

The Biology of Invasive Alien Plants in Canada.

5. *Polygonum cuspidatum* Sieb. & Zucc. [= *Fallopia japonica* (Houtt.) Ronse Decr.]

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Barney, J. N., Tharayil, N., DiTommaso, A. and Bhowmik, P. C. 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. *Polygonum cuspidatum* (Japanese knotweed) is an introduced perennial geophyte in the buckwheat family (Polygonaceae). The phyto-geographic distribution of *P. cuspidatum* in North America suggests a large number of intentional introductions via ornamental plantings from 1870 to 2000, followed by secondary spread from these foci. This species is most pernicious along riparian corridors and road and railroad rights-of-way, reducing visibility, displacing native species, negatively affecting native wildlife, and causing alterations in natural hydrologic processes. Although non-hybrid seed recruitment has not been observed in Europe because of the presence of male-sterile clones only, dispersal of seeds and stem and rhizome fragments by flowing water does occur in North America and populations are readily established from these sources. The primary means of local and regional range expansion is human-mediated transport of rhizome-infested soil. Hybridization is common with the congener *P. sachalinense* in the introduced ranges of North America and Europe resulting in the equally noxious *P. × bohemicum*.

Key words: Japanese knotweed, Mexican bamboo, *Polygonum*, *Fallopia*, *Reynoutria*, POLCU, invasive plant, weed biology

Barney, J. N., Tharayil, N., DiTommaso, A. et Bhowmik, P. C. 2006. **La biologie des plantes exotiques envahissantes au Canada. 5. *Polygonum cuspidatum* Sieb. & Zucc. [= *Fallopia japonica* (Houtt.) Ronse Decr.]**. Can. J. Plant Sci. **86**: 887–905. La renouée japonaise (*Polygonum cuspidatum*) est une géophyte vivace exotique de la famille du sarrasin (Polygonacées). Sa répartition géographique en Amérique du Nord donne à penser qu'elle a été introduite sciemment en grand nombre comme plante ornementale entre 1870 et 2000. La propagation secondaire est survenue par la suite, à partir de ces foyers. L'espèce s'avère particulièrement pernicieuse dans les corridors riverains et routiers ou sur les servitudes de passage ferroviaires. Elle réduit la visibilité, supprime les espèces indigènes, nuit à la faune locale et modifie l'hydrologie naturelle. Bien que la croissance de semences non hybrides n'ait pas été rapportée en Europe, où l'on ne trouve que des clones mâles stériles, en Amérique du Nord, les graines ainsi que des fragments de tige et de rhizome se dispersent par l'écoulement des eaux, si bien que des peuplements réussissent à s'établir. Le principal moyen pour l'espèce de prendre de l'expansion localement et régionalement demeure le transport de sol infesté de rhizomes par l'être humain. L'espèce se croise aisément avec sa congénère *P. sachalinense* dans les régions d'Amérique du Nord et d'Europe où elle a été introduite, ce qui entraîne la multiplication de l'hybride tout aussi nuisible *P. × bohemicum*.

Mots clés: Renouée du Japon, bambou du Mexique, *Polygonum*, *Fallopia*, *Renoutria*, POLCU, plante envahissante, biologie des mauvaises herbes

1. Species Name and Taxonomic Relationships

Polygonum cuspidatum Sieb. & Zucc. — Synonym: *Fallopia japonica* (Houtt.) Ronse Decr., *Reynoutria japonica* Houtt., *Polygonum zuccarinii* Small, *Pleuropterus zuccarinii* (Small) Small, *Pleuropterus cuspidatus* (Sieb. & Zucc.) H. Gross, *Polygonum japonicum* Meissn. — **Japanese knotweed**, Japanese bamboo, Mexican bamboo, fleecflower, horse-buckwheat, Japanese fleecflower; **renouée du Japon**, bamboo, canne, Jérusalem, jonc canadien, jonc de Saint-Joseph, renouée japonaise, Sainte-Anne, sarrasin des Indes, renouée de Siebold, and persicaire cuspidée (Darbyshire 2003). Bayer code: POLCU. Polygonaceae, buckwheat family, Polygonacées.

The genus in a broad sense is composed of approximately 250 extant species, with about 90 and 160 species occurring in the western and eastern hemispheres, respectively (Small

1895). These figures have been corroborated in more recent surveys of *Polygonum* (Griffiths 1994; Gleason and Cronquist 1995). There are a reported 70 species occurring in North America, ranging from the arctic to temperate zones (Small 1895). Scoggan (1978–1979) reports 83 species in 9 genera of Polygonaceae occurring in Canada, with 26 species being introduced. The Flora of North America (Freeman and Hinds 2005) considers *Fallopia* a separate genus with 12 species (eight in the flora), while *Polygonum* has 65 species (33 in the flora).

The name *Polygonum* is derived from Greek roots for *many* and *knee* or *joint*, referring to the swollen nodes often found on

Abbreviations: a.s.l., above sea level; LAI, leaf area index; LMA, leaf mass area; RAPD, randomly amplified polymorphic DNA; SLA, specific leaf area; WAT, weeks after treatment

stems of this genus (Small 1895). These swollen nodes are often accompanied by sheathing ocrea, which are unique to the Polygonaceae (Lamb Frye and Kron 2003). Taxonomists continue to debate the classification and nomenclature of *P. cuspidatum*, with most European researchers splitting *Polygonum* and using *Fallopia japonica*, while their North American colleagues use *P. cuspidatum*. This taxon was first described as *Reynoutria japonica* from Japanese material by Houttuyn (1777), but was largely unavailable to scientists for nearly a century as the account was published in Dutch. Almost a century later it was independently described from additional Japanese samples as *Polygonum cuspidatum* by Siebold and Zuccarini (1846), only to be later determined that the two taxa were the same (Makino 1901). Morphological evidence suggests that *Polygonum* sensu lato should be split into several genera, with *Fallopia* (including *Reynoutria*) having three sections: (i) erect rhizomatous perennials (including *Fallopia japonica*), (ii) climbing perennials, and (iii) climbing annuals (Ronse Decraene and Akeroyd 1988). Recent molecular evidence has placed *P. cuspidatum* in a monophyletic group with all other sampled *Polygonum* (sensu lato) taxa within Polygonaceae, but was unable to resolve whether *Fallopia* should be segregated as a distinct genus (Lamb Frye and Kron 2003). Therefore, we have decided to use *Polygonum cuspidatum* because of the lack of consensus on nomenclatural placement, the focus on North America for this review (where *Fallopia* is little used), and following Darbyshire et al. (2000).

The nomenclatural debate also confounds reference to the congeneric Sakhalin knotweed (*P. sachalinense* Maxim.) and their hybrid Bohemian knotweed (*P. × bohemicum* (Chrtek & Chrtková) Zika & Jacobson), with which *P. cuspidatum* is commonly confused (Zika and Jacobson 2003).

2. Description and Account of Variation

(a) *Species Description* — We have based the following description using in situ individuals, herbarium sheets from the United States of America and Canada, and published literature accounts (Beerling et al. 1994; Gleason and Cronquist 1995; Zika and Jacobson 2003). Figures 1 and 2.

Polygonum cuspidatum is a stout rhizomatous perennial geophyte. Rhizomes are dark brown, knotty, up to 8 cm in diameter, and often bright orange inside. A deep taproot is present in plants originating from seeds, becoming woody with age and often protruding from the soil surface. Adventitious roots are white, fine, and thread-like. Stems are terete, 1–3 m tall with reddish-purple spots, glaucous, erect, becoming striate-ridged, and hollow throughout. Leaves are alternate, broadly ovate (8–15 cm by 5–12 cm), with bases ranging from truncate to strongly cuneate, becoming distally acuminate to strongly cuspidate. Leaf margins are entire, with abaxial veins minutely scabrous with scattered swollen cells or knobs. Petioles <1–3 cm long with thin membranous ocrea at each base. Extrafloral nectaries composed of numerous ball-like projections of nectar-cells are borne on stem nodes or at the petiole base (Kawano et al. 1999). Flowers borne on axial or terminal ocreolate racemes or panicles (8–15 cm long). Inflorescence internodes are densely pubescent. Flowers are creamy-white (2–3 mm diameter), with five ovate tepals (outer three keeled, enclosing the inner

two), eight stamens (filaments 0.3–0.8 mm long), longitudinally dehiscent anthers small (0.2–0.7 mm long) and flat, three distinct styles, stigmas fimbriate. Individuals are gynodioecious (male-sterile or hermaphroditic) with some flowers having reduced pistils, appearing female-sterile. Perianth becomes enlarged during fruit formation, becoming winged and completely enclosing the trigonous achene. The glossy dark-brown achenes are 2–4 mm long by 1–2 mm wide and have a mean weight of 1.6 mg.

Chromosome numbers for *P. cuspidatum* vary greatly with geographic location, with diploid numbers of $2n = 44, 52, 66,$ and 88 reported (Doida 1960; Bailey and Stace 1992; Kim and Park 2000; Mandák et al. 2003). The most common base chromosome numbers for *Polygonum* sensu lato are $x = 10$ or 11 (included are the four knotweed taxa considered here), with some taxa having $x = 12$ or 13 (Bailey and Stace 1992). Polyploidy in *Polygonum* is restricted to the erect rhizomatous perennials of section *Reynoutria*, which include all four of the knotweed taxa considered here (Bailey and Stace 1992).

(b) *Distinguishing Features* — *Polygonum cuspidatum* is commonly confused with its hybrid, *P. × bohemicum*, in its introduced range of Europe and North America. However, Zika and Jacobson (2003) have developed a set of distinguishing characters for *P. cuspidatum*, *P. sachalinense* and *P. × bohemicum*. *Polygonum cuspidatum* has the smallest leaves of the species complex, generally (8–15 cm long by 5–12 cm wide) compared with >30 cm length in *P. sachalinense*, and leaves of *P. × bohemicum* are of intermediate size. The mid-stem leaves are the most useful for discrimination. In *P. cuspidatum* they are basally truncate to slightly cuneate and apically acuminate or cuspidate, while *P. × bohemicum* is slightly to deeply cordate at the base to essentially truncate, and having an acute or acuminate apex, while *P. sachalinense* is basally deeply cordate with an abruptly narrowed apex being blunt to acute. Abaxial leaf vein morphology varies from blunt scabers or knobs in *P. cuspidatum*, to stout single-celled (sometimes three-celled) hairs in *P. × bohemicum*, to narrow-based, long multicellular hairs in *P. sachalinense*. The final distinguishing feature is the ratio of panicle length to subtending leaf length. Panicle length is equal to or greater than the length of the subtending leaf in *P. cuspidatum*, while *P. × bohemicum* panicle length is equal to or less than the leaf length, and *P. sachalinense* panicle length is less than the leaf length.

Key to the four invasive knotweed taxa found in North America.

1. Abaxial leaf veins minutely scabrous; leaf bases truncate to slightly cuneate; leaves usually < 15 cm long; panicle \geq subtending leaf length.....2
 2. Late summer height 1–4 m; largest leaves < 18 cm long; green foliage.....*P. cuspidatum* var. *cuspidatum*
 2. Late summer height 0.5–1 m; largest leaves < 10 cm long; often reddish foliage*P. cuspidatum* var. *compactum*
1. Abaxial leaf veins slightly to densely pubescent; leaf bases slightly to deeply cordate; leaves usually > 20 cm long; panicle \leq subtending leaf length3

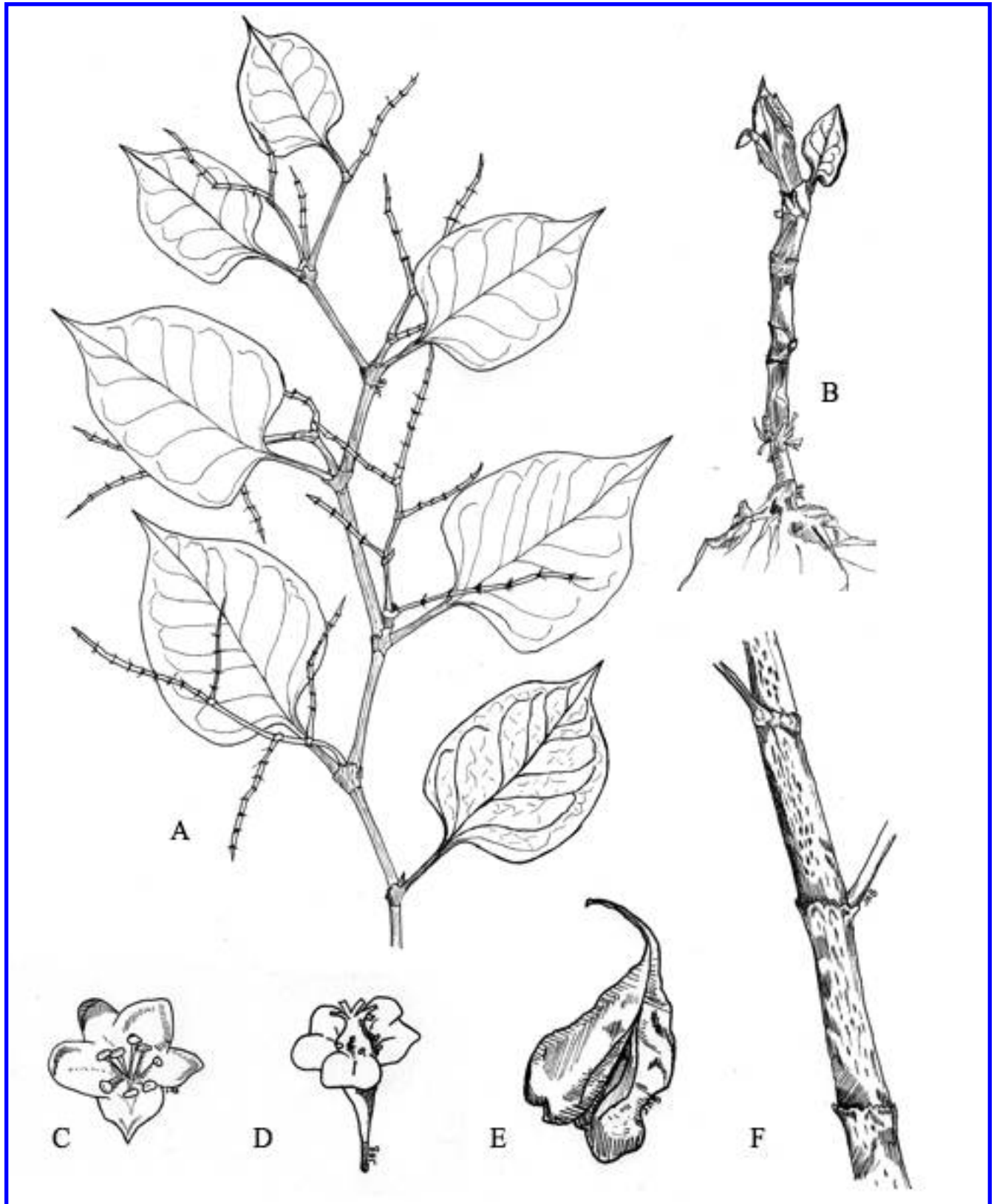


Fig. 1. *Polygonum cuspidatum* A. flowering stalk after fruit shed; B. emerging ramet from rhizome fragment showing nodes and fibrous roots; C, male flower; D, female flower; E, winged-sheath covered trigonous-achene; F, bamboo-like stalk showing spots and ocreae (Drawings by J. N. Barney).

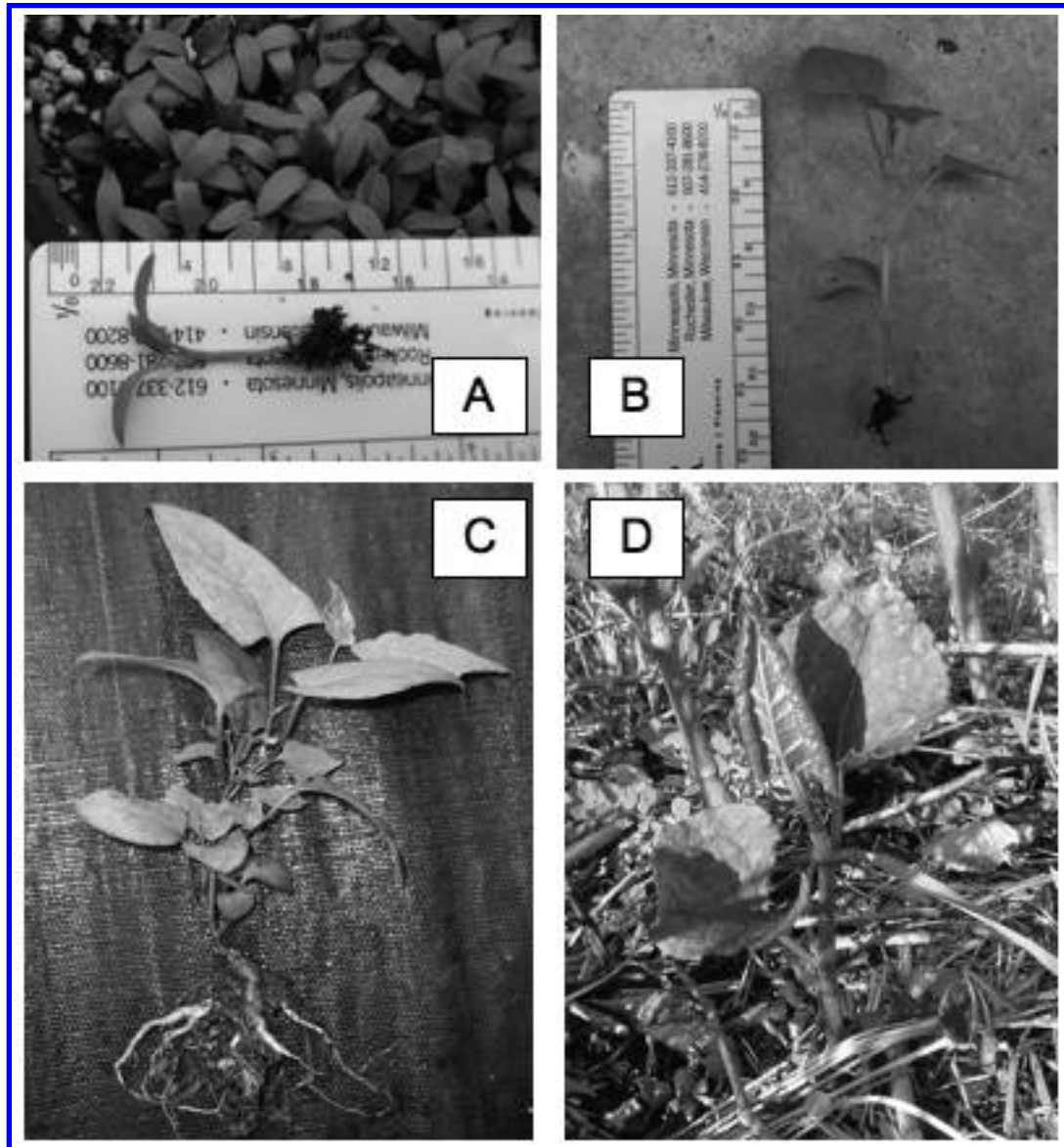


Fig. 2. *Polygonum cuspidatum*. A, seedling with emerging first true leaf; B, 2-wk-old seedling; C, general habit of seed-grown individual showing rhizome formation; D, ramet emerging from rhizomes in situ.

- 3. Abaxial leaf veins with scattered single-celled (sometimes three-celled) stout hairs; leaf bases nearly always cordate; leaves 15–25 cm long*P. × bohemicum*
- 3. Abaxial leaf veins with many long (multi-cellular) hairs; leaf bases deeply cordate; leaves 20–35 cm long*P. sachalinense*

(c) *Intraspecific Variation* — *Polygonum cuspidatum* sensu stricto exhibits wide morphological variation throughout its introduced range. However, Zika and Jacobson (2003) point out that the hybrid *P. × bohemicum* has been largely overlooked in North America, and has been commonly mistaken for *P. cuspidatum*, further obfuscating the ability to accurately assess intraspecific variation from published accounts.

Only anecdotal evidence exists for intraspecific variation of *P. cuspidatum* in North America. The few studies that have examined *P. cuspidatum* in North America have identified their taxa as *P. cuspidatum* sensu lato, precluding any judgments on intraspecific variation. However, large variation in specific leaf area (SLA) has been documented between full sun (SLA = 18.69 cm² g⁻¹) and deep shade (SLA = 41.67 cm² g⁻¹) individuals — likely a phenotypic response to irradiance (J. N. Barney, unpublished data).

A cytological study of *Polygonum* taxa of the British Isles revealed that *P. cuspidatum* populations did not vary in chromosome number, all being 2n = 88 and female (Bailey and Conolly 1985; Bailey and Stace 1992). However, Bailey and Stace (1992) found the diploid number of the dwarf knotweed variety *P. cuspidatum* var. *compactum* and *P.*

sachalinense to be $2n = 44$, while the hybrid *P. × bohemicum* diploid number was $2n = 44, 66, \text{ or } 88$. Populations of *P. cuspidatum* from the native range in Korea and Japan were found to vary in ploidy levels, $2n = 44, 66, \text{ or } 88$ (Bailey and Stace 1992; Kim and Park 2000). Kim and Park (2000) also found all Korean populations of *P. sachalinense* to be dodecaploids, $2n = 132$, a truly surprising result! Molecular analysis of more than 150 *P. cuspidatum* populations from the United Kingdom, Czech Republic, Germany, France, and the United States of America revealed a single haplotype with the same multi-primer RAPD (randomly amplified polymorphic DNA) profile, suggesting a single genet (Hollingsworth and Bailey 2000a). Populations in the Czech Republic have been found to be identical cytologically ($2n = 88$) (Mandák et al. 2003) and genetically (a single female genotype found using multi-primer RAPD) (Hollingsworth and Bailey 2000a). In contrast, *P. sachalinense* from the United Kingdom has revealed high levels of genetic diversity using RAPD primers (Hollingsworth and Bailey 2000b), providing further evidence for clonal spread of a single *P. cuspidatum* genotype, and seed production and/or multiple introductions of *P. sachalinense*. As expected, genetic variability of *P. cuspidatum* is very high in the native range (Mt. Fuji, Japan). All 155 populations examined at a primary successional site on Mt. Fuji were found to be polymorphic, with the number of genets per patch ranging from 1 to 8 (Zhou et al. 2003). Morphological variation in *P. cuspidatum* leaf characters in the native range of Korea was much less than interspecific variation (Kim and Park 2000).

(d) *Illustrations* — Figure 1 depicts *P. cuspidatum* branch, flowers, fruit, and rhizome. Seedling stages and an emerging ramet from a rhizome are shown in Fig. 2.

3. Economic Importance and Environmental Impact

(a) *Detrimental* — The widespread geographic distribution, and astonishing rate at which *P. cuspidatum* spreads locally, has resulted in marked alterations in the physical environment and community composition of habitats it invades, as well as having indirect effects at various trophic levels.

Polygonum cuspidatum is primarily an environmental weed that causes major ecological alterations to invaded communities by forming persistent and extensive mono-specific stands that exclude native vegetation (Holzner 1982; Beerling et al. 1994). In Canada and the United States of America it rarely occurs as an agricultural weed, though Missouri lists *P. cuspidatum* as a weed of pastures and agricultural fields (Fishel 1999), and it has been cited as a serious threat to wildlife in Wales (Palmer 1994). A 50-m transect through a *P. cuspidatum* stand showed percent cover of native vegetation to vary from 100% at the invasion front to 0% within the *P. cuspidatum* canopy (Maerz et al. 2005). Correspondingly, green frog (*Rana clamitans* Latrelle) biomass was negatively related to *P. cuspidatum* percent cover (Maerz et al. 2005).

A survey of Welsh authorities (local and National Park personnel, public and private utilities, water authorities, wildlife conservation bodies, farmer's unions, and herbicide

manufacturers) rated *P. cuspidatum* damage to river banks and protected works as widespread, while rating damage to paved surfaces, loss of wildlife habitat, and disturbance of planted vegetation as occasional but serious (Palmer 1994). *Polygonum cuspidatum* causes flood hazards by increasing resistance to water flow (Edward and Howel 1989) and by damaging flood prevention structures (Beerling 1991). Rhizome and shoot growth in this species is prolific and can displace foundations, walls, pavements, and drainage works (Locandro 1973; Beerling 1991). Topsoil mineral content was significantly greater under *P. cuspidatum* than under native vegetation, especially K and Mn (Vanderhoeven et al. 2005).

In addition to the parental species *P. cuspidatum* and *P. sachalinense*, the hybrid *P. × bohemicum* can have detrimental effects on native riparian communities. A study on intraspecific competition between *P. × bohemicum* and the native forb *Eupatorium perfoliatum* L. and tree *Acer saccharinum* L. revealed that competition for light and soil-mediated processes were important in determining the performance of *P. × bohemicum* (Siemens and Blossey, unpublished data). When the native species were grown within the *P. × bohemicum* canopy without direct competition for light (i.e., surrounding *P. × bohemicum* shoots were removed), they did not survive, nor when transplanted into a closed canopy with the soil amended with activated carbon to remove organic compounds. However, when the native species were grown in plots where both *P. × bohemicum* shoots were removed and activated carbon mixed soil was used, plants survived. These findings suggest that *P. × bohemicum* may achieve competitive dominance both by reducing light availability and through the alteration of the soil environment, either through the release of allelochemicals and/or via other microbially mediated processes.

(b) *Beneficial* — The most widespread use of this species was as an ornamental, especially throughout the 19th century when it was widely disseminated in both Europe and North America (Beerling et al. 1994; Barney 2006). Because of its showy blossoms, *P. cuspidatum* became a popular plant in Victorian gardens of Europe, winning a gold medal in 1847 from the Society of Agriculture and Horticulture at Utrecht as the most “interesting” plant of the year (Bailey and Conolly 2000). A staunch supporter of *P. cuspidatum* in late 19th century Europe was William Robinson, exclaiming in laughable irony that if plants like *P. cuspidatum* “were introduced along the sides of woodland walks and shrubbery borders, how much more enjoyable such places would be...instead of which such parts are generally bare, or given up to weeds” (Robinson 1881). Liberty Hyde Bailey (1916) espoused this plant for “bold mass effects” and “clouds of bloom,” while stating that *P. sachalinense* becomes “inveterately persistent once established.” North American nurseries followed the sentiment of Bailey, touting *P. cuspidatum* as “a bold, handsome plant...which bloom in great clouds, producing a very soft and pleasing effect” (Townsend 1997). A survey of North American herbarium records revealed more than 150 collections of *P. cuspidatum* labeled as an ornamental escape and

distributed across the whole of North America (Barney 2006). The red-leaved cultivar “Crimson Beauty”, a shorter, less-aggressive perennial has been sold and planted in North America as well (Townsend 1997).

Andros (2000) reported that *P. cuspidatum* makes an excellent food source for honey bees, exclaiming that one hive gained 45 kg in 5 days from a *P. cuspidatum* stand. Several authors state the use of *P. cuspidatum* as a human food source both in its native range and in its introduced range of North America (Siebold and Zuccarini 1846). Fogg (1945) wrote that despite its weediness “it is perhaps of small comfort to learn that the young shoots of [*P. cuspidatum*] when cooked like asparagus furnish an estimable article of diet.” Cherokee Indians are also known to eat the cooked leaves of *P. cuspidatum* (Perry 1974). A host of beneficial secondary compounds have been isolated from *P. cuspidatum*, including the anti-cancer phytoalexin resveratrol [Kimura and Okuda (2001) and see Section 10].

The potential use of *P. cuspidatum* as a heavy metal hyper-accumulator has been investigated in Europe and Japan. Populations in Japan sampled from copper- (3000 $\mu\text{g Cu g}^{-1}$ dry matter), zinc- (10 000 $\mu\text{g Zn g}^{-1}$ dry matter) and cadmium- (100 $\mu\text{g Cd g}^{-1}$ dry matter) contaminated soils, showed that this species hyper-accumulates these heavy metals in both roots and leaves, especially in cell walls (Nishizono et al. 1989). Typical levels of these elements in non-contaminated soils in this same study were 20, 110, and 2 $\mu\text{g g}^{-1}$ dry matter Cu, Zn, and Cd, respectively. Heavy metal concentrations in *P. cuspidatum* tissue (2300 $\mu\text{g Cu}^{2+}$ g^{-1} dry matter, 6700 $\mu\text{g Zn}^{2+}$ g^{-1} dry matter, and 62 $\mu\text{g Cd}^{2+}$ g^{-1} dry matter) were found to be significantly higher than those at the control site, and compared with other angiosperms growing on similar metalliferous soils. A similar study in Croatia found higher than average levels of Cu, Zn, Pb, and Cd in *P. cuspidatum* leaves (Hulina and Dumija 1999). In Japan the concentration of a copper-binding protein isolated from *P. cuspidatum* cytoplasm of plants collected from a metalliferous habitat increased proportionally to the copper concentration in the cytoplasm (Kubota et al. 1988). *Polygonum cuspidatum* may have a competitive advantage in regions receiving high levels of SO_2 pollution (Japan), as net photosynthesis was little affected by SO_2 fumigation (Natori and Totsuka 1984).

(c) **Legislation** — *Polygonum cuspidatum* is not listed on any federal lists in either Canada or the United States of America. However, *P. cuspidatum* is listed in British Columbia under the Invasive Plants Regulation of the Forest and Range Practices Act (British Columbia Ministry of Forests and Range 2004). In the United States of America, *P. cuspidatum* is considered a Class B Noxious Weed in California, Washington, Oregon, and Vermont (Invaders Database System 2003), and a Class C Noxious Weed in Alabama (Germplasm Resources Information Network 2005). Connecticut has made the import, sale, purchase, transplant, cultivation, or distribution of *P. cuspidatum* illegal (State of Connecticut General Assembly 2005). *Polygonum sachalinense* is also listed as a Class B Noxious Weed in California, Washington, and Oregon (Invaders Database System 2003). In the United Kingdom the Wildlife

and Countryside Act (United Kingdom Parliament 1981) made it an “offense to actively plant or otherwise cause the species [*P. cuspidatum*] to grow in the wild.” A decade later *P. cuspidatum* was classified as “controlled waste,” which requires disposal at a licensed landfill (United Kingdom Parliament 1990).

4. Geographical Distribution

For a detailed analysis of the phytogeographic distribution of *P. cuspidatum* in North America see Barney (2006), on which all of the following is based. The current Canadian distribution is concentrated in southern Ontario, Quebec, and Newfoundland, and throughout Prince Edward Island, Nova Scotia, and New Brunswick (Fig. 3). Isolated populations exist in Winnipeg, Manitoba, southwestern British Columbia, and the southern Alaska panhandle.

Few populations have been recorded between longitude 90 and 110°W, with the highest collection frequency occurring east of the Mississippi River (~90°W). The latitudinal distribution of *P. cuspidatum* appears to be concentrated between 40 and 50°N. The Pacific coast distribution is likely the result of an independent introduction from that of the east coast with saltational populations following inland. *Polygonum cuspidatum* has been documented in 71% of the counties in the northeastern US (Pennsylvania, New York, Maryland, Massachusetts, New Hampshire, Vermont, Connecticut, Rhode Island, and Maine). As of 2000, *P. cuspidatum* has been collected in 93 Canadian municipalities and 577 US counties. The local density (sub-municipality/county) of *P. cuspidatum* in Canada and the United States of America is not known, but the large-scale distribution appears to be reaching environmental equilibrium (see Section 10). This species is not known to extend south to Mexico (Seiger 1997; Barney 2006).

Polygonum cuspidatum is native to Japan, Korea, Taiwan, and northern China (Ohwi 1965; Beerling et al. 1995), generally occurring as a pioneer species on volcanic slopes (Tezuka 1961; Adachi et al. 1996a). From these sites *P. cuspidatum* was introduced to Europe in 1825 (Bailey and Conolly 2000). The historical spread across the United Kingdom of *P. cuspidatum*, *P. sachalinense*, and their hybrid *P. × bohemicum* is well documented (Conolly 1977; Bailey et al. 1996; Dawson and Holland 1999; Bailey and Conolly 2000). By 1994, this species had been documented in nearly half of the 3500 10 × 10-km square regions into which the United Kingdom is divided (Wade et al. 1996). The most recent Atlas of the British and Irish Flora reports *P. cuspidatum* in 1877 of 2852 10 × 10-km cells in Great Britain and 627 of 1007 cells in Ireland (Preston et al. 2002). Additionally, *P. × bohemicum* is reported in 170 and 12 cells in Great Britain and Ireland, respectively, while *P. sachalinense* is reported in 324 and 44 cells (Preston et al. 2002). In addition, *P. cuspidatum* has become widespread in most countries across Europe, generally occurring between latitudes 43 and 63°N (Beerling et al. 1994). The northernmost regions of colonization occur in Norway and Finland, while the southernmost sites are in northern Portugal and Bulgaria (Beerling et al. 1994). *Polygonum cuspidatum* has been found naturalized in Vladivostok, Russia (43°08'N,

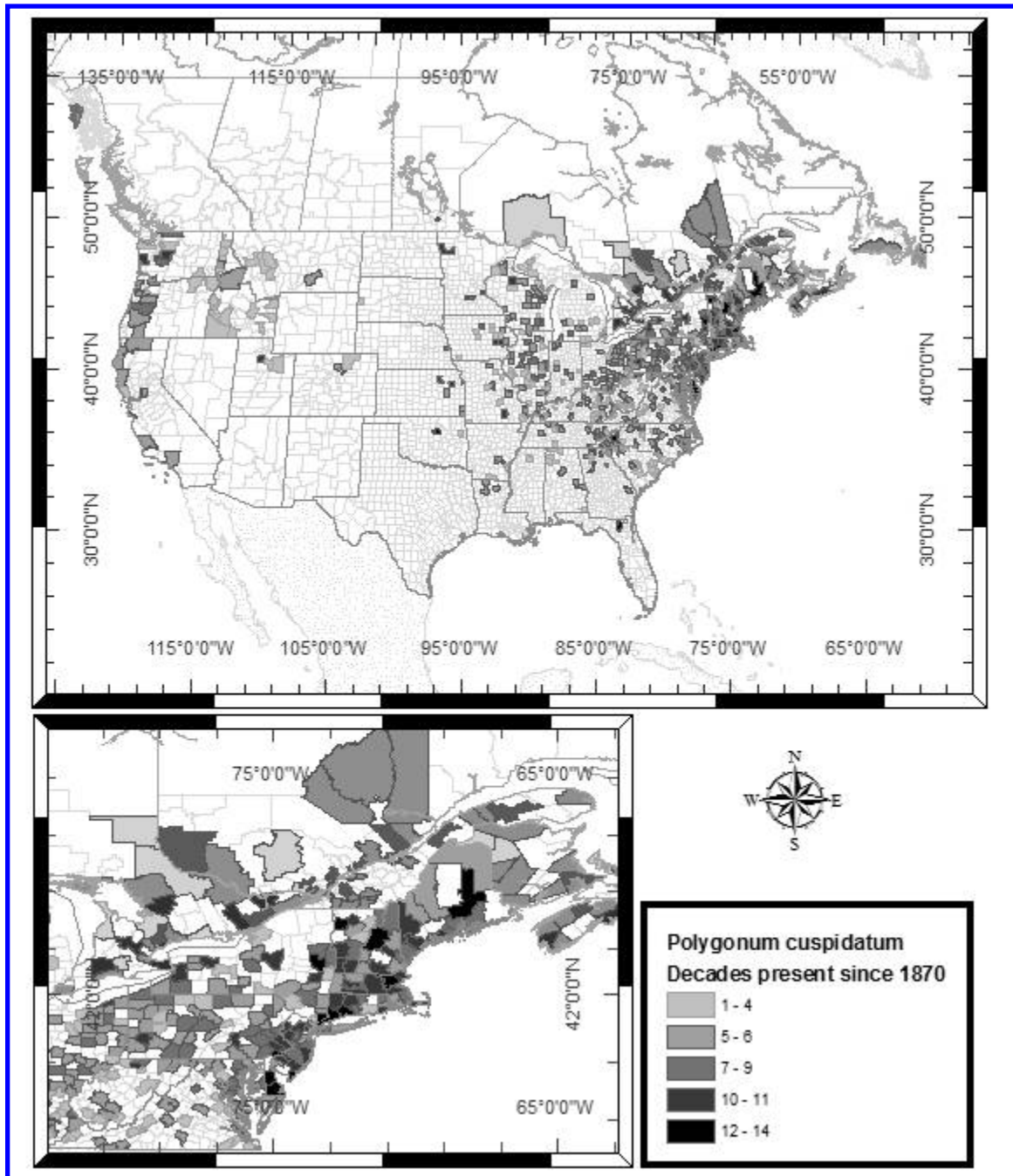


Fig. 3. Distribution of *Polygonum cuspidatum* in Canadian municipalities and US counties. A, North America; B, Southeast Canada/Northeast United States of America based on herbarium collections [adapted from Barney (2006)].

131°54'E) and is hardy in St. Petersburg (59°56'N, 30°20'E) (Komarov 1936).

Herbarium collections exist for the Australian provinces of New South Wales, Victoria, and Tasmania (Royal Botanic Gardens Melbourne 1995). Impressive monoclonal stands have been documented in Canada, many US States, Great Britain, Switzerland, Spain, Czech Republic, Sweden, Norway, Yugoslavia, and New Zealand (Webb et al. 1988; Beerling et al. 1994; Beerling and Palmer 1994; Seiger

1997), demonstrating the breadth of environmental tolerance exhibited by this species.

5. Habitat

(a) *Climatic Requirements* — In contrast to its European distribution, *P. cuspidatum* has a more southerly range in North America, primarily occurring between 33°N and 48°N (Fig. 3A). Only one population has been documented north of the 50th parallel, Baranof Island, Alaska (Barney

2006). To date, there are 93 Canadian political units (municipalities) where at least one *P. cuspidatum* population has been found, most of which occur in southern Ontario and Quebec. In an effort to estimate the large-scale distribution of *P. cuspidatum* in Canada and the United States of America, Barney (2006) applied the Verhulst-Pearl population growth model to the cumulative number of invaded political units. The estimated carrying capacity for Canada is 99 municipalities, six short of the current number of invaded municipalities. Ignoring local range expansion and density changes, these occurrences suggest that *P. cuspidatum* is approaching large-scale geographic equilibrium in Canada, as it has in Europe (see below). Therefore, the Canadian climate appears to be limiting expansion northward and to the Prairie Provinces.

In Europe, this perennial is most abundant between 45°N and 55°N, with populations declining northward (maximum of 63°19'N) and southward (minimum of 43°N). The northern limits of this species have been shown to be controlled by the length of the growing season (in growing degree days) and absolute minimum temperature (Beerling 1993). Beerling (1993) found that the climatic correlation with *P. cuspidatum* distribution occurs in regions with a heat sum equal to or above 2505 day-degrees and absolute minimum temperature equal to or above -30.2°C. This very low minimum temperature demonstrates the cold tolerance of underground rhizomes, allowing this species to expand northward without relying on persistence of frost susceptible shoots to produce seeds for recruitment. A similar pattern of growing season length was found in the native range on Mt. Fuji, Japan, where seedlings must attain a minimum dry weight of >10 mg to survive regardless of altitude (Maruta 1983).

Beerling (1993) predicted changes in the distribution of *P. cuspidatum* with increasing temperatures expected from global climate change; surmising that with a 1.5°C increase in minimum temperature, *P. cuspidatum* could potentially colonize southern Iceland, western Norway, and northern Sweden; while a 4.5°C increase would allow colonization of nearly the entire Scandinavian Peninsula and Iceland. A more comprehensive forecast of *P. cuspidatum* distribution in Europe was undertaken using minimum temperature of the coldest month, growing degree days >5°C, and the ratio of actual to potential evapotranspiration (Beerling et al. 1995). Results suggest that the current distribution of *P. cuspidatum* in Europe is driven by these three environmental predictors, and is in equilibrium with current climatic conditions (i.e., there is little chance of further large-scale geographic spread, as *P. cuspidatum* has colonized all available "climatic sites"). Beerling et al. (1995) then used minimum temperature, growing degree days, and the evapotranspiration ratio under two general circulation climate forecast models to make predictions on future range changes and found a general trend for northward and southward migration with extirpation of central European populations. As noted in the study, this forecast ignores the ability of *P. cuspidatum* to reach these sites, and only makes forecasts as to potential sites based on climate.

(b) *Substratum* — Herbarium specimen labels from Canada and the United States of America report *P. cuspidatum*

growing in varied terrain: sandy soil, swampy ground, waste ground, rocky bank, and alluvial floodplain with most emphasizing high soil moisture. No specific information regarding soil types was available. Locandro (1973) noted populations in the United States of America growing on sand (including beach sand), loam, and silt, while soil pH ranged from 4.5 to 7.4 and phosphorus and potassium concentrations of <23–137 kg ha⁻¹ and <37–284 kg ha⁻¹, respectively.

In a survey of 17 *P. cuspidatum* stands in Wales, no correlation was found between stand size/vigor and various soil properties (Palmer 1994). Populations occurred on soils ranging in pH from 3 to 8, organic matter content from 2 to 25%, and soil nutrient concentrations (K, Na, Mg, Ca, and P) that varied by orders of magnitude. Though *P. cuspidatum* prefers nutrient rich soils, it also thrives in nutrient poor soils where its growth is much reduced.

In a river habitat survey conducted between 1994 and 1996 in the United Kingdom, *P. cuspidatum* was found growing on: (i) bank material from inhospitable bedrock, rip-rap, and gabions to clay and peat; (ii) stream flow types from free-fall to standing water; (iii) bankside habitats from mixed woods, conifer plantations, scrub, to urban lots; and, (iv) bank features from eroding cliffs, bare side bars, and point bars (Dawson and Holland 1999). In Belgium, *P. cuspidatum* has been reported in soils ranging in pH 4.4–7.3 (Vanderhoeven et al. 2005). *Polygonum cuspidatum* maintains a high relative growth rate even under nitrogen-limited conditions (Chiba and Hirose 1993), and heavy metal contaminated soils (Kubota et al. 1988; Imahara et al. 1992; Mizuno et al. 2002).

In the native range of Japan, *P. cuspidatum* is often the first species to colonize recent lava flows (Mt. Aso, Sakurajima Island, Mt. Nakadake, and Mt. Fuji). As with many early successional species, *P. cuspidatum* has been shown to increase soil formative processes, specifically by decreasing soil bulk density and increasing organic matter content, water content, and nutrient levels (Hirose and Tateno 1984). Tateno and Hirose (1987) found organic nitrogen, ammonium, and nitrate concentrations to be 14, 4, and 2-fold higher, respectively, under *P. cuspidatum* stands than adjacent bare soil in primary successional stands on Mt. Fuji.

(c) *Communities in Which the Species Occurs* — In both Europe and North America, *P. cuspidatum* is a frequent colonizer of water-course banks, road and railroad rights-of-way, gardens, disturbed settings, waste places, and forest edges. A survey of North American herbarium records with site descriptions (195 Canadian and 1017 US) showed that the communities most frequently invaded are roadsides (15% Canada and 23% US) and waterway rights-of-way (17% Canada and 22% US) including streams, rivers, ponds, lakes, and oceans (Barney 2006). Figueroa (1989) found that *P. cuspidatum* density was lower along paved versus unpaved roads in Washington State, which he attributed to differences in right-of-way management. Species often found with *P. cuspidatum* along watercourses in Canada and the United States of America include reed canarygrass

(*Phalaris arundinacea* L.), white oak (*Quercus alba* L.), bur oak (*Q. macrocarpa* Endl.), American basswood (*Tilia americana* L.), hawthorn (*Crataegus* spp.), buckthorn (*Rhamnus cathartica* L.), alder (*Alnus* spp.), Oregon ash (*Fraxinus latifolia* Benth.), myrtle (*Umbellularia* spp.), maple (*Acer* spp.), ferns (*Polystichum* spp.), and aspens (*Populus* spp.) (herbarium label data). Along roadsides in North America, *P. cuspidatum* is commonly found growing in association with mugwort (*Artemisia vulgaris* L.), goldenrod (*Solidago* spp.), willow-herb (*Epilobium* spp.), wild rye (*Elymus* spp.), common ragweed (*Ambrosia artemisiifolia* L.), and chicory (*Cichorium intybus* L.) (herbarium label data). Along central New York State roadsides, *P. cuspidatum* also occurs with wild parsnip (*Pastinaca sativa* L.), perennial sowthistle (*Sonchus arvensis* L.) and wild carrot (*Daucus carota* L.) (A. DiTommaso, personal observation). Not surprisingly, *P. cuspidatum* was labeled as a “cultivated escape” in 19 and 11% of Canadian and US specimen labels, respectively (Barney 2006).

In the native range of East Asia, *P. cuspidatum* is a primary colonizer of lava flows and polluted areas (Natori and Totsuka 1984; Adachi et al. 1996a). These areas are generally open habitats receiving full sunlight with no competing vegetation and minimal species richness. On Mt. Fuji, *P. cuspidatum* serves as a nurse plant for secondary succession, as colonizing species such as *Miscanthus oligostachyus* Stapf and *Aster ageratoides* subsp. *ovatus* (Franch. & Savat.) Kitam. establish exclusively within stands of *P. cuspidatum* (Adachi et al. 1996a). The dense closed canopy of *P. cuspidatum* facilitates succession on lava flows in East Asia, but suppresses growth of other plants in its introduced range of Europe and North America. Light levels are reduced by >90% at ground level, shading out all competing vegetation despite often low stem densities (3–12 stems m⁻²) (J. N. Barney, unpublished data).

6. History

The historical spread of *P. cuspidatum* in North America has been reviewed by Barney (2006), from which the following has been adapted. For an extensive review of the distribution and historical spread of *P. cuspidatum* and related species in the British Isles see Conolly (1977).

The introduction into North America of *P. cuspidatum* is likely of horticultural provenance at a private estate on Long Island, NY, in the early 1870s. As with most invasive species, the geographic spread of *P. cuspidatum* has witnessed a near 50-yr lag before becoming widely established. Up to the turn of the 20th Century, *P. cuspidatum* was found in only 15 US states, primarily in the northeast, and in localized populations in southern Ontario and British Columbia (Fig. 3A). However, many of the herbarium labels documenting these locations indicate that these populations were in cultivation or had escaped from cultivation. A total of 264 Canadian and 1476 US unique population collections (i.e., only considering one herbarium sheet per population) have been documented to date from North American herbaria. By 1950, *P. cuspidatum* had become well established in the northeastern United States of America, while becoming sparingly distributed throughout the Midwest and Pacific

Northwest, and becoming more common in southern Ontario and Quebec. However, by the turn of the 21st Century, there has been a rapid spread of the species across the Northeastern United States of America, with 71% of counties having naturalized populations (Fig. 3B). This aggressive riparian weed is expanding southward and westward from a northeastern front into the Midwest and Southeastern US. An additional invasion front is moving east from what is likely an independent introduction in the Pacific Northwestern US (Fig. 3A).

7. Growth and Development

(a) *Morphology* — Geographic dispersal is primarily achieved via rhizome and stem fragments and secondarily via winged achenes. The rhizome system assists in perennation, but does not facilitate dispersal. However, fragments of either stems or rhizomes may be transported and subsequently established. The hollow stems float along moving water bodies, and have been observed crossing open seas. The tri-winged fruits facilitate both wind and water dispersal.

(b) *Perennation* — *Polygonum cuspidatum*, *P. sachalinense*, and their hybrid *P. × bohemicum* are perennial, herbaceous geophytes. They overwinter via an underground woody rhizome system. Above-ground shoots are highly susceptible to both late spring and early autumn frosts, causing leaf drop, while the rhizome systems are able to survive in frozen soils (J. N. Barney and P. C. Bhowmik, personal observation). Early spring frosts often cause dieback, followed by regeneration from the rhizome and completion of life cycle. Hollow stems from the previous year can be seen throughout the next growing season, but are often broken by wind or water currents. A major source of local and regional dispersal is via human-transported soil contaminated with *P. cuspidatum* rhizomes.

(c) *Physiological Data* — Maintenance respiration of field-collected seeds grown in growth chambers was measured in low and high altitude ecotypes from Mt. Fuji, Japan, at 15 and 25°C. The high altitude ecotype (2420 m a.s.l.) had maintenance respiration values 1.7-fold higher than the low altitude ecotype (700 m a.s.l.) at both temperatures, likely reflecting the costs of inhabiting a harsher environment (Mariko and Koizumi 1993). Net photosynthetic rate was positively correlated with respiration rates in both ecotypes at both temperatures, where carbon fixation rates were always greater in high altitude ecotypes, but no differences in growth respiration were detected (Mariko and Koizumi 1993). However, leaf photosynthesis was measured at irradiance values of 400 μmol m⁻² s⁻¹ for 15°C plants and 300 μmol m⁻² s⁻¹ for 25°C plants, values much lower than would be experienced in situ, thus results should be considered accordingly. Kogami et al. (2001) found a positive correlation between leaf mass per area (LMA: g m⁻²) and altitude in field populations, with the lowland ecotype (10 m a.s.l.) LMA at 48 g m⁻² and the highland ecotype (2600 m a.s.l.) LMA at 90 g m⁻². Highland *P. cuspidatum* had higher mesophyll thickness, cell wall thickness (palisade and

spongy cells), lower mesophyll porosity, higher area-based nitrogen and chlorophyll content, and less negative $\delta^{13}\text{C}$ (‰). Gas exchange parameters were taken at both high and low irradiance values (750 and 190 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in both lowland and highland ecotypes. Photosynthetic rate was greater in lowland ecotypes (14.2 versus 10.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 750 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance and 5.5 versus 5.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 190 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance), as was nitrogen-content based assimilation rates [198.6 versus 83.6 $\mu\text{mol CO}_2 (\text{mol N})^{-1} \text{ s}^{-1}$ at 750 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance and 78.3 versus 41.2 $\mu\text{mol CO}_2 (\text{mol N})^{-1} \text{ s}^{-1}$ at 190 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance], and stomatal conductance (0.22 versus 0.16 $\text{mol m}^{-2} \text{ s}^{-1}$ at 750 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance and 0.14 versus 0.12 $\text{mol m}^{-2} \text{ s}^{-1}$ at 190 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ irradiance).

The O_2 -dependency of leaf-level photosynthesis was compared between highland (2250 m a.s.l.) and lowland (100 m a.s.l.) *P. cuspidatum* populations from Japan at native atmospheric conditions (Sakata and Yokoi 2002). The lowland ecotype had higher carboxylation efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ per $\mu\text{mol CO}_2 \text{ mol}^{-1}$) than the highland ecotype at their respective native atmospheric conditions (22% lower CO_2 and O_2 partial pressures in highland environment). Additionally, the carboxylation efficiency was greater in the lowland ecotype at all four O_2 concentrations.

In Japan, limitation in photosynthetic capacity has been shown to vary with season, leaf age, and atmospheric CO_2 concentration (Onoda et al. 2005). The photosynthetic rate of *P. cuspidatum* grown at 700 $\mu\text{mol CO}_2$ was 36% greater in young leaves in August, 44% greater in young leaves in October, and 27% greater in old leaves in October than equivalent leaves grown at 370 $\mu\text{mol CO}_2$. The rate of CO_2 assimilation at saturating intercellular CO_2 partial pressure (V_{cmax} : $\mu\text{mol m}^{-2} \text{ s}^{-1}$) was 10% less in young August leaves, 13% less in young October leaves, and 24% lower in old leaves in October than equivalent leaves grown at 370 $\mu\text{mol CO}_2$, with similar results for ribulose biphosphate regeneration rates (J_{max}).

Net assimilation rate ($\text{g m}^{-2} \text{ d}^{-1}$) in populations of *P. cuspidatum* from Japan increased with increasing leaf nitrogen content (g N m^{-2}) to a maximum of 6 $\text{g m}^{-2} \text{ d}^{-1}$ (Hirose 1984; Osone and Tateno 2003). Stem and root nitrogen concentrations were strongly correlated with leaf nitrogen content in field populations (Osone and Tateno 2003). In greenhouse grown individuals Osone and Tateno (2003) found specific absorption rates for nitrogen ranging from 1.2 to 27.0 $\mu\text{g N mg}^{-1} \text{ d}^{-1}$, while Hirose (1984) found values between 0.1 and >20 $\mu\text{g N mg}^{-1} \text{ d}^{-1}$ depending on the growth nutrient solution. Leaf area was inversely related to leaf nitrogen content, while growth rate (net assimilation rate \times leaf area) increased sharply followed by a gradual decline (Hirose 1984). Removal of nitrogen from the growth solution resulted in a shift in available nitrogen to root tissue, but had little effect on net assimilation rate (Hirose and Kitajima 1986). Onoda et al. (2004) found that greenhouse grown *P. cuspidatum* seedlings that germinate early in the season allocate proportionally more nitrogen to cell walls than do late germinators, which use their nitrogen for building photosynthetic machinery. This shift in allocation likely reflects an adaptation to growth in regions having relatively short growing seasons.

Photoassimilates of *P. cuspidatum* shift from shoots to roots near the end of the growing season before senescence, reducing nutrient loss over the winter months (Price et al. 2002). A ^{14}C labeling experiment showed that photoassimilates allocated to roots totaled <10% in May and September, while rhizome allocation was 5% in May and 67% in September. Allocation to flowers in September was <5%, perhaps reflecting the lack of sexual reproduction in British *P. cuspidatum* populations.

Polygonum cuspidatum seedlings grown under fluorescent light contained pigmented spherical bodies called anthocyanoplasts within the vacuoles of epidermal cells (Kubo et al. 1995). In contrast, seedlings grown in the dark contained unpigmented anthocyanoplasts, which accumulate anthocyanins upon irradiation. The site of anthocyanin accumulation in *P. cuspidatum* seedlings is dependent on the temperature at which the irradiation occurs (Yamaguchi et al. 2000). Initial accumulation occurs in the lower section of the hypocotyls, gradually extending toward the upper section of the hypocotyls when irradiated with white light at 25°C, with variations depending on light source and temperature.

Adachi et al. (1996b) reported that the phenomenon of central die-back exhibited by *P. cuspidatum* clumps in the native habitat on Mt. Fuji, Japan, was caused intrinsically by the modification of the rhizome branching angle to 40°. The authors identified this adaptation as a means of clonal expansion, maintenance of clump density, and facilitation of effective light acquisition. Nitrogen translocation by the rhizomes from the center of the clump towards the periphery is thought to play a major role in the radiation of *P. cuspidatum* (Adachi et al. 1996c). Suzuki (1994) identified the translocation of assimilates, nutrients, and water between ramets through rhizomes, as a mechanism regulating the production of shoots in *P. cuspidatum*. In small and medium-sized clumps where leaf area index (LAI) was small, the horizontal leaves are distributed evenly through the canopy. In large clumps where the LAI is higher, a large proportion of horizontal leaves are distributed in the lower part of the canopy, with upper leaves showing a more vertical arrangement (Suzuki 1994).

(d) *Phenology* — The phenology described below is based on Locandro (1973) and the personal observations of the authors of eastern US populations. Seedlings of *P. cuspidatum* emerge in mid-spring (late March-May) depending on latitude and altitude (Fig. 4). Rhizome sprouts emerge from late-spring (April) through mid-summer (June–July), until the canopy closes. Rhizome sprouts often resemble asparagus shoots, being pointed at the apex, broad-based, and fleshy. Flowering in North America generally begins in August and continues through mid-September, with fruit-set beginning in September and fruits generally remaining on the plants throughout the winter. Leaves are photosynthetically active until autumn frosts when senescence begins, and drop throughout the winter months. Maximal total dry biomass of 976 g m^{-2} was achieved in mid-June in a Czech Republic population (Horn 1997).

(e) *Mycorrhiza* — Mycorrhizal associations with *P. cuspidatum* have been investigated for populations residing on

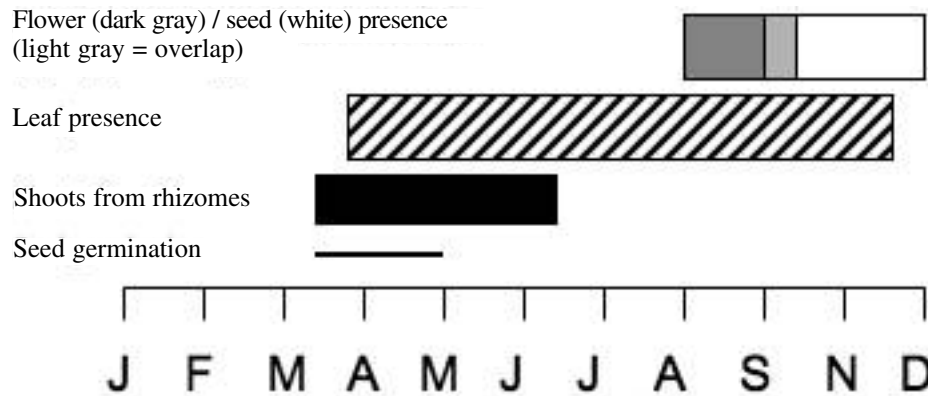


Fig. 4. Phenology of *Polygonum cuspidatum* in North America [from author observations and Locandro (1973)].

the slopes of Mt. Fuji, Japan. Contrary to previous studies, two independent researchers discovered arbuscular mycorrhizal fungal associations with *P. cuspidatum* in stands at various stages of succession (Wu et al. 2004; Fujiyoshi et al. 2005). Wu et al. (2004) found that percentage mycorrhiza colonization and spore density decreased with increasing altitude (1500–1930 m a.s.l.), with uncolonized root hairs averaging 303 μm . The arbuscular mycorrhizal morphology in *P. cuspidatum* roots is described as both *Paris*-type and *Arum*-type (Wu et al. 2004). Both studies found robust stands of *P. cuspidatum* lacking any mycorrhizal associations, indicating that this early colonizer is a facultative mycotrophic species (Wu et al. 2004). No data exist on mycorrhizal associations in North American populations.

8. Reproduction

(a) *Floral Biology* — As with other features of this species, its floral biology in North American populations is paradoxical, with reports of populations being completely male sterile, male only, gynodioecious, or subdioecious (Locandro 1973; Forman and Kesseli 2003; Bram and McNair 2004). This variation in floral biology is likely a product of either misidentification of *P. cuspidatum* with congeners, or the result of inherent variation in the native genome established via multiple introductions. However, in the United Kingdom, *P. cuspidatum* is reported to be exclusively female, having no stamen-containing flowers throughout the region, thus earning the moniker of “world’s largest female” (Bailey 1994; Hollingsworth and Bailey 2000a).

A study of Mid-Atlantic US *P. cuspidatum* populations found male flowers to be very rare, but when present produced viable pollen (Locandro 1973). Populations in central New York State have been found to contain individuals with hermaphroditic flowers and male-sterile flowers (gynodioecious), producing large numbers of viable, presumably non-hybrid (no other knotweed taxa within 1 km), seed (J. N. Barney, personal observation).

In Japan, insects in the Hymenoptera, Diptera (Bibionidae and Mycetophilidae), and Coleoptera (Pyrochroidae) have been observed visiting the extrafloral nectaries of *P. cuspi-*

datum (Kawano et al. 1999). Visiting Hymenoptera include: *Camponotus obscuripes* Mayr, *Camponotus japonicus* Mayr, *Formica fukaii* Wheeler, *Formica japonica* Motsch., *Lasius japonicus* Santschi, *Leptothorax congruus* var. *spiniosior* Forel, *Pheidole fervida* Fr. Smith, *Pristomyrmex pungens* Mayr, *Polistes* spp., *Allantus luctifer* Smith, *Dolerus* spp. (Kawano et al. 1999). In addition, Tanaka (1966) documented both male-fertile and male-sterile populations being visited by flies, bees, and wasps. Analysis of extrafloral nectaries, composed of 10–15 elongated cells longitudinally arranged, showed that the nectar solution is composed of 24% sugars; primarily fructose (43%), glucose (37%), sucrose (15%), and trisaccharide (5%) (Kawano et al. 1999). *Polygonum cuspidatum* appears to be exclusively entomophilous in all naturalized ranges, including North America.

(b) *Seed Production and Dispersal* — Despite numerous published accounts related to the vegetative mode of reproduction of *P. cuspidatum* in its native and introduced range, seed production and recruitment may also play a role in the geographic expansion of this invader. However, the identity of the parental taxa involved in seed production is often unknown, especially in the United Kingdom where only female clones exist. There are no reports of agamospermi- cally produced seeds in any populations throughout its range.

The number of flowers per stem of several *P. cuspidatum* individuals from the United Kingdom ranged from 95 000 to >190 000, with the actual number of seeds per stem ranging from 283 to 6152 (Bailey 1994). This suggests a very low percentage of the male sterile flowers being fertilized, likely due to a lack of nearby compatible congeneric pollen donors. A similar estimate of potential seed production in a North American population (Philadelphia, PA) approaches 127 000 per stem, assuming all flowers are successfully pollinated (Bram and McNair 2004).

Average *P. cuspidatum* seed weight of populations at 2500 m a.s.l. on Mt. Fuji, Japan, was 1.9 mg (Maruta 1994), while seeds from 0 to 1400 m a.s.l. had a mean seed weight

of ~ 0.9 mg, and those from 1500 to 2500 m a.s.l., ~ 1.7 mg (Mariko et al. 1993).

When seed is produced, the winged achenes are primarily wind dispersed (Beerling et al. 1994). The fruits have also been observed floating in streams in North America, facilitating colonization of riparian corridors (J. N. Barney and P. C. Bhowmik, personal observation).

(c) *Seed Banks, seed Viability and Germination* — Bram and McNair (2004) showed that a moist chilling (4°C) of 30 d immediately after mid-September through mid-October seed collection generally increased maximum percent germination compared with the same stratification treatment given the following year in Philadelphia, PA populations. Maximum germination was generally achieved after late-September, with seeds from some sites reaching maximal germination in late October (Bram and McNair 2004). However, maximum percentage germination varied drastically (40–>90%), which may be due to either intraspecific variation in seed germinability or sites containing different *Polygonum* species, since identification to species was not confirmed.

North American *P. cuspidatum* seeds were found to begin germinating in the greenhouse 7 d after planting and continue to germinate until 36 d after planting (Forman and Kesseli 2003). The mean germination for seeds collected from 24 parent plants in three sites in eastern Massachusetts and grown in the greenhouse was 30%, with 65% of these seedlings surviving to maturity, and 81% flowering (i.e., 16% of seeds sown flowered). Seedling survival in the field the year following germination is achieved if sufficient growth is reached in year one (five or more true leaves) (Forman and Kesseli 2003). Seeds from a single site in Philadelphia, PA were found to have 82% germination when buried 1–2 cm in early winter in pre-existing *P. cuspidatum* stands (Bram and McNair 2004). Bram and McNair (2004) also documented in situ seedling recruitment in *P. cuspidatum* along an urban riparian corridor. However, as noted above, it was not determined if these populations were *P. cuspidatum* sensu stricto or a congener, and results should be viewed accordingly. Seedlings were noted in plots in a Connecticut population the year following glyphosate treatment (Ahrens 1975). Seeds collected from a population of *P. cuspidatum* in central New York State, with both male-sterile and hermaphroditic individuals, and no *P. sachalinense* or *P. × bohemicum* nearby, yielded viable seeds (J. N. Barney, unpublished data). Hybrid seeds that have been collected exhibited dormancy and required after-ripening at room temperature (Hrušková and Hofbauer 1999). Seeds identified as *P. cuspidatum* were collected at 5–10 cm depth from an urban garden in Sheffield, UK (Thompson et al. 2005).

A considerable amount of research has been conducted on seed recruitment in the native range of Japan, particularly on Mt. Fuji, where *P. cuspidatum* is a primary colonizer of recent lava flow areas. Winter survival following germination of *P. cuspidatum* at 2500 m a.s.l. on Mt. Fuji was found to be 2%, with a seedling threshold size of 12 mg dry weight (Maruta 1994). Altitudinal variation in germination has

been observed, with seeds near the upper altitudinal limit on Mt. Fuji (2400 m a.s.l.) germinating from late April through mid-May, and lowland (Shizouka) populations germinating from mid-March through early-May (Nishitani and Masuzawa 1996). Seeds collected from Mt. Fuji (2400 m a.s.l.) and Shizouka (10 m a.s.l.), which spent the winter months on Mt. Fuji buried 1–3 cm in mesh bags, were tested for their response to light and temperature; light (500–700 $\mu\text{mol m}^{-2} \text{s}^{-1}$) treated seeds of both populations reached 80% germination at 10°C with non-treated seeds reaching 80% germination at 25°C (Nishitani and Masuzawa 1996). However, Mariko et al. (1993) describe two ecotypes of *P. cuspidatum* along the same altitudinal gradient on Mt. Fuji, with a distinct ecotype at 1400–1500 m a.s.l. The “upland” ecotype produced seeds 1.5-fold heavier, reached 50% germination at lower temperatures (15°C), and had higher total leaf area and plant biomass (at 15°C) compared with the “lowland” ecotype. Seeds collected and germinated the year of production (late September or late October) from both ecotypes showed little response to light or temperature treatments, suggesting innate seed dormancy. Moist chilling (0–4°C) or dry warm (25°C) storage for 30 d resulted in 90% germination, breaking seed dormancy (Nishitani and Masuzawa 1996). After-ripening shifted the temperature requirement from 35°C to an optimum of 20–25°C for germination (Nishitani and Masuzawa 1996).

(d) *Vegetative Reproduction* — Asexual reproduction via stem and rhizome fragments is the reputed primary means of reproduction and colonization throughout the introduced range in central Europe, the United Kingdom, and North America. Vegetative spread has also been documented in the native range of Japan (Mt. Fuji), but appears to be less important than seedling recruitment for colonization. This geophyte overwinters with perennating buds on underground stems (rhizomes), with aboveground shoots highly susceptible to cold/frost damage.

Polygonum cuspidatum produces an extensive network of rhizomes reaching 15–20 m in length and penetrating 2–3 m deep in soil (Locandro 1973; Conolly 1977), and accounting for two-thirds of total plant biomass (Alder 1993). Rhizome fragments can regenerate from various depths, with 2 cm being optimal, but can also sprout from as deep as 1 m (Locandro 1973). The vegetative reproductive potential for rhizome tissue grown in water or soil (buried and surface sown) was examined in four *Polygonum* taxa (*P. cuspidatum*, *P. cuspidatum* var. *compactum*, *P. sachalinense*, and *P. × bohemicum*) in the Czech Republic (Bímová et al. 2003). Regeneration from rhizomes was generally poor (<20%) in water, while varying greatly between taxa in soil treatments. *Polygonum cuspidatum* had 100% rhizome regeneration when buried 5 mm in a loam-sand mix and ~ 50% regeneration when surface-sown. The hybrid *P. × bohemicum* had a high regeneration percentage (90–100%) in all soil treatments. Further investigation showed that regeneration capacity varied by genotype in *P. × bohemicum*, but not in *P. sachalinense* (Pyšek et al. 2003). Beerling (1990a) showed that rhizome fragments as small as 8 g fresh weight are able to regenerate, provided a node is present. Single

season biomass can increase 26-fold from May to September, with rhizome biomass increasing 18-fold and accounting for 48% of the total biomass (Price et al. 2002).

Stem tissue regeneration has been examined in populations from the United Kingdom and the Czech Republic as the shredding of above-ground shoots is a common control practice in both regions. de Waal (2001) showed that *P. cuspidatum* stem tissue is able to regenerate and produce adventitious roots regardless of season. However, the sprouts from the spring cutting failed to establish further due to low nutrient and growth hormone content of the cuttings. Stem tissue produced up to one new shoot per three stem nodes reaching a maximum height of 80 mm in 4 wk, and began to regenerate within 1 wk following harvest. Bimová et al. (2003) found all four *Polygonum* taxa exhibited >75% regeneration from stem tissue floating on water, while stem regeneration in soil treatments (surface or buried) was <30% (except for *P. cuspidatum* var. *compactum* on soil surface, ~ 55%). The internodal tissues are also found to have some regenerative capacity (Locandro 1973). Even nodes split in half are capable of regenerating when exposed to favorable conditions (de Waal 2001).

Approximately 238 propagules could be produced from 1 m² of a typical rhizome network (Brock and Wade 1992). Child (1999) indicated that the minimum rhizome weight that could regenerate was 0.7 g, which extrapolates to ~2000 propagules per meter square of *P. cuspidatum*. Similar estimates of propagules per meter square from the stem tissue suggests that 8 and 90 propagules could be produced from split and intact nodes, respectively (de Waal 2001).

Disturbance and transportation of soil profiles containing *P. cuspidatum* are a significant mechanism of colonization, precluding management of this species via soil removal. Roadsides are a common habitat colonized by *P. cuspidatum* in North America, with spread being facilitated by roadwork and right-of-way maintenance (Weston et al. 2005). Spread via waterways, both fresh and saltwater, of fractured stems and rhizomes has been documented in both the United Kingdom and the United States (Beerling et al. 1994; Barney 2006). Short-term cutting of *P. cuspidatum* shoots in a management study in Wales resulted in an expanded clonal radius (Beerling 1990a) and increased shoot density (Beerling and Palmer 1994), suggesting that either lateral rhizome production and/or shoot formation from existing rhizome nodes was stimulated. This robust rhizome system has been documented penetrating asphalt 8 cm thick, and is able to regenerate at burial depths of up to 1 m (Pridham and Bing 1975; Locandro 1978).

9. Hybrids

Hybridization of *P. cuspidatum* with some congeneric species in the introduced ranges of Europe and North America is reported to be common and widespread. All viable seeds produced by *P. cuspidatum* in Europe are putatively the result of pollen donation by one of several species: *P. sachalinense*, *P. cuspidatum* var. *compactum*, *P. × bohemicum*, or *P. baldschuanicum* Regel (Bailey 1994).

The most common hybrid in both Europe and North America appears to be from a cross between *P. cuspidatum*

var. *cuspidatum* and *P. sachalinense* = *P. × bohemicum*. The reported diploid numbers of *P. × bohemicum* are $2n = 66$ (Hart et al. 1997), $2n = 44$ (from *P. cuspidatum* var. *compactum* × *P. sachalinense*) or $2n = 88$ (Mandák et al. 2003). In England, all hexaploid *P. × bohemicum* (from *P. cuspidatum* var. *cuspidatum* × *P. sachalinense*) populations examined have the chloroplast haplotype of *P. cuspidatum* (Hollingsworth et al. 1999). *Polygonum × bohemicum* plants show a high level of genetic diversity in the United Kingdom (Hollingsworth and Bailey 2000b), but genetic variability has yet to be examined in North American populations. This is the most common and wide-spread hybrid in Europe, where it is reported to be more aggressive than either of the parental taxa (Ellestrand and Schierenbeck 2000; Mandák et al. 2004). In Washington State, many staminate populations of *P. × bohemicum* have been observed, although few fruiting populations have been documented (Zika and Jacobson 2003). Zika and Jacobson (2003) speculated that most of the *P. × bohemicum* populations observed in the wild in the US Pacific Northwest were the result of garden escapes rather than recurrent hybridization between the two parental species. Few attempts have been made to distinguish *P. × bohemicum* from either of its parents in Canada or the eastern United States of America, which has confounded interpretation of research results.

Hybridization between *P. cuspidatum* and *P. cuspidatum* var. *compactum* has been reported in the United Kingdom (Bailey and Stace 1992), resulting in male fertile or hermaphroditic individuals (Bailey 1994). This hybrid has yet to be reported in North America.

The "railway-yard knotweed" *Fallopia × conollyana* J.P. Bailey, a cross between *P. cuspidatum* and *P. baldschuanicum*, was first reported in Wales in 1983 and is now found in the United Kingdom, the Czech Republic, and Germany (Bailey 2001). Deemed an unlikely hybrid because of its deciduous woody perennial habit and unique chromosomal base number ($2n = 54$), very few seedlings or mature plants of *F. × conollyana* have been confirmed in the wild. No record of this hybrid exists in North America.

10. Population Dynamics

The population structure of *P. cuspidatum* colonizing the slopes of Mt. Fuji, Japan, was assessed using aerial photographs between 1962 and 1999 (Zhou et al. 2003). Of the 155 populations detected in 1999, 90 could be located in the 1962 photographs, while the other 65 were either too small to be detected in the photos, or were the result of later colonization. The patches ranged in coverage from 0.5 to 139 m² and averaged 30 patches ha⁻¹. Patch sexuality varied greatly: 62 patches had solely male shoots, 56 patches contained female shoots only, 11 patches were exclusively monoecious, six patches had both unisex and monoecious individuals, and 20 patches had a mixture of male and female individuals. Genetic analysis revealed that individuals between patches, and male and female individuals within patches, were different genets. A strong correlation was detected between patch size and area of the largest genet, with new genet recruitment occurring at the patch boundary.

As a primary colonizer of lava flows in Japan, *P. cuspidatum* facilitates primary succession by reducing its shoot density at the patch center, a phenomenon known as central die-back (Adachi et al. 1996a). This is not a result of intra- or inter-specific competition, but an outcome of rhizome orientation and structure, a function of patch size and age. *Aster ageratoides* subsp. *ovatus* and *Miscanthus oligostachyus* are two species that colonize the patch centers.

A host of secondary compounds have been isolated and characterized from both the above- and below-ground structures of *P. cuspidatum*, mostly pharmaceuticals, but also allelochemicals. The phytoalexin resveratrol (3,5,4'-trihydroxystilbene), the noted ingredient of red wine which has also been isolated from *P. cuspidatum* roots, has received considerable attention for its anti-cancer properties (Kimura and Okuda 2001). Resveratrol concentrations in *P. cuspidatum* range from 2.96 to 3.77 mg g⁻¹ dry weight (Vastano et al. 2000). The concentration of resveratrol is found to be tissue specific, with perennial roots, leaf, stem and annual roots containing 1024.96, 764.74, 123.57, and 26.88 µg g⁻¹ dry weight resveratrol, respectively. Liver peroxidation in rats was found to be mitigated by several components of *P. cuspidatum* root extracts; namely the stilbenes piceid, resveratrol, and 2,3,5,4'-tetrahydroxy stilbene-2-O-D-glucoside (Kimura et al. 1995). Other *P. cuspidatum* root constituents that have been identified include the anthraquinones chrysophanol, physcion, emodin, emodin-8-O-D-glucoside; the phenolics physcion-8-O-D-glucoside, fallacinol, citerorosein, quercetin, quercetinol, protocatechuic acid, (+)-catechin [the toxic phytochemical found in knapweed (sensu Bais et al. 2003)], 2,5-dimethyl-7-hydroxy chromone, 7-hydroxy-4-methoxy-5-methylcoumarin, and torachryson-8-O-d-glucoside; and the hydroquinone 2-methoxy-6-acetyl-7-methyljuglone (Kimura et al. 1983).

11. Response to Herbicides and Other Chemicals

Formal studies on the control of *P. cuspidatum* began in the early 1960s. The earliest published study in North America (Connecticut) compared control of regrowth from cut stems (August) following applications of dicamba (1.68 and 3.36 kg a.i. ha⁻¹ in June) and glyphosate (3.36, 6.72, and 10.08 kg a.e. ha⁻¹ in June and September) on 1.8–2.4 m plants. The single dicamba application showed poor control. However, the two glyphosate applications reduced shoot densities from 5 to 16 shoots m⁻² to 0 to 2 shoots m⁻² (Ahrens 1975). A second experiment performed was identical to the first but included the additional treatments of stem cutting 10 or 30 d after treatment. The 30-d cutting was more effective, especially when combined with an additional late-season glyphosate application. However, in all treatments, live *P. cuspidatum* roots were found and produced viable shoots (Ahrens 1975). Figueroa (1989) found differences in early-June applied glyphosate (3.4 kg a.e. ha⁻¹) efficacy between *P. cuspidatum* stands along paved and unpaved roads, attributing the poor control along unpaved roads to the presence of dust on the leaves. However, imazapyr (0.6 kg a.i. ha⁻¹) was found to be effective regardless of roadside condition, but unfortunately no quantitative results were reported (Figueroa 1989).

Gover et al. (2000) found that an early and a late summer treatment with dicamba (2.2 kg a.i. ha⁻¹) and clopyralid

(0.21 kg a.i. ha⁻¹) combined with a mid-summer grass overseeding [55:35:10 mixture of hard fescue (*Festuca brevipila* Tracey), red fescue (*Festuca rubra* ssp. *rubra* L.), and annual ryegrass (*Lolium multiflorum* L.)] in Pennsylvania gave >90% reduction of *P. sachalinense* biomass 16 mo later, but gave poor control of *P. cuspidatum*. A follow-up study using a high volume application (1870 L ha⁻¹) of glyphosate (3.4 kg a.e. ha⁻¹) to roadside *P. cuspidatum* populations provided 96% biomass reduction 47 wk after treatment (WAT), while imazapyr (0.84 kg a.i. ha⁻¹) and a glyphosate (3.4 kg a.e. ha⁻¹) – imazapyr (0.14 kg a.i. ha⁻¹) mixture gave 89% control 47 WAT (Gover et al. 2005). The Roadside Research Project at Pennsylvania State University recommends management for *P. cuspidatum* include an initial treatment phase followed by annual spot treatments (A. E. Gover, personal communication). The initial treatment phase comprises an early summer cutting of stems to ground level and a mid- to late-summer glyphosate (3–4 kg a.e. ha⁻¹) application. This is followed by a mid-summer glyphosate application to any remaining live stems in year two. Subsequent to the initial 2 yr of treatment, the managed area is then spot treated using selective herbicides if desirable vegetation has established.

Early autumn (late-September) stem injections of concentrated glyphosate at a volume of 5 mL stem⁻¹ provided complete season long control of an Ithaca, NY *P. cuspidatum* population. Stem density reductions of more than 90% were observed the following year compared with plants not receiving the late autumn glyphosate application (J. N. Barney, unpublished data). Using C¹⁴ tracer studies have demonstrated increased translocation of photosynthates to rhizomes beginning in June (Price et al. 2002), suggesting optimal timing for systemic herbicide application. However, since most of the perennating structures are quiescent buds that exhibit very low metabolic activity, repeated application of the chemical is needed throughout the season.

In a British study assessing the efficacy of nine herbicides applied in a single season or two consecutive seasons versus stem cutting, a single application of picloram (2.6 kg a.i. ha⁻¹) was found to reduce shoot density 8-fold (4 versus 31 shoots m⁻²), while consecutive applications reduced stem density from 33 to 1 shoot m⁻² (Scott and Marrs 1984). The other herbicides tested reduced *P. cuspidatum* stem density, but were deemed to provide inadequate control. Application of 2,4-D (2.79 kg a.i. ha⁻¹) in May and July on riparian populations of *P. cuspidatum* in South Wales, UK, reduced above-ground dry biomass 90% 14 wk after initial treatment, while application of glyphosate (2.15 kg a.e. ha⁻¹) resulted in a 60 % (May only) and 85% (May and July) reduction in biomass (Beerling 1990b). Treatment with 2,4-D gave the added benefit of allowing monocot establishment in the treated plots thus facilitating restoration efforts.

12. Response to Other Human Manipulations

Polygonum cuspidatum often occurs in sensitive riparian corridors or near desirable native species, removing herbicide application as a viable management option. Several studies have examined mechanical control as an alternate

management strategy. Seiger and Merchant (1997) conducted a cutting study on container-grown *P. cuspidatum* rhizome segments (each containing three nodes), comparing the timing and number of cuts on rhizome biomass. A single cutting of above-ground material reduced rhizome dry biomass by 13%, two cuts by 31%, and three cuts by 65% compared with intact controls. Regression analysis revealed that four cuts within a single season would be required to achieve net rhizome biomass depletion. Timing of cutting did not affect rhizome biomass so long as cutting was performed 7 wk prior to senescence. Mowing at 2-wk intervals for 2 yr completely eliminated *P. cuspidatum* in Wales, while hand pulling for 10 yr did not exhaust the rhizome reserve (Baker 1988). However, Baker (1988) noted a rapid re-colonization of the hand-pulled area with native herbs, but noted that herbicides would likely be required to ensure eradication.

13. Response to Herbivory, Disease and Higher Plant Parasites

(a) Herbivory

(i) *Mammals, including both domestic and wild animals* — The young shoots of *P. cuspidatum* are reported to be palatable to sheep, donkeys, goats, cattle, and horses (Bond and Turner 2005).

(ii) *Birds and/or other vertebrates* — No known reports of bird or other vertebrate herbivory on *P. cuspidatum* in North America or the native range of East Asia. House sparrows have been observed removing the achenes from the perianth in the United Kingdom (J. Bailey, personal communication).

(iii) *Insects* — Large numbers of herbivorous insects were observed feeding on the foliage of both *P. cuspidatum* and *P. sachalinense* in Japan, often consuming >40% of the total leaf area (Kawano et al. 1999). The following insects are noted herbivores of *P. cuspidatum*; (Coleoptera) *Blitopertha conspurcata* Harold, *B. orientalis* Motsch., *Maladera japonica* Motsch., *Arthrotus niger* Motsch., *Cryptocephalus approximatus* Baly, *Smaragdina aurita* L., *Lixus* spp., *Phyllobius* spp., *Rhinoncus* spp., *Apoderus geminus* Sharp, *A. rubidus* Motsch., *Euops punctatostriatus* Motsch., and *E. splendidus* Voss. *Polygonum cuspidatum* has been a reported host for the strawberry leaf beetle (*Galerucella vittaticollis* Baly, Coleoptera) in Japan, but with little damage to the leaves (Adati and Matsuda 2000). In the native range of Japan, the leaf feeding chrysomelid beetle *Gallerucida nigromaculata* Baly regulates *P. cuspidatum* population growth, and is under consideration as a biocontrol agent in the United Kingdom and United States of America (Shaw and Seiger 2002). Despite the large number of herbivorous insects observed on *P. cuspidatum* foliage, the extrafloral nectaries present at the base of the leaves attract predatory ants, which, in turn, reduce overall feeding by insects and leaf loss (Wade et al. 1996; Kawano et al. 1999). Two detritivorous insects (*Nemurella pictetii* Klapalek (Plecoptera), *Sericostoma personatum* Kirby & Spence (Trichoptera), and *Gammarus fossarum* Koch (Amphipoda) have been shown to feed on *P. cuspidatum* leaf litter in French waterways (Dangles et al. 2002).

(iv) *Nematodes and/or other non-vertebrates* — No known reports of nematodes or non-insect invertebrates on *P. cuspidatum* in North America, Europe, or the native range of East Asia.

(b) *Diseases* — No known reports of diseases on *P. cuspidatum* in North America, Europe, or the native range of East Asia.

(i) *Fungi* — The following fungi have been identified as using *P. cuspidatum* as a host: *Aecidium polygoni-cuspidati* Dietel, China and Japan; *Ceriospora polygonacearum* (Petr.) Piroz & Morgan-Jones, England; *Chaetoconis polygoni* (Ellis & Everh.) Clem., England; *Hymenoscyphus menthae* (Phill.) Baral, Netherlands; *Leptosphaeria fusispora* Niessl (on stems.), New York; *Puccinia antenori*, China; *P. phragmitis* (Schumach.) Korn., Japan; *P. polygoni-amphibii* Pers., China; *P. polygoni-amphibii* var. *tovariae* Pers., Japan; and, *Schizothyrium pomi* (Mont. & Fr.) Arx., North Carolina (Farr et al. 2002 onwards).

(ii) *Bacteria* — No known reports of bacteria on *P. cuspidatum* in North America, Europe, or the native range of East Asia.

(iii) *Viruses* — No known reports of viruses on *P. cuspidatum* in North America, Europe, or the native range of East Asia.

(c) *Higher Plant Parasites* — No known reports of higher plant parasites on *P. cuspidatum* in North America, Europe, or the native range of East Asia.

14. Prognosis

Polygonum cuspidatum was initially introduced into North America in the 1870s as an ornamental, with its current geographic distribution the result of many independent introductions as nursery stock followed by secondary spread from these locations. The broad scale distribution of *P. cuspidatum* in Canada is reaching climatic equilibrium, while in the United States there remain many regions suitable to *P. cuspidatum* colonization. Local population expansion is facilitated by both vegetative fragments and seed recruitment dispersed primarily via waterways and movement of contaminated soil.

Once introduced to a new area, *P. cuspidatum* populations rapidly expand, displacing nearly all resident vegetation. Alterations in natural flooding cycles and water quality, soil physical properties, and native species recruitment have been documented in invaded habitats. Evidence suggests that *P. cuspidatum* has the ability to alter the soil and light environment such that native species cannot establish within infested sites, greatly threatening native species survival in infested areas. *Polygonum cuspidatum* has become such a nuisance in the United Kingdom that officials have made it an offense to knowingly distribute or contribute to the spread of this species. North American regulatory agencies should follow this example and mandate management and eradication of this noxious invader as soon

as possible. The first step should be containment; reducing further spread of this perennial into new areas. Public outreach and education has proven beneficial in the United Kingdom, and could serve as a model for the management of *P. cuspidatum* in North America.

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