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The introduction of Japanese knotweed, *Reynoutria japonica*, into North America[1]

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Abstract. This article presents the discovery of earliest known references to the cultivation of Japanese knotweed, *Reynoutria japonica*, in North America. As described in articles from 1868, 1872, and 1875 there were three distinct introductions of the plant in the 1860s, two from Europe and one from Japan. The European introductions consisted of the now widespread, seedless female clone introduced into commerce by Philipp von Siebold in the 1840s and a dwarf, seed-producing variety with reddish stems, probably also introduced by von Siebold. The introduction from Japan was sent by Thomas Hogg to his brother James's nursery in New York City and produced "an abundance of rose-colored fruits." Serendipitously, an herbarium specimen collected from Hogg's plant in 1873 was discovered in in 2006 and its examination strongly suggests that the introduction consisted of at least one male and one female plant. Thomas Hogg's independent introduction of the species from Japan could well explain the higher levels of genetic diversity displayed by Japanese knotweed populations in eastern North America compared to those in Europe.

Key words: *Fallopia japonica*, George Thurber, James Hogg, *Polygonum cuspidatum*, Thomas Hogg, Torrey Botanical Club

As remarkable as it may seem, the historical details surrounding the introduction of Japanese knotweed, *Reynoutria japonica* Houtt., into North America are unknown. The species is widely considered to be one of the most problematic invasive plants in the temperate world and its intentional propagation and distribution has been banned by many European countries and American states (IUCN 2013). *Reynoutria japonica* is native to eastern Asia—encompassing Japan, Korea, Taiwan, and southwest China—where it grows in a wide variety of habitats including riversides, swamp forests, disturbed forest edges, mountain slopes, and roadway verges (Beerling, Huntley, and Bailey 1995). One of its most well-studied natural occurrences is on the southeast slopes of Mt. Fuji, on barren lava flows between 1,500 and 2,500 m, where it reproduces from both seeds and rhizomes to form patches covering up to 100 m^2 (Zhou *et al*. 2003). The taxonomy of the Japanese knotweed has a long and complicated history, but recent molecular and morphological research (Schuster, Wilson, and Kron 2011) has clearly established the priority of its original 1777 Latin binomial, *Raynoutria japonica* Houtt. over the more widely used names, *Fallopia japonica* (Houtt.) Ronse Decr. and *Polygonum cuspidatum* Siebold and Zucc.

Reynoutria japonica was successfully introduced into Europe at Leiden in the Netherlands by Phillip von Siebold in the early 1840s (Bailey and Conolly 2000) and into North America sometime prior to 1873, the date of the earliest known herbarium specimen (Barney 2006). The species was widely cultivated on both continents for a variety of utilitarian purposes and quickly began spreading outside its intended planting areas. As an invasive species, Japanese knotweed grows particularly well in riparian habitats, abandoned agricultural fields, polluted postindustrial wastelands, roadway verges, and infrastructure edges (Barney *et al*. 2006). Once established, the plant spreads aggressively from its deep underground rhizomes and is highly resilient in the face of repeated disturbance. In eastern North America, its wind-dispersed seeds have the capacity to germinate on bare ground and establish seedlings some distance from their source (Forman and Kesseli 2003; Gammon *et al*. 2007, 2010).

[1] The author thanks Jacob Barney for his advice and his help in tracking down the oldest specimen of Japanese knotweed from North America, Christina Harris for help with the research on the writings of William Robinson, Walter Kittredge of the Harvard University Herbaria for his thoughtful comments, Koichi Watanabi for information concerning von Siebold's introduction of Japanese knotweed, Marion Dietrich for help with German translations, and the Herbarium of the University of Massachusetts in Amherst for providing the author with a scan of their historic specimen of Japanese knotweed.

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Japanese Knotweed in Europe. *Reynoutria japonica* was first commercially distributed in Europe in 1848 by Philipp von Siebold, a Bavarian doctor who worked for the Dutch government in Japan between 1823 and 1829. Von Siebold had a strong interest in botany and natural history and he sent a large shipment of live plants—over 500 different kinds—to the Netherlands upon his departure from that country (Siebold 1863, Bailey and Conolly 2000). Following his return to Europe, von Siebold settled in Leiden and, in 1842, cofounded the Royal Society for the Advancement of Horticulture in the Netherlands sanctioned by King Willem II. One goal of the organization was to commercialize the Japanese plants that von Siebold or other Dutch botanists had collected in Japan. The venture was not profitable and von Siebold bought out his partners in 1844. He renamed the enterprise Von Siebold & Company and established an "acclimatization" nursery on property that he owned in Leiderdorp, just across the river from Leiden (Compton and Thijsse 2013).

In his catalogue from 1848, von Siebold first offered Japanese knotweed for sale to the general public (under the name *Polygonum sieboldii*) at the exorbitant price of 500 francs for a "mother" plant plus 25 young ones. Eight years later, in his 1856 catalogue, the price had dropped by a factor of *eighty*, down to 100 plants for 25 francs (Bailey and Conolly 2000). This catalogue, as well as the one from 1863, contained a glowing description of Japanese knotweed:

> This knotweed is one of our most important introductions from Japan, a perennial ornamental plant, inextirpable, with shining foliage, clusters of very graceful flowers, useful in creating groves, sheltering young plantings, and fortifying sandy hills and dunes. The plant, which can be cut in the spring many times over, provides an excellent forage for fattening livestock, which eat it out of preference; the flowers, which appear in autumn, are very sweet and give bees winter food; the bitter and tonic root is a medicine of repute among the Chinese and Japanese; finally, even the stalks which die in winter are good for burning and for matches. Already there have been very satisfactory trials stabilizing trenches and slopes along railroad tracks and sandbanks with plantings of this arborescent, inextirpable plant. (Siebold 1863, translated by Townsend 1997)

Curiously, von Siebold's description makes no mention of the fact that the young shoots are edible in spring, a lapse that he made up for by twice referring to the plant as inextirpable; the description also says nothing about the plant setting seed. In 1866, shortly before he died at age 76, von Siebold asserted that "almost a thousand species or varieties of trees or shrubs, herbaceous and bulbous plants from the magnificent flora of this fertile archipelago [Japan] are cultivated in my acclimatization garden [in Leiden]." When two British horticulturists visited von Siebold's former garden site in 1883, they reported—not unexpectedly—that it had been overrun by both *R. japonica* and the giant knotweed (*Raynoutria sachalinensis* (F. Schmidt) Nakai), which had been introduced from northeast Asia into St. Petersburg, Russia, in 1864 (Sharman 1990, Bailey and Conolly 2000, Christenhusz and von Uffelen 2001).

Japanese Knotweed in Britain. Although Japanese knotweed was first sent to England from China around 1825, this early introduction did not flourish and died without being distributed (Lindley and Paxton 1850). In 1850, von Siebold sent an unsolicited shipment of plants—including *R. japonica*—to Kew Gardens in London in hopes that they would reciprocate by sending him some of their newly collected plants from China and Japan. While there is no written record of the fate of von Siebold's Japanese knotweed plant after its arrival, secondary evidence suggests that it was planted in the garden and shared with at least one nursery (Bailey and Conolly 2000). In an article about *R. japonica* from 1867, the famous horticulturist William Robinson noted that "Mr. Standish [Standish & Co. of Ascot] has, I think, a large stock of it, and there is plenty of it at Kew, or used to be." Robinson goes on to take a not so subtle dig at the institution for failing to recognize the ornamental potential of Japanese knotweed: "This is a fine strong herbaceous species of a genus which, as cultivated in our botanic gardens, it does not appear likely to afford an elegant or a graceful subject. But it is one of the best things which I can recommend for their embellishment" (R. 1867).

Once Japanese knotweed had established a beachhead in Britain, its subsequent rapid spread was facilitated by horticultural writers like the

aforementioned William Robinson, who, in the first edition (Robinson 1870) of *The Wild Garden* provided advice for how best to use the plant:

> Siebold's Persicaria. *Polygonum Sieboldii*. Japan. Herbaceous perennial; 4 to 6 feet; yellowish green; summer; division or cuttings.—Isolated specimen near wood or pleasure-ground walks, but most striking in the former position; or associated with the most vigorous herbaceous plants cultivated for the effect of their leaves or habit.

By 1874, with a few more years of experience under his belt, Robinson ramped up his enthusiasm for the ornamental attributes of Japanese knotweed but also warned about its aggressiveness (Robinson 1874):

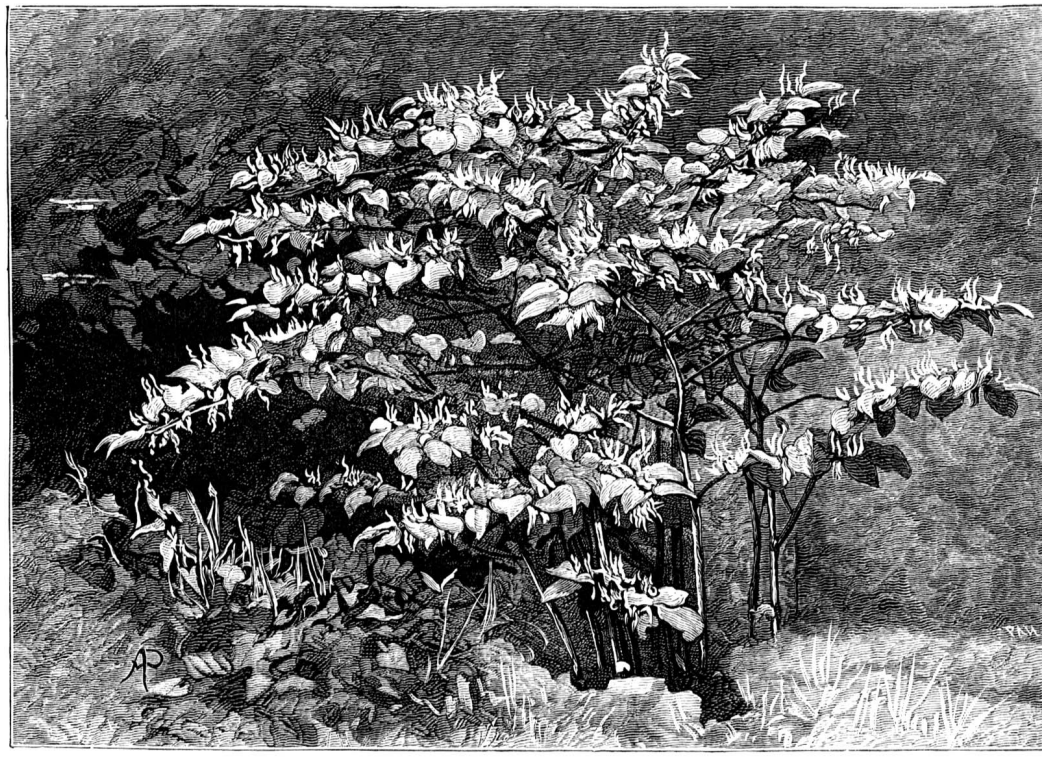
> As I now write, one of our finest and most effective plants, in respect of habit, as well as bloom, is the Japanese Polygonum Sieboldi, sometimes called also cuspidatum; it has this season attained a height of 9 or 10 feet, carrying its foliage from the very base, in fully developed perfection, and now its beautiful branches are pendent in graceful curves, with the weight of the feathery flowers, individually small, and inconspicuous, but in mass and arrangement, the very perfection of beauty. One fault it has is, that it is a sad rambler, so much so, that in a very few years, a single plant would cover half an acre of ground, and it will hold its own with a vigour and persistency that annihilates all competitors.

In the various editions of his books, including *The Wild Garden, The English Flower Garden*, and *The Subtropical Garden*, Robinson's descriptions of Japanese knotweed walked a wavering line between beauty and danger (Fig. 1). He was, quite literally, schizophrenic about the plant: recommending and condemning it simultaneously. It was not until the 1921 edition *The English Flower Garden*—some 54 yr after his first description—that Robinson finally admitted that the plant was "easier to plant than to get rid of in the flower garden; a rank weed" (Robinson 1921).

Remarkably, virtually all of the *R. japonica* currently growing in England (as well as much of northern and central Europe) consists of a vigorously growing female (male-sterile) clone that seldom, if ever, sets seed and reproduces vigorously by means of underground rhizomes. It is now generally agreed that this plant was originally introduced into commerce by Von Siebold & Company in 1848 (Bailey, Bímova and Mandák 2009).

Japanese Knotweed Arrives in America. In contrast to the well-document introduction and spread of *R. japonica* throughout Europe, the details of the plant's arrival in the USA have remained unknown until now. In the course of doing research on the plant introductions of Thomas Hogg, a famous New York City plantsman who sent numerous plants from Japan to America between 1862 and 1875 (Del Tredici 2014, 2017), the author has discovered the earliest known reports of the cultivation of Japanese knotweed in North America. The first article appeared in the March 1868 issue of *American Agriculturist* under the title, "The Japanese Knotweed (*Polygonum cuspidatum*)." The article, which is accompanied by a line drawing of a plant that is clearly producing young fruits (Fig. 2), was written by the journal's editor, the botanist George Thurber. After giving a general description of the genus *Polygonum*, Thurber (1868) goes on to provide the following description:

> We have for some years known a species which is really worth cultivating, but which does not seem to be much disseminated—the *Polygonum cuspidatum*, a native of Japan. It is a perfectly hardy perennial, which throws up branching stem three or four feet high, bearing large oval leaves, which are long pointed at the apex,—hence the name *cuspidatum*. The small white flowers are succeeded by the fruit, or seeds, which being of a pale rose color are more showy than the flowers themselves. Though the flowers individually are small, they are produced in such abundance and have such a graceful droop that the plant is quite showy in flower and fruit, and its effect is heightened by the reddish color of the stems. The plant increases rapidly, and soon forms a large clump, indeed this is its greatest fault, and one which unfits it for use in small borders. It is very effective for planting where there is plenty of room, and it will grow in any soil and situation, even under the shade of trees. It blooms in July and August, and continues for a long time. There is a variegated leaved form



The Great Japan Knotweed (Polygonum cuspidatum).
(Showing the plant in flower.)

Polygonum cuspidatum.—If, instead of the formal character of much of our gardening, plants of bold types similar to the above were introduced along the sides of woodland walks and shrubbery borders, how much more enjoyable such places would be, as at almost every step there would be something fresh to attract notice and gratify the eye, instead of which such parts are generally bare, or given up to weeds and monotonous rubbish.

FIG. 1. *Reynoutria japonica* from the 1881 edition of *The Wild Garden* by William Robinson, illustrated by Alfred Parsons (Robinson 1881).

which is rather curious, but the variegation is not constant.

Four elements of this description distinguish the Japanese knotweed plant that Thurber describes from the von Siebold clone: (a) it bloomed earlier; (b) it produced rose-colored fruits; (c) it grew only three to four feet tall, suggesting it was a dwarf variety; and (d) it produced stems that were reddish in color as opposed to the typical green mottled with purple. While the identity of Thurber's plant cannot be determined with certainty, von Siebold's nursery catalogues from 1856 and 1863 list, without description, the species, *Polygonum pictum* Sieb., that was later (1849) reduced to synonymy with *R. japonica*. Based on limited evidence, Bailey and Conolly (2000) suggested that von Siebold's species *P. pictum* could have been the dwarf early-blooming variety of Japanese knotweed (*R. japonica* var. *compacta* (Hook. f.) Modenke) which grows at high

FIG. 2. Illustration of *Reynoutria japonica* from the George Thurber's article in the March 1868 issue (page 101) of the *American Agriculturist* (Thurber 1868).

elevations on Mt. Fuji, produces hermaphroditic flowers, and is suffused with red pigmentation. If this speculation is correct, then it's reasonable to assume that the plant Thurber described was the *compacta* variety of Japanese knotweed imported from Europe.

The second newly discovered reference to Japanese knotweed in North American appeared in the May 1872 issue of *The Gardener's Monthly and Horticulturist* written by someone identified only as "J.C., Philadelphia." The author begins his article by stating this:

> As this gigantic, hardy perennial has grown for many years in our garden, attaining somewhat extraordinary proportions, the following description may prove to be of interest. It grows in a six feet circular bed on the lawn, and early in April sends up a

> hundred smooth, round, hollow jointed canes of a bright green color, thickly mottled with purple. (J.C. 1872)

He describes the plant's stems and branching pattern in detail and then notes the following:

> . . .at an elevation of over ten feet, it forms a large spreading and arching head, densely clothed with graceful foliage, and late in August crowned with abundant panicles of small white flowers. These in England are succeeded by rosy white seed vessels, but our plant has never born seed. When it has completed its growth, its spreading branches cover a space of over thirty feet in circumference, and its whole appearance is striking and beautiful. To show the great rapidity of its growth, it was found that from the first of April to the beginning of May, it reached the height of nine feet, and on the warmest days in April, its strongest shoots grew from six and a half to seven and a half inches in 24 hours. (J.C. 1872)

The remarkable vigor of J.C.'s plant coupled with the fact that it "has never born seed," strongly suggests he was growing the female clone of *R. japonica* that von Siebold had distributed throughout Europe. Indeed, J.C. mentions von Siebold by name in his concluding statement about the plant:

> One fault it has, and that is, that it sends up a forest of suckers to the distance of twelve feet from the plant, and they are difficult to eradicate. This property of running at the root in all directions just below the soil, has been take advantage of in Japan, according to Von Siebold, for fixing the sand. (J.C. 1872)

When J.C. might have imported his propagule of von Siebold's clone of Japanese knotweed from Europe is impossible to determine, but the size of his clump in 1872—100 stems filling a 2-m-diameter planting bed—suggests that it was probably sometime in the mid-1860s. J.C.'s statement that Japanese knotweed plants growing in England produced "rosy white seed vessels" is hard to make sense of given the dominance of von Siebold's seedless clone in England today, but it's possible he was referring to the self-fertile *R. japonica* var. *compacta* variety that Thurber described, assuming it was more common in the England in the 1860s than it is now.

The third newly discovered article in the saga of Japanese knotweed's introduction into North America appeared in the June 1875 issue of an obscure horticultural publication, *The American Garden*, published in Brooklyn, NY, and edited by Thomas Hogg's older brother James. The author discovered this rare periodical in its alphabetically correct but undocumented location in the stacks of the Frances Loeb Library at the Harvard Graduate School of Design. The article is titled "POLYGONUM CUSPIDATUM" and begins with the sentence: "Seven or eight years ago we [James Hogg] received from Mr Thomas Hogg, in Japan, a beautiful, hardy and striking perennial Buckwheat," a statement which puts the plant's arrival in North America in 1867 or 1868. Hogg goes on to note the following:

> It grows from five to seven feet high, throwing from the ground great, strong shoots. At first it resembles some mammoth Asparagus, but eventually it becomes thickly studded with long, green, horizontal branches, which are striped or washed with rose-color. The leaves are very large, oval or oblong-oval, of a bright green color, and are produced quite thickly on the branches. The flowers, which are produced in large bunches from the axils of the leaves, are small and of a greenish white color. They are succeeded, in September, by an abundance of rose-colored fruits, which give the plant an elegant appearance. The shoots, which are often an inch in diameter, have lately been used in France as a substitute for Asparagus. We have not yet tried them, but intend to do so. Should they prove valuable as a vegetable, the plant will be very desirable for that purpose, as it is of easy cultivation. (Hogg 1875)

There are two important pieces of information in Hogg's article: first, the plant was sent to him by his brother directly from Japan in 1867 or 1868 and second, it produced "rose-colored" fruits. Is it just a coincidence that both Hogg and Thurber mention this distinctive trait, or is it possible that both authors were describing the same plant? The latter explanation is a distinct possibility given that Thurber was a good friend of Hogg's and described visiting his garden on at least three separate occasions in the 1860s (Thurber 1866, 1870, 1878). There are several problems with the idea that both articles were describing the same

plant, the first of which is timing. Hogg states that his plant arrived, at the very earliest, in the winter/spring of 1867, while Thurber's plant was described no later than the fall of 1867. Assuming that the dates in both articles are correct, Hogg's newly arrived plant would have had to grow "three or four feet" in height and flower in its first growing season—a rather unlikely scenario given the small size of the plants Hogg had to ship from Japan. The second problem is that Thurber's plant was described as being three to four feet tall while Hogg's plant was nearly twice that size. Thirdly, George Thurber was a friend and botanical colleague of James Hogg and it seems unlikely that he would have written an article about a plant in Hogg's garden without giving him credit. In light of the above considerations, it seems unlikely that the two plants—despite the fact that they both produced rose-colored fruits—were the same clone.

Hogg (1875) ended his article about Japanese knotweed with this statement:

> Another and very similar species, P. sachalinense [*Reynoutria sachalinensis*] has, within three or four years past, been introduced into Europe from the Amoor river country in Eastern Asia. The leaves are similar in shape to those of P. cuspidatum, but are larger—being from 6 to 8 inches long;—have red footstalks and are traversed by a red mid-rib.

This information, as well as the illustration of "POLYGONUM SACHALINENSE" that accompanied the text, were copied from an earlier article about the species by Eduard Regel (Regel 1874). Hogg gives no indication that giant knotweed was growing in his garden and a review of the horticultural literature of the period indicates that *R. sachalinensis* was probably not introduced into North America until after 1893 (André 1893, Plank 1893).

The Torrey Botanical Club Connection. James Hogg's nursery was located in the Yorkville section of New York City, located on the upper east side of Manhattan near the East River. The nursery had been established in 1822 in lower Manhattan by his father, Thomas Hogg, Sr., who moved it to Yorkville around 1840. James also maintained a large private garden in Yorkville filled with the plants that his brother Thomas Hogg, Jr., had sent him from Japan (Fig. 3). Thomas had been appointed US Marshall to Japan by President Abraham Lincoln in 1862 and served in that position through 1869 when he returned to America. He went back to Japan in 1873 to work as an advisor for the Japanese Customs Service and stayed through the end of 1875. During his first sojourn in Japan, Thomas Hogg mainly collected vegetable seeds and horticultural plants in small containers from Japanese nurseries, which he shipped to his brother in Yorkville. During his second trip, Hogg collected mainly seeds from wild-growing woody plants which he sent to Samuel Parsons' Kissena Nurseries in Flushing, NY (Moring 1893; Del Tredici 2014, 2017).

According to Professor C.S. Sargent, Director of the Arnold Arboretum, writing in 1888:

> More than twenty years ago, Mr. James Hogg began to plant in his grounds at Eighty-Fourth Street and the East River the novelties which his brother Thomas Hogg was then sending from Japan. At one time there were collected here more than 300 species of trees, shrubs, and herbaceous plants, mostly from Japan and China. Most of these were the first specimens of their kind to reach the country, and many were received here some time before their introduction into Europe. (Sargent 1888)

Japanese knotweed was clearly part of James Hogg's plant menagerie in Yorkville and it would undoubtedly have drawn the attention of his many botanical colleagues, including members of the fledgling Torrey Botanical Club, of which James Hogg had been a founding member in 1870 (Cooney 2000). Thomas Hogg became a member of the Torrey Botanical Club in 1882 and served as its vice-president from 1886 until his death in 1892 (Moring 1893). George Thurber was another founding member of the Torrey Botanical Club and served as its second president from 1873 to 1880 following the death of John Torrey on March 10, 1873 (Cooney 2000). The fourth member of the club to play a role in the Japanese knotweed story—and another one of its founders—was a Mr. M. Ruger who served "the chief organizer and leader of the club's excursions" and is now remembered for having collected the earliest known herbarium specimen of *R. japonica* in North America (A.B. 1879, Cooney 2000, Barney 2006).

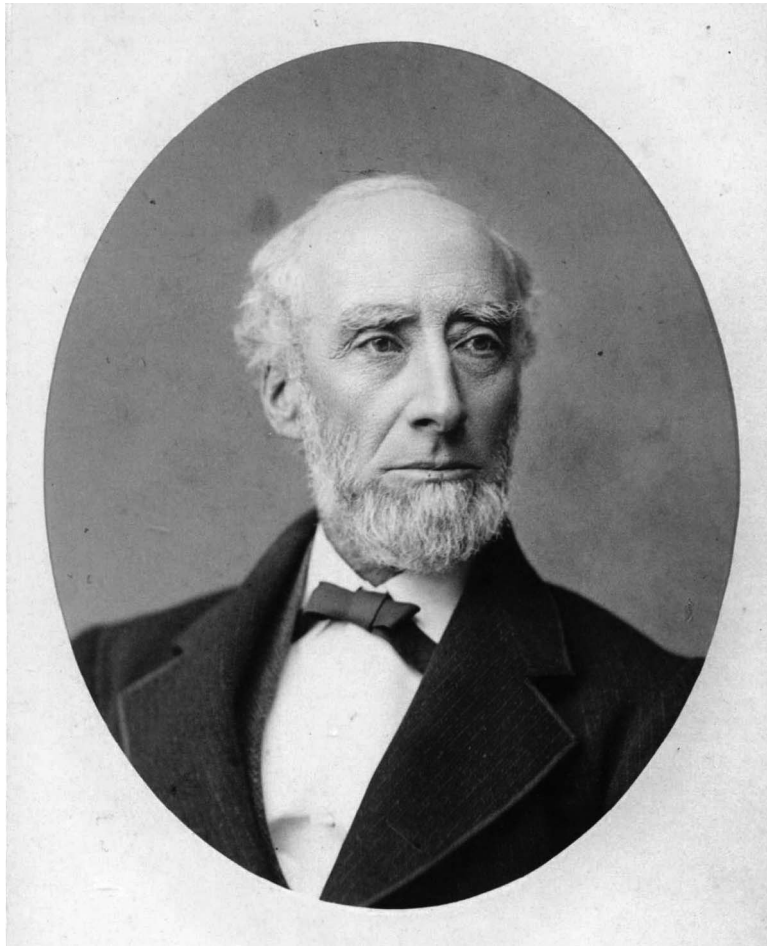


FIG. 3. Photograph of Thomas Hogg, Jr. (circa 1887), courtesy of the LuEsther T. Mertz Library of the New York Botanical Garden.

The label on right-hand side of Ruger's historic *R. japonica* specimen is printed with his name and the collection data reads "*Polygonum cuspidatum*; Cultivated at Yorkville, N. Y. City; Sept. 1873." It is stamped with the number 9693 from the Amherst College Herbarium, but now resides in the Herbarium of the University of Massachusetts, Amherst (Fig. 4). Given that Ruger's Yorkville specimen overlapped James Hogg's cultivation of the plant in both space and time, the unescapable conclusion is that it came from Hogg's garden.

An examination of the specimen by the author under a dissecting microscope revealed a female plant in the early stages of flowering. Many of the flowers have clearly observable ovaries (or very young fruits) up to 2 mm long, topped with glistening stigmas. The few stubby, underdeveloped anthers at the base of the flowers appear to be sterile and show no signs of producing pollen. These observations suggest that the plant Ruger collected his specimen from could only have produced the reported "abundance of rose-colored fruits" if a second, pollen-producing, individual was growing nearby.

In terms of its sexuality, *R. japonica* is generally considered to be either strictly dioecious or gynodioecious, with separate hermaphrodite and male-sterile (female) individuals that require insect pollination in order to produce seed. There are a few reports of male plants setting seed, but this is uncommon and the seed is never abundant. Hermaphroditic individuals are considered self-incompatible and make poor female parents and generally function as male plants (Beerling *et al.* 1995, Forman and Kesseli 2003, Barney *et al.* 2006, Bailey, Bímová and Mandák 2009).

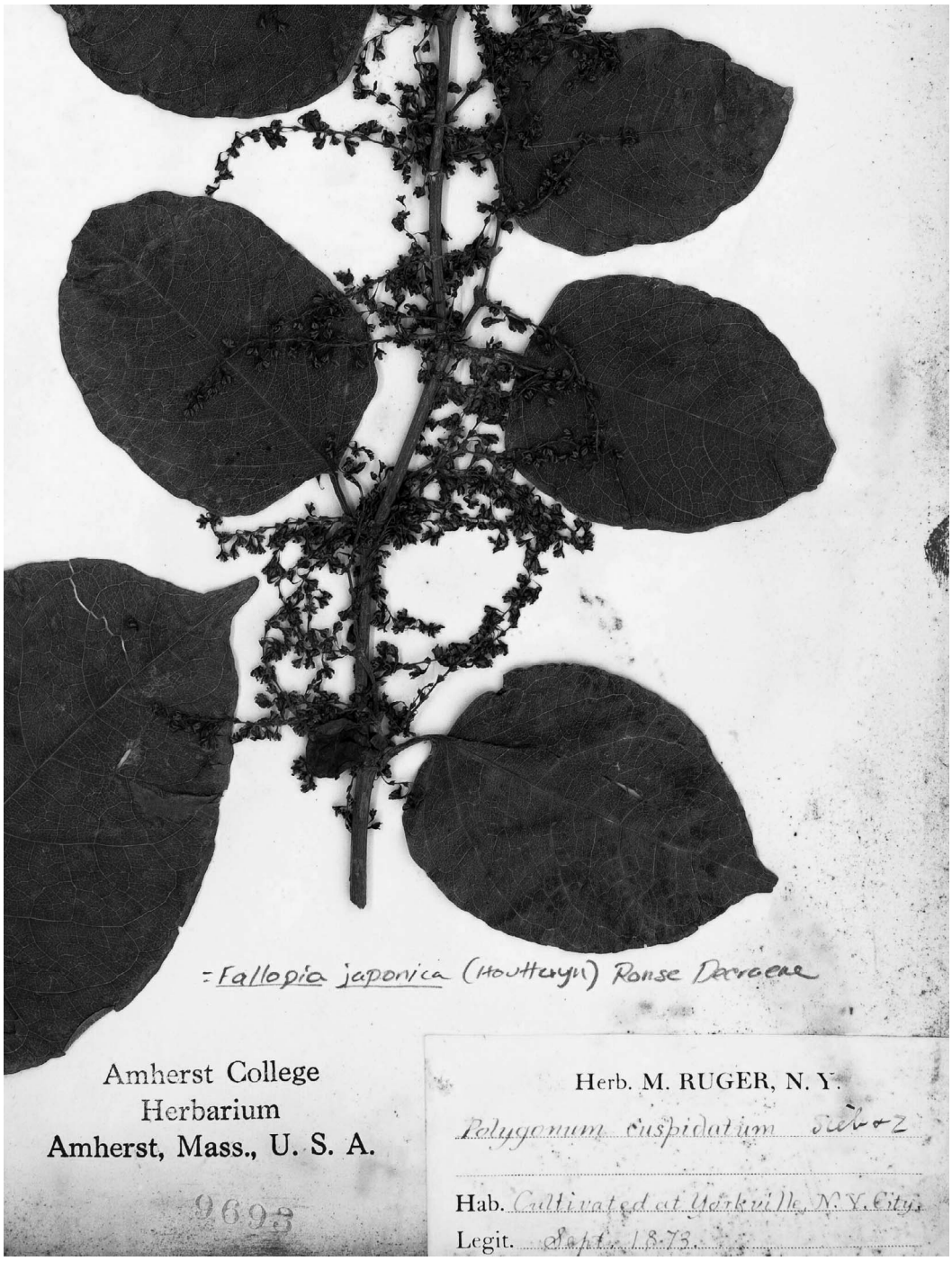


FIG. 4. The lower right-hand quadrat of the earliest known herbarium specimen of *Reynoutria japonica* in North America collected by M. Ruger in September 1873 from the Yorkville garden of James Hogg. Scan courtesy of the Herbarium of the University of Massachusetts, Amherst.

Discussion. Barney (2006) discovered Ruger's historic knotweed specimen while he was documenting the spontaneous spread of *R. japonica* across North America based on the collection dates and locations off herbarium specimens from 273 American and Canadian herbaria. He discovered that relatively few specimens of *R. japonica* were collected prior to 1900, a steady increase in the number of specimens through the 1940s, and a literal explosion of collections in the 1950s and 1960s. Most invasive plants show a clear "lag phase" during which population numbers are low and spread is minimal before population numbers expand rapidly—the so-called "log phase." For *R. japonica* in North America, Barney calculated its lag phase at 50 yr, a relatively short time period best explained by the widespread planting of Japanese knotweed for ornamental and utilitarian purposes in the late 19th and early 20th centuries (Townsend 2000). Indeed, by 1893—roughly 30 yr after its introduction—the horticulturalist E.N. Plank sounded the alarm about Japanese knotweed based on its performance in New York City: "The vigor of this plant will not be doubted by anyone who has seen it growing in the Central Park of this city, where it quickly becomes an aggressive weed."

Studies on *R. japonica* populations in New England (Forman and Kesseli 2003; Gammon *et al*. 2007, 2010; Grimsby *et al*. 2007; Gammon and Kesseli 2010; Grimsby and Kesseli 2010) have shown that the levels of genetic diversity and seedling regeneration are significantly higher than those reported for Europe and western North America, where a single female clone of *R. japonica* is widespread and seed production is rare (Hollingsworth and Bailey 2000, Bailey, Bímová and Mandák 2009, Gaskin et al 2014). If one assumes that seeds from James Hogg's plants were propagated and distributed within northeastern North America, then one has a source of genetically distinct individuals capable of pollinating the von Siebold clone as well as establishing new, fully fertile populations of Japanese knotweed. Such an assumption also provides a credible explanation for why the levels of genetic diversity in both *R. japonica* and its hybrid with *R. sachalinensis* (*R.* × *bohemica* Chrtek & Chrtková) are much higher in New England than they are in both Europe and western North America. The history of Japanese knotweed, as reconstructed in this article, clearly demonstrates how an understanding of the circumstances surrounding the introduction of invasive species can help elucidate the patterns underlying their modern distribution.

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