therefore, they have a greater potential to spread quickly and adapt to new environmental conditions. Gaskin et al. (2014) postulated that the presence of novel Bohemian genotypes scattered over many locations suggests relatively frequent spread by seed, even though Bohemian knotweed is also capable of spreading vegetatively. The prospect of long-range spread thus requires drastically different management approaches than for clonal knotweed populations as seen in Great Britain and in earlier phases of the knotweed invasion of North America (Gaskin et al. 2014).

Hybridization appears to have increased the invasiveness of the exotic knotweed complex. As seed production emerges as a potentially major aspect of this increased invasiveness, research is needed to understand the seed biology, dispersal, and seed banks of Bohemian knotweed and how these might vary by genotype. Furthermore, hybrid knotweed plants have been found to be more competitive than their parents (Parepa et al. 2014). Knotweed hybrids performed significantly better in competition with a native community by suppressing the growth of the native plants (Parepa et al. 2014). The hybrid also has a greater capacity to regenerate and form shoots, making it a more successful invader (Bímová et al. 2003); furthermore, it is more tolerant of clipping and loss of aerial biomass (Rouifed et al. 2011). Given these and other differences between Bohemian knotweed and other knotweed species, taxon identification is becoming much more critical in understanding and managing knotweed invasion (Gaskin et al. 2014).

Phenotypic Plasticity and Epigenetic Change as Mechanisms for Local Adaptation. Knotweed can grow in poor soil conditions and has been found to be capable of tolerating high levels of salt (Rouifed et al. 2012). Although salt treatment slowed regeneration and shoot growth, Rouifed et al. (2012) found all three *Fallopia* taxa exhibited tolerance to strong salt stress. Salt tolerance is an advantage to knotweed species and may allow them to colonize polluted environments and brackish conditions. The ability of their rhizomes to survive in saltwater has also facilitated their distribution via seawater in coastal areas (Beerling et al. 1994). However, Richards et al. (2008) found no difference between salt marsh and control knotweed plants from roadside habitats when both were exposed to high salt concentrations in a greenhouse study. Thus it appears that knotweed does not exhibit specific adaptations to high salt concentrations, and salt tolerance is a plastic response to ambient conditions.

Richards et al. (2012) grew knotweed from different populations in a common garden. Although these plants showed almost no genetic diversity, they did exhibit a great deal of epigenetic differentiation and phenotypic plasticity in response to salt treatments. The findings indicate that epigenetic effects could contribute to phenotypic variation in invasive populations, in particular those with little genetic variation, and be facilitating the colonization of knotweed in a multitude of environments. Whether these findings also apply to F. × *bohemica* hybrids requires further study.

Recent research indicates epigenetics may be an important aspect of increasing the diversity of invasive plants. Environmental stresses, such as salt treatments, can trigger methylation changes, and this may have evolutionary consequences, even in the absence of gene sequence variation (Verhoeven et al. 2010). For a review of epigenetics, see Bossdorf et al. (2008) and Schrey et al. (2013). Epigenetics may provide clonal plants such as knotweed with the potential for optimizing plasticity and acclimation in response to the environment at a rate much faster than natural selection (Douhovnikoff and Dodd 2015). Epigenetic responses to hybridization and autopolyploidy formation in plants can be very complicated; see review by Rapp and Wendel (2005). In their review they highlight our lack of understanding of gene expression modulation when hybridization, polyploidization, or both occurs. In some species, global

repatterning of DNA methylation occurred, and in others, methylation was additive (Rapp and Wendel 2005). Further research on epigenetics of hybrid knotweed is needed.

Ecological Consequences of Knotweed. The spread of invasive knotweed throughout North America has had profound ecological consequences. Urgenson et al. (2009) found the invasion of riparian areas by giant knotweed has resulted in a loss of richness and abundance (cover or density) of native herbs, shrubs, and juvenile trees, and suggests the loss of foundation species in these systems can have cascading effects. Stoll et al. (2012) found the average plant species richness in Japanese knotweed plots was 50% lower compared with control plots. Japanese knotweed contributes a lower nutritional quality leaf litter than the native species it has displaced. This change in the composition and quality of riparian leaf litter input may affect aquatic food webs (Urgenson et al. 2009). Lecerf et al. (2007) showed that knotweed leaf litter has a strong effect on stream detritus food webs, altering assemblages and spore production of aquatic hyphomycetes.

Flooding events are important in the spread of knotweed. Colleran and Goodall (2014) found that 70% of new plants originated from rhizome fragments and 30% from stems carried by floodwaters. In a recent study by Duquette et al. (2015), establishment of both Japanese and Bohemian knotweed in riparian areas occurred only from propagation of rhizome or stem fragments. In both of these studies, seeds did not contribute to the spread of invasive knotweed along rivers or streams.

Although seeds might not currently play an important role in the spread of Bohemian knotweed in riparian areas, Rouifed et al. (2011) found knotweed seeds were buoyant; after nearly 2 d in the water, 50% of seeds were still floating. After 3 d, seeds germinated in the water and the seedlings also floated. Moreover, the exposure of seeds to water significantly increased their germination rate, without affecting seedling survival, compared with direct planting in soil (Rouifed et al. 2011). We therefore cannot ignore seed production in riparian areas.

The effect of knotweeds on the communities they invade is not limited to native plant species. Invertebrates and other animals can be affected by altered plant communities. Invertebrates were found to be reduced by almost 50% in knotweed-invaded plots compared with control plots (Gerber et al. 2008). Beetle species richness and diversity in Japanese knotweed stands were reduced, and knotweed had a negative effect on total beetle abundance (Topp et al. 2008). Maerz et al. (2005) found that green frogs had reduced foraging success in habitats invaded by Japanese knotweed, which resulted in a significant decrease in mass compared with frogs in noninvaded plots. Stoll et al. (2012) found that average snail species richness was significantly reduced in Japanese knotweed plots. The reduction was pronounced in large ($\geq$ 5 mm shell size) and long-lived ($>$ 2 yr) snail species, but not in slugs or small and short-lived snails.

Allelopathic Influence on Plant Germination and Growth and Soil Biota. Many successful invasive species have allelopathic properties. Here we will use the definition of allelopathy from Rice (1984): "the effects (stimulatory and inhibitory) of a plant on other plants through the release of chemical compounds into the environment." This definition also includes microorganisms (Lorenzo et al. 2013). Allelochemicals are secondary plant compounds with a variety of roles in the plant's native distribution. However, in a new habitat, native species are not adapted to the allelochemicals of the invading plant (Lorenzo et al. 2013). There is evidence that knotweed achieves competitive superiority primarily by limiting access to light; however, many studies indicate knotweed is also allelopathic (Murrell et al. 2011; Siemens and Blossey 2007). The allelopathic compounds found in knotweed are phenolics—stilbenes and catechins—which have antimicrobial and fungicidal properties (Murrell et al. 2011; Vrchotová and Šerá 2008).

Piola et al. (2013) analyzed the secondary metabolites from Japanese knotweed, giant knotweed, and hybrid Bohemian knotweed. They found the secondary metabolites of the hybrids were closer to Japanese knotweed, although hybrids expressed compounds of both parent species. They identified three dianthrones for the first time in *Fallopia* species. The most significant result of this study suggests that postintroduction hybridization has resulted in the evolution of new chemical traits.

The role of allelopathy in knotweed invasiveness has recently been the focus of a number of studies (e.g., Murrell et al. 2011; Parepa et al. 2013; Siemens and Blossey 2007). Many studies use bioassays of seeds from a limited number of species and compare germination rates, seedling growth, or both under laboratory, greenhouse, or garden conditions. Researchers have used different plant parts from leaves (green or senesced), stems, and rhizomes. Some have also used soil from knotweed sites to see if there is any lasting allelopathic activity in knotweed-contaminated soil. These studies allow researchers greater control of variables; however, it is difficult to compare data from these experiments to each other or to those done in the field.

One of the tools used in allelopathic research that separate allelopathy from resource competition is the use of activated charcoal (Inderjit and Callaway 2003). Several recent knotweed studies used activated charcoal as a control (Murrell et al. 2011; Parepa et al. 2013, Siemens and Blossey 2007) because it can absorb organic compounds (Inderjit and Callaway 2003). The addition of activated carbon, however, has been found to interfere with the availability of nutrients and plant growth (Lau et al. 2008; Weißhuhn 2009).

Šerá (2012) found the type of seed tested was a more important factor affecting germination than the type of knotweed leaves used to contaminate the soil; the tested crop plants were more sensitive than either of two weed species, *Chenopodium album* L. (common lambsquarters) or *Echinochloa crus-galli* (L.) Beauv (barnyardgrass). Moravcová et al. (2010) also found that knotweed extracts inhibited germination of several species and that it varied by knotweed species. Giant knotweed exerted the largest negative effect on the germination of *Urtica dioica* L. (stinging nettle), Bohemian knotweed most affected the germination of *Calamagrostis epigejos* (L.) Roth (bushgrass), and Japanese knotweed had the lowest inhibitory effect on all test species. Several studies found that knotweed allelopathy acts on growth rather than germination. Vrchotová and Šerá (2008) tested Japanese, Bohemian, and giant knotweed rhizome extracts for allelopathy in white mustard seeds. Their results show that Bohemian and giant knotweed inhibited growth more strongly than Japanese. There were significant differences in the length of radicles and hypocotyls and root : shoot ratio between the control and treated seeds. Parepa et al. (2012) tested nine native species and found that knotweed leaf litter leachate, an aqueous extract of knotweed leaves added to the soil, and trained soil with a history of knotweed precultivation did not suppress the germination or early growth of native species. When using experimental native communities, they found that the presence of Bohemian knotweed caused significant shifts of life history strategy in two dominant natives. Similar effects could be elicited through litter leachates or trained soil (soil with a history of knotweed growth) alone (Parepa et al. 2012).

There have been few experiments in the field, but as efforts are being turned to restoration in ecosystems affected by knotweed, it becomes important to understand their long-term effects. Dommanget et al. (2014) investigated the phytotoxic effect of Japanese knotweed on resprouting capacity and the growth of three Salicaceae species with potential value for restoration. Their results indicate the existence of allelopathic effects—direct, indirect, or both—of Japanese knotweed on the growth of *Salicaceae* species cuttings. The three species were not equally affected, however, suggesting that the choice of resistant species could be crucial for restoration success. Knotweed removal in riparian ecosystems resulted in rapid and abundant colonization of native woody species and of native and nonnative forbs (Urgenson et al. 2014). Knotweed litter was found to benefit perennial native forest forbs adapted to natural burial by canopy litterfall relative to nonnative forbs (predominantly light-demanding annuals). These studies show that understory regeneration may be quite successful in restoration of riparian areas. However, Claeson and Bisson (2013) suggest successful reestablishment of native vegetation after knotweed removal along large, complex rivers may require active restoration, such as the control of secondary invasions by other exotic plants or replanting native species as conditions change over time.

Knotweed has also been found to exert strong controls on the late seral species, reducing survival by 24%, height growth by 91 to 122%, and diameter growth by 37 to 55% (Urgenson et al. 2009). These effects were not correlated with reductions in light. Instead, in the presence of knotweed, ectomycorrhizal colonization was significantly reduced (64%) and root : shoot ratio was significantly increased, suggesting a disruption of soil mutualisms.

It is possible that the phytotoxicity seen in knotweed may relate to the presence of soil biota. Parepa et al. (2013) found that invasive knotweed benefited more from the overall presence of soil biota than any of the six native species. In particular, the presence of the full natural soil biota strongly shifted the competitive balance in favor of knotweed. Soil biota promoted both regeneration and growth of the invader, which suggests that soil organisms may be important both in the early establishment of knotweed and possibly its later dominance of native communities. Additions of activated carbon to the soil made the advantage of knotweed disappear, which suggests that the mechanisms underlying the positive soil biota effects are chemically mediated. Their study demonstrates that soil organisms play a key role in the invasion success of exotic knotweed. Allelopathic interference or interaction with microbial soil organisms may contribute to the lack of native species in populations of Bohemian knotweed (Parepa et al. 2013). Knotweed leachates applied in a field experiment showed knotweed had a strong effect on population growth of the soil fauna (Heděnec et al. 2014). Further evidence of the importance of soil biota comes from Maerz et al. (2009), who found invasive earthworms facilitated knotweed establishment.

Is Knotweed an "Ideal Weed"? Baker (1974) listed 12 "ideal weed" characteristics. He pointed out that some major weeds might be successful, even if only exhibiting a few of the ideal traits, but that certain species did possess a large number of these traits which compounded the plant's weediness; knotweed clearly fits the latter category (Table 1). Although Baker's (1974) listing of weediness is somewhat outdated and does not include all possible weediness traits, it is a useful starting point. Of the 12 traits listed by Baker (1974), knotweed clearly exhibits all except four traits to some degree. We were unable to find published information on seed longevity (trait 2), and in any case, seed banks are not generally thought to be a major life history strategy, although soil within knotweed patches has been observed to contain ungerminated seeds (S. Balzer, unpublished data). Knotweed does not always produce large quantities of viable seeds (trait 3), and production of seeds takes place over a relatively short period of time (trait 4). Furthermore, large clones, such as the English clone of Japanese knotweed, are not self-fertile (trait 5). Thus, the

Table 1. Ideal weed characteristics (ca. Baker 1974) possessed by knotweed plants (*Fallopia* spp.). Wording of Baker's traits modified according to Chaney and Baucom (2012).

Ideal weed trait	Knotweed trait(s)?
1. Germinates in many environments	May grow under a wide range of soil types, pH (e.g., pH 4.4–7.3) (Vanderhoeven et al. 2005)
2. Great longevity of seed	Insufficient data, but 80% germination rate after overwintering (Nishitani and Masuzawa 1996)
3. Rapid growth through vegetative phase to flowering	Capable of extremely rapid growth, high relative growth rate (Chiba and Hirose 1993)
4. Continuous seed production	Seed production period relatively short—September–November in North America (Barney et al. 2006)
5. Self-compatible	Most frequently not but occasionally self-compatible (Barney et al. 2006)
6. When cross-pollinated, unspecialized visitors or wind used	Pollinated by a wide variety of insects (Barney et al. 2006)
7. Very high seed output	A single stem may produce 191,892 seeds (Bailey 1994), but viability is not always high; varies with species
8. Tolerant and plastic	Many features of knotweed clones vary with environment and have been observed to adapt via epigenetic mechanisms (Richards et al. 2012); the Bohemian knotweed also exhibits genetic variation
9. Has adaptations for short- and long-distance dispersal	Short-range dispersal via stem and rhizome fragments, long-distance dispersal via wind-dispersed seeds (Gaskin et al. 2014)
10. Vigorous vegetative reproduction or regeneration from fragments	Extensive rhizome system, extending several meters underground and representing two-thirds of plant biomass (Alder 1993)
11. Plant not easily drawn from the ground	Knotweeds notoriously difficult to uproot (stem injection of herbicides recommended to ensure the whole plant is killed)
12. Ability to compete interspecifically by special means (rosette, choking growth, allelochemicals)	Strong competitive ability through forming monospecific stands and shading; allelochemicals produced (Murrell et al. 2011)

Achilles heel of knotweed species has generally been their inability to produce large numbers of seeds; however, with the advent of large populations of Bohemian knotweed in North America via frequent hybridization between giant and Japanese knotweed and subsequent reproduction by seed among Bohemian knotweed hybrids (Gammon et al. 2010; Gaskin et al. 2014), the role of seed reproduction is now being re-evaluated, and research is being conducted to understand this emerging potential.

It should also be noted that in terms of Baker's ideal trait 1, whereby a weed is capable of germinating in a wide variety of environments, knotweed does have its limits. Although it utilizes all soil types, it tends to prefer fairly moist soil and is a plant that prefers edge habitats (i.e., riparian zones, roadsides, railroad rights-of-way, disturbed sites, and forest edges) (Barney et al. 2006). It is also limited climatically to relatively temperate areas with mild winters, although there are indications it has not realized its potential climatic range in North America (Bourchier and Van Hezewijk 2010), in contrast to Europe, where it has spread to most available climatic niches (Beerling et al. 1995). Even given the limitations of knotweed reproduction by seed and being largely restricted to edge habitats, the other ideal traits possessed by knotweed represent a challenging array of

characteristics that may often work together synergistically to foil management attempts.

The invasion of North American by knotweed species is ongoing, with many uninvaded areas identified as being suitable for knotweed growth. As temperatures increase, knotweed is predicted to travel farther north and to higher elevations (Bourchier and Van Hezewijk 2010; Clements and DiTommaso 2012). With the ability to regenerate from fragments and through dispersal by seeds, invasive knotweed is on the move. An arsenal of chemical weapons, the ability to shade out competitors, the production of hybrids, and the ability to adapt rapidly through epigenetic change makes knotweed a formidable invader. Furthermore, as highlighted throughout this review, most of these weapons are poorly understood, especially in light of emerging implications of hybridization. Research is needed to address key questions. For example, how does hybridization affect knotweed epigenetics? Under what conditions might seed production become a major source of regeneration? What kind of niche expansion is possible with the increased variability of *F. × bohemica*? Given the considerable challenges posed by knotweed species that promise to become even greater with the proliferation and spread of Bohemian ecotypes, only a thoroughly researched, well-informed

approach to knotweed management across North America can be successful. For a review of efforts to date to manage the multifaceted threat posed by knotweed, see Clements et al. (2016).

Acknowledgments

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