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Front cover: *Ailanthus altissima*, the tree-of-heaven, in the courtyard of Wuhan Temple, China. Photograph by Peter Del Tredici.

Inside front cover: The first illustration of *Ailanthus altissima* to appear in the West, from a 1788 article by the French botanist René L. Desfontaines. Courtesy of the Archives of the Gray Herbarium.

Inside back cover: Kudzu (*Pueraria lobata*) twines over roadside vegetation in South Carolina. Photograph by Peter Del Tredici.

Back cover: This *Ailanthus altissima*, seen growing in the wall that surrounds the courtyard of Wuhan Temple, also appears in the left corner of the photograph on the front cover.



Amur Honeysuckle, Its Fall from Grace

James O. Luken and John W. Thieret

This account of the history and biology of *Lonicera maackia* explains how and why the plant became so wildly successful as an “exotic invasive.”

Scientists throughout the world are concerned about the apparent homogenization of regional floras being caused by invasive, nonindigenous plant species. A new term for this process, *biological pollution*, has come into use, and removal of nonindigenous plants to protect native species and to maintain the integrity of communities is now a common practice in many parks and nature reserves. However, human activity is an important determinant of the eventual rate and extent of diffusion of a non-native species into a new geographic range, whether the plant was introduced intentionally or accidentally.¹ Therefore, as the time, effort, and resources committed to managing non-indigenous plants increases, a need is emerging for greater understanding of the naturalization process on the part of people who may either facilitate or limit plant invasions, especially since human influences can often be modified by effective policy decisions.

In this article we trace the almost 150-year-long involvement of Western plant scientists with the eastern Asiatic shrub Amur honeysuckle—*Lonicera maackii*, a member of the Caprifoliaceae. The story of Amur honeysuckle parallels that of various other Eurasian deciduous shrubs—for instance, Russian olive (*Elaeagnus angustifolia*), Tatarian honeysuckle (*Lonicera tatarica*), and buckthorn (*Rhamnus cathartica*)—that were introduced for their floral, fruit, and foliage displays but eventually became troublesome.

Less than a century after its deliberate introduction into North America, Amur honeysuckle is growing and reproducing in at least twenty-four states of the eastern United States and in Ontario, Canada.² The plant is perceived

by many resource managers as an undesirable element in parks, natural areas, and preserves: “It would be difficult to exaggerate the weedy potential of this shrub.”³ This perception, however, is not shared by gardeners and horticulturists—W. J. Bean wrote that “[I]t is one of the most beautiful of bush honeysuckles”⁴—and its garden value has encouraged widespread introduction. Such varied and sometimes opposing values must be considered along with ecological data as future management policies for non-indigenous species are debated.

Our case study will address the following questions: How and why was Amur honeysuckle intentionally introduced into cultivation in the United States? What life-history traits of the species contribute to present-day valuations of the species, both positive and negative? To what extent are these differing perceptions reflected in management policies?

The Species

Amur honeysuckle (also known as bush honeysuckle, tree honeysuckle, or Maack’s honeysuckle) is an upright, multistemmed, deciduous shrub that can achieve heights of twenty feet. The leaves are dark green, with a variety of shapes ranging from lance heads to broad ellipses that taper to a slender point. Amur honeysuckle leaves are particularly noticeable in early spring as they open well before those of other plants. Likewise, in autumn this honeysuckle holds its leaves later than its neighboring plants.

In its native range—central and northeastern China, the Amur and Ussuri river valleys of Korea, and isolated parts of Japan—Amur honeysuckle is commonly found on floodplains

The bright red berries of Amur honeysuckle remain on the shrub until January unless removed by birds.



Native and invaded ranges of Amur honeysuckle. Isolated occurrences in Japan are not shown.

and in open woodlands. In the invaded areas of the eastern United States and Ontario, it occurs mostly in urban or urban-fringe landscapes, where it occupies open sites, forest edges, and the interiors of forest patches. Its reproductive characteristics give Amur honeysuckle its greatest appeal. It consistently produces an early spring profusion of white flowers that turn dull yellow with age. Fruit set can be heavy, and the bright red berries remain on the shrubs until January unless removed by birds.

Introducing Amur Honeysuckle in the West

Anecdotal evidence suggests that Amur honeysuckle was cultivated in gardens of China long before European plant hunters discovered the species. In the nineteenth century, these gardens offered many new species to the landed aristocrats of the West who had grown weary of standard cultivars and were eager for novelties. The first herbarium specimen of Amur honeysuckle was collected in 1843 by an English plant

explorer, Robert Fortune, probably from a Chinese garden; but it was specimens collected near the Amur River in 1855 by the Russian plant explorer Richard Maack that served as the basis for eventual description of the species.⁵

Beginning in the late 1800s, European and American plant hunters who exported living plant materials from Asia played a pivotal role in introducing Amur honeysuckle to Western horticulture. A German horticulturist, E. Regel, reported the first successful cultivation of Amur honeysuckle outside its native range, at the Imperial Botanical Garden in St. Petersburg in 1883, using propagules sent from Manchuria in 1880. Regel's 1884 report was soon translated into English and used as the basis for writings on Amur honeysuckle published in Great Britain. It was being cultivated in Germany by 1889 and at the Royal Botanic Gardens at Kew by 1896. The original plants in western Europe probably came from St. Petersburg, which was distributing seeds of Amur honeysuckle as early as 1887.⁶



Basal stems of Amur honeysuckle.



An Amur honeysuckle grown in an open environment.

The St. Petersburg Garden was also the source of the first seeds recorded in the United States, which arrived at the Arnold Arboretum in 1897. The second record of introduction—sent to the New York Botanical Garden by the United States Department of Agriculture—followed by only a year. However, the earliest known report of Amur honeysuckle cultivation in North America is in the archives of the Dominion Arboretum in Ottawa, indicating that plants of Amur honeysuckle were received there in 1896, from Spaeth Nurseries in Germany.⁷

Major botanical gardens, commercial nurseries, and horticultural societies of that time worked together to inform private gardeners about new introductions. During the late 1800s and early 1900s, botanical gardens in Europe maintained active seed-exchange programs and annually published inventories of available seeds. In 1907 and 1915 the plant received awards of merit from the Royal Horticultural Society. Since 1900, it has been described frequently in horticultural literature published in Belgium, France, Germany, Great Britain, and the United States.

Location of garden	Year of listing
St. Petersburg	1887
Cambridge	1913
Oslo	1917
Dublin	1919
Copenhagen	1924
Edinburgh	1924
Amsterdam	1929
Paris	1931

This table gives the year that European botanical gardens first listed Amur honeysuckle in their inventories of seeds available through their exchange programs.

Disseminating Amur Honeysuckle in the United States

In an effort to obtain potentially valuable, cold-resistant varieties of alfalfa, the USDA dispatched an agricultural explorer, Niels E. Hansen, to Russia in 1897. Hansen unilaterally expanded his charge and began shipping seeds of many other species to Washington, D.C. His seed packets began arriving at the same time that a new unit within the USDA, the Section of Foreign Seed and Plant Introduction (SPI), was being funded and organized. Amur honeysuckle seeds gathered in Russia by Hansen and received in 1897 were among the first seeds catalogued by the SPI.⁸

The SPI facility in Washington, D.C., served as a center for distributing seeds to commercial growers, botanical gardens, and private individuals throughout the United States. Seed distributions were designated as "Plant Introduction Experiments," and it was assumed that recipients would report back to the SPI regarding their success or failure with the seeds. Indeed, the 1898 introduction of Amur honeysuckle to the New York Botanical Garden was a Plant Introduction Experiment. The results of this introduction are not known, but almost certainly it was successful, considering the ease with which the species can be propagated.

The SPI's records indicate that its facility received at least seven shipments of Amur honeysuckle between 1898 and 1927. (This represents a minimal number of shipments because imported honeysuckles were often not identified as to species.) These importations originated at botanical gardens in Great Britain or were collected in Manchuria by agricultural explorers working for the USDA. Clearly the Amur honeysuckle now naturalized in the United States represents a variety of genotypes, although the specific geographical range over which these genotypes were collected is not known. The SPI's introduction effort was successful: In 1931, the species was available from at least eight commercial nurseries throughout the country.⁹

From the 1960s to 1984, the USDA Soil Conservation Service (SCS; now known as the Natural Resource Conservation Service) sponsored a program to develop improved cultivars of Amur

honeysuckle. These plants were intended for the traditional SCS functions—soil stabilization and reclamation—as well as improving habitat for birds and serving as ornamental landscape plantings.

Five introductions occurred during this period. From plants already naturalized in various parts of the United States, specimens were selected for more abundant fruit production, propagated vegetatively, and then cultivated at centers for plant materials around the country. Occasionally the SCS would make seedlings available to other government agencies involved in reclamation work. Although Amur honeysuckle did not prove particularly useful for soil stabilization, the ease of harvesting its seeds mechanically and the high survivability of seedlings after cold storage facilitated its distribution and establishment in large reclamation projects. In addition, the consistently high flower and fruit production of Amur honeysuckle proved well suited for wildlife habitat improvement. More commonly, however, seeds were made available on request to commercial nurseries and the resulting plants were sold to private individuals. The most successful of these cultivars, 'Rem-Red', is still recommended by the SCS (now the NRCS) and is commercially available.¹⁰

Escape of the Amur Honeysuckle

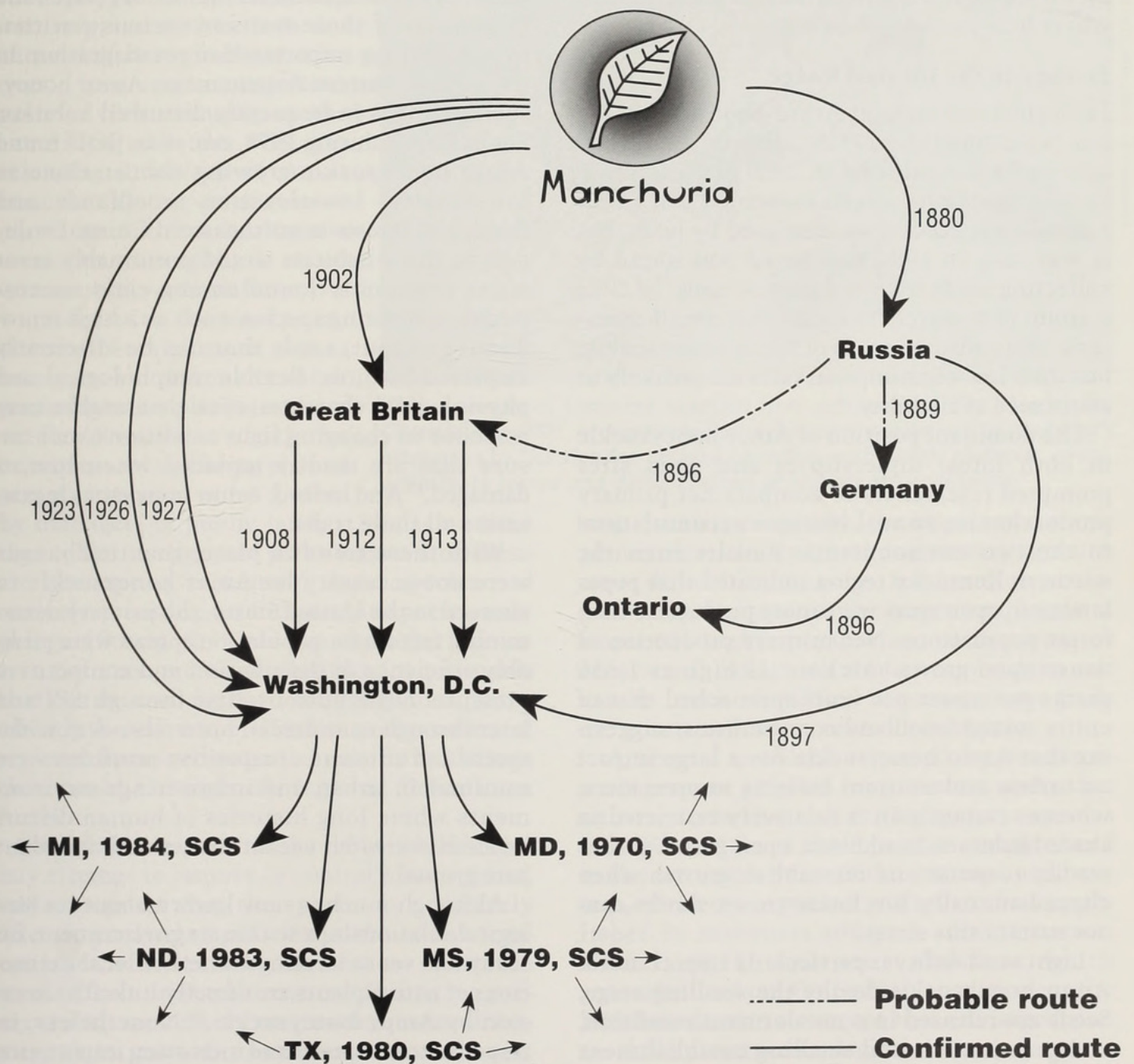
The first record of Amur honeysuckle's tendency to spread beyond the point of initial planting is found in the archives of the Morton Arboretum, near Chicago, and dates from the mid-1920s. In spite of this early warning, the Morton Arboretum was still touting the virtues of the plant more than a decade later. Evidence of naturalized populations did not begin to appear until the late 1950s, continuing through the early 1970s. These initial reports were harbingers of the invasion to come. For example, Lucy Braun, in her 1961 book on Ohio woody plants, noted that the Amur honeysuckle was "reported only from Hamilton County, where it is becoming abundant in pastures and woodlands." Thirty-three years later the species was reported in thirty-four Ohio counties.¹¹

The relative delay between first introduction (1897) and widespread escape (1950s) of Amur

honeysuckle was to be expected for a plant with its life-history traits and mode of introduction. First, it is a long-lived woody plant that does not produce fruit until it is three to five years old and, therefore, will increase slowly compared to an annual plant. Second, during this earlier period (1898–1950s) Amur honeysuckle was typically used in small quantities in landscape plantings, so the area of subsequent spread was for some time more limited than would be the case with annual weeds, which often con-

taminate crop seed and are thereby disseminated quickly.

In Europe, Amur honeysuckle has been intensively cultivated longer than in the United States, but no naturalization has been reported. Fruit production by the species, at least in western Europe, seems to be less regular and abundant than in eastern North America. Although the first report of Amur honeysuckle flowering in eastern Europe (in St. Petersburg in 1883) mentioned the "sanguineous" fruit, early west-



Pathways and dates of Amur honeysuckle introduction to Europe and North America. "SCS" indicates release of improved cultivars by the U.S. Department of Agriculture Soil Conservation Service.

ern European notes included data on flowers only, or remarked on lack of fruit development. Not until approximately two decades after the shrub's introduction into England were the fruits described in British horticultural literature. Even as late as 1934, the merits of the plant as a fruiting shrub were said to be not well known in England, although "in warm seasons and on certain soils" fruiting could be abundant.¹² Western European regions apparently lack certain environmental conditions shared by the eastern United States and eastern Asia, where fruit production is heavy.

Ecology in the Invaded Range

Ecological research on Amur honeysuckle did not begin until the 1980s, after the plant had achieved a critical level in local plant communities.¹³ Earlier reports had assumed that Amur honeysuckle seeds were dispersed by birds, but it was only in 1983 that proof was found by collecting seeds from the guts of birds. In 1992 a group of researchers found that small mammals also consume seeds of Amur honeysuckle, but their low consumption rates are unlikely to affect seed availability.¹⁴

The dominant position of Amur honeysuckle in both forest understories and open sites prompted researchers to compare net primary production (or annual biomass accumulation) in the two environments. Results from the northern Kentucky region indicated that populations in open areas were more productive than forest populations. Net primary production of dense open-grown thickets (as high as 1,350 grams per meter per year) approached that of entire mixed woodland communities, suggesting that Amur honeysuckle has a large impact on carbon and nutrient budgets in open sites, whereas carbon gain is relatively restricted in shaded habitats. In addition, open-grown shrubs readily resprout and reestablish growth when clipped annually, but forest-grown shrubs cannot sustain this stress.¹⁵

Light availability is particularly important for Amur honeysuckle during the seedling stage. Seeds are released in a nondormant condition, and germination and seedling establishment may occur year-round, with a distinct increase in activity during relatively warm, wet periods

in winter and early spring. However, seedling growth in forests is severely curtailed by low light conditions, which inhibit production of the long shoots that enable seedlings to reach better light environments. Even as adults, Amur honeysuckle shrubs are moderately shade intolerant and are not likely to replace themselves in shady environments unless past disturbances create a window of opportunity.¹⁶

The success of Amur honeysuckle in a wide range of habitats and light conditions has logically led to research on its life-history traits, the expression of those traits in various environments, and the importance of preadaptation. In its original, eastern Asiatic range, Amur honeysuckle thrives in frequently disturbed habitats. For example, during 1994, one of us (JOL) found Amur honeysuckle growing almost alone in low-density, low-elevation woodlands and floodplain forests in northeastern China. Evolution in these habitats would presumably favor traits commonly found among early successional, colonizing species, such as a high reproductive output, seeds that can be efficiently dispersed by birds, flexible morphological and physiological characteristics that enable easy response to changing light conditions, and tissues that are readily replaced when lost or damaged.¹⁷ And indeed, Amur honeysuckle possesses all these traits.

With these traits in place, genetic changes were not necessary for Amur honeysuckle to succeed in the United States; the primary determining factors for population spread were probably efficiency of distribution and competitive pressure. Distribution—first through SPI and later through commercial nurseries—was widespread and efficient; competitive pressures were minimal in urban and urban-fringe environments where long histories of human disturbance had created vacant niches and abundant bare ground.¹⁸

Although much is now known about its biological relationships within its environment, no study has yet determined whether local extinctions of native plants are directly linked to invasion by Amur honeysuckle.¹⁹ Nonetheless, in response to its spread and increasing importance in various plant communities, the Illinois Department of Conservation adopted a policy in

1989 that made its use unacceptable in that state, and many methods have been developed for eliminating this species from natural areas.²⁰

Lessons for the Future

Considering the varied functions that scientists envisage for the new cultivars they develop and the differing values that people hold regarding nature preservation, it is not surprising that conflicts arise over resource-management policies. For example, at the same time that the SCS was releasing cultivars of Amur honeysuckle for conservation plantings and horticulturists were recommending it as an ornamental, various botanists were decrying its weedy tendencies. Furthermore, Amur honeysuckle and many other nonindigenous plants—crown-vetch (*Coronilla varia*), for example—are still being planted across large areas of land, often by managers of public land, at the same time that other managers of parks and natural areas are attempting to control these species and actively pursuing an indigenous-species-only policy. Clearly, the time has come for innovative policies and multidisciplinary protocols that can be used for both nonindigenous plants already firmly established as components of regional floras and potential new introductions that could homogenize regional floras even further.

Sound science, which should be the basis for any attempt to remove or control plant species, requires proof that the species is negatively affecting management efforts in natural communities, whether the goals of those efforts are to establish presettlement conditions, to preserve rare species, to maximize species diversity, or to maintain patterns of disturbance. However, unlike the effect of a weed in agricultural plots, which can be measured in terms of



This drawing of *Lonicera maackii* first appeared in *The Gardeners' Chronicle* in 1907, accompanied by a description attributing the plant's attraction to "its slender, arching branches with nearly glabrous, ovate, acuminate leaves and dense clusters of creamy-white flowers."

crop quantity or quality, the impact of a single plant species in a natural community is much more difficult to measure. Furthermore, ecologists may disagree on the important levels of impact (whether population, community, or ecosystem). Still, such studies can be done and can be much simplified if management goals are prioritized before research is begun.

A special problem is posed by resource-management policies for preserves and other natural areas that call for indigenous species only. The origin of these policies can be traced to the formative years of our national park system, when conservation goals were first established by scientists and park administrators. Underlying the goals set at that time, which generally used pre-Colombian conditions as the benchmark, was a concept that envisaged successfully preserved ecological systems as assemblages of native species that were balanced, stable, and free of human influence. However,

achievement and maintenance of the pre-Colombian benchmark has become increasingly difficult, if not impossible, because the disturbances that operated historically in natural areas have been suppressed or altered and the contexts in which species compete have been changed.²¹

Some researchers have devised a new paradigm for conservation that recognizes the dynamic nature of all ecological systems.²² This paradigm does not call for nonindigenous plants to be eliminated from biological communities simply because they were not present in the past. Instead, they would be evaluated on the basis of their roles in ecological processes. In addition, as ecologists Hobbs and Huenneke rightfully pointed out in 1992, certain management activities that attempt to modify ecological processes for the benefit of indigenous species, such as prescribed burning to stimulate seed germination, may at the same time facilitate invasion by nonindigenous plants. Resource managers may therefore need to choose from a menu of conservation goals; some of these goals may call for inclusion of nonindigenous species while others call for their elimination.

Increased effort should be devoted to studying the interactions between indigenous and nonindigenous species and the functional roles that nonindigenous species now play in biological communities with long histories of human influence. For example, Schiffman found that endangered giant kangaroo rats (*Dipodomys ingens*), indigenous to California grasslands, facilitate colonization and dispersal of nonindigenous plants by creating bare ground and dispersing seeds. Indeed, "eradication of [these] exotic plants would probably have a significant negative impact on populations of this endangered species."²³ Amur honeysuckle, to give another example, achieves its greatest dominance in heavily disturbed, urban landscapes. The impact of the species in these systems is not well understood, but it is possible that valuable ecological functions—nutrient retention, carbon storage, animal habitat improvement—are served by Amur honeysuckle in the absence of indigenous species or when niches are unfilled.²⁴ Assessing the function of non-

indigenous species in urban landscapes and surrounding areas is likely to require the kind of large-scale research that is now mostly limited to pristine systems.

Finally, careful examination of the life-history traits of the thousands of plants that have been accidentally or intentionally introduced, coupled with an analysis of when, where, and if these species have naturalized, would be a useful exercise. Such an analysis would likely have some predictive value when new introductions are proposed or when new cultivars are being developed.²⁵ Attention should focus on seed production and germination, as suggested by the case of Amur honeysuckle as well as by a 1985 survey of other plants that eventually became problem weeds and by a rating system for management of nonindigenous plants established in 1993.²⁶ Species with high and consistent seed output, poorly developed seed dormancy, rapid germination, and the ability to germinate at low temperatures and low light may be most likely to spread rapidly across a wide range of habitats. Since the proportion of all introduced horticultural species and cultivars that have naturalized is small (usually about one percent) and eventually become components of our regional floras, the goal of such a screening process would not be to drastically reduce plant introductions but to lessen the risk of future problems.

Endnotes

¹ Mack 1985.

² Trisel and Gorchov 1994.

³ Swink and Wilhelm 1994, 474.

⁴ Bean 1973.

⁵ Bretschneider 1898, Herder 1864.

⁶ Regel 1884, Thatcher 1922, Anonymous 1884a, b, Dippel 1889, Royal Gardens Kew 1898, Imperial Botanic Garden 1887.

⁷ Rehder 1903.

⁸ Fairchild 1938, USDA 1899.

⁹ Farrington 1931.

¹⁰ Sharp and Belcher 1981, Belcher and Hamer 1982, Gaffney and Belcher 1978, Lorenz et al. 1989.

¹¹ Kammerer 1939, Braun 1961, Pringle 1973, Trisel and Gorchov 1994.

¹² Anonymous 1934.



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