Amur Honeysuckle, Its Fall from Grace

Lessons from the introduction and spread of a shrub species may guide future plant introductions

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Scientists throughout the world are concerned about the appar-ent homogenization of regional floras due to exchange and introduction of nonindigenous plant species. A new term for this process, biological pollution, has come into use. Removal of nonindigenous plants to protect native species and to maintain the integrity of typal communities is now a common practice in many parks and nature reserves. As more time, effort, and resources are committed to management of nonindigenous plants, there is an emerging need for greater understanding of the values and actions of the various people who may, through time, facilitate or limit plant invasions. For intentionally or accidentally introduced plant species, interactions with people are important determinants of eventual areal extent and rate of spread in the new geographic range (Mack 1985). Moreover, these anthropic factors may also be easily modified by effective policy decisions.

In this article, we present a chronology of events documenting nearly 150 years of interaction between western plant scientists and the east-

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The introduction history of Amur honeysuckle reveals many interactions between humans and the plant

ern Asiatic shrub Amur honeysuckle—Lonicera maackii (Rupr.) Herder; Caprifoliaceae. The story of Amur honeysuckle parallels that of various other Eurasian deciduous shrubs (e.g., Russian olive, Elaeagnus angustifolia; Tatarian honeysuckle, Lonicera tatarica; and buckthorn, Rhamnus cathartica) that were originally introduced for their floral, fruit, and foliage displays but became problems.

Within less than a century after its deliberate introduction into North America, Amur honeysuckle is growing and reproducing in at least 24 states of the eastern United States and in Ontario, Canada (Figure 1; Trisel and Gorchov 1994). The plant is perceived by many resource managers as an undesirable element of parks, natural areas, and preserves: "It would be difficult to exaggerate the weedy potential of this shrub" (Swink and Wilhelm 1994, p. 474). This perception, however, is not shared by gardeners and horticulturists: "[I]t is one of the most beautiful of bush honeysuckles" (Bean 1973, p. 611). Its garden value has contributed to widespread introduction. Such varied and sometimes competing values regarding nonindigenous species must be considered as future management policies are debated.

Through the use of a historical chronology we address the following questions: Why and how was Amur honeysuckle intentionally introduced into cultivation? What lifehistory traits of the species contribute to both positive and negative interactions with humans? How have the different perceptions of Amur honeysuckle created divergent management policies? This case-study approach demonstrates that anthropic factors as well as ecological data must be considered in the development of management policies for nonindigenous plants.

The species

Amur honeysuckle (also known as bush honeysuckle, tree honeysuckle, or Maack's honeysuckle; Figure 2) is an upright, multistemmed, deciduous shrub that can achieve heights of 6 m. The leaves are dark green. with a variety of shapes ranging from lance heads to broad ellipses that taper to a slender point. The leaves are particularly noticeable in early spring throughout the invaded range because Amur honeysuckle leaf expansion occurs well before that of other plants (Trisel and Gorchov 1994). Likewise in autumn, this honeysuckle holds its leaves later than its community associates.

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In the native range—central and northeastern China, the Amur River and Ussuri River valleys, Korea, and isolated parts of Japan (Figure 1) the species is commonly found in floodplains and as a component of open woodlands. In the invaded range—eastern United States and Ontario—Amur honeysuckle occurs mostly in urban or urban-fringe landscapes, where it successfully occupies open sites, forest edges, and interiors of forest patches.

The reproductive characteristics of this species have the greatest appeal. In both native and invaded habitats, Amur honeysuckle consistently produces an early spring profusion of white flowers that turn dull yellow with age. Fruit set (Figure 2c) can be heavy. The bright red berries, unless removed by birds, remain on the shrubs until January.

Botanical gardens and commercial nurseries

Anecdotal evidence suggests that Amur honeysuckle was cultivated in gardens of China long before European plant hunters described the species (Bretschneider 1898). Indeed, these gardens, which held plants highly valued by Chinese horticulturists, 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 by plant explorer Robert Fortune in 1843, probably from a Chinese garden (Bretschneider 1898). Specimens collected later near the Amur River in 1855 by the Russian plant explorer Richard Maack served as a basis for eventual description of the species (Herder 1864).

Beginning in the late 1800s, European and US plant hunters intent on export of living plant materials from Asia played a pivotal role in the introduction of Amur honeysuckle to horticulture. Because of its floral and fruit display, the species was widely collected (Figure 3). The first successful cultivation outside of the native range occurred in Russia at the St. Petersburg Botanical Garden in 1883 (Regel 1884) with propagules sent from Manchuria in



Figure 1. Native and invaded ranges of Amur honeysuckle. Isolated occurrences in Japan are not shown.

1880 (Thatcher 1922). Regel's 1884 report was soon translated and used as the basis for publications on Amur honeysuckle in Great Britain (Anonymous 1884a, b). Within ten years, detailed morphological data obtainable only from living plants (Dippel 1889) indicated successful cultivation in Germany; the Royal Botanic Gardens at Kew reported cultivation in 1896 (Royal Gardens Kew 1896). These first plants in western Europe probably came from St. Petersburg, which was distributing seeds of Amur honeysuckle as early as 1887 (Imperial Botanic Garden 1887).

The earliest North American notice of Amur honeysuckle cultivation we have located is in archives of the Dominion Arboretum, Ottawa, which recorded that plants of Amur honeysuckle were received there in 1896¹ from Spaeth Nurseries in Germany (Figure 3). The first US record is in archives of the New York Botanical Garden, indicating that seeds of Amur honeysuckle were received there in 1898² as part of a US Department of Agriculture (USDA) experiment. In 1903, the Arnold

²Bruce K. Riggs, 1994, personal communication. New York Botanical Garden, Bronx, NY. Arboretum at Harvard University (Rehder 1903) reported successful cultivation of the species.

Major botanical gardens of that time period, commercial nurseries, and horticultural societies worked together to keep private gardeners informed 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 (Table 1). In 1907 and 1915 the plant received awards of merit from the Royal Horticultural Society (Floral Committee 1908, 1916). Since 1900, it has been frequently described in horticultural literature published in Belgium, France, Germany, Great Britain, and the United States.

Table 1. Seeds of Amur honeysuckle were first listed in the following years by botanical gardens,

Year of listing
1887
1913
1917
1919
1924
1924
1929
1931

¹Trevor Cole, 1994, personal communication. Dominion Arboretum, Ottawa, Ontario, Canada.



Figure 2. Amur honeysuckle in northern Kentucky. (a) Basal stems. (b) Growth form in an open environment. Shrub height is approximately 2.5 m. (c) Fruiting branch.

Section of Foreign Seed and Plant Introduction

In an effort to obtain new, potentially valuable plants that could be grown by farmers, USDA dispatched an agricultural explorer, Niels E. Hansen, to Russia in 1897. Hansen was sent to search for cold-resistant alfalfa varieties, but he unilaterally expanded his charge and began shipping seeds of many different species to Washington, DC. Hansen's seed packets began arriving at the same

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time a newly organized unit within USDA, the Section of Foreign Seed and Plant Introduction (SPI), was funded and organized (Fairchild 1938). Amur honeysuckle seeds gathered in Russia by Hansen and received in 1897 were among the first seeds catalogued by SPI (USDA 1899).

The SPI facility in Washington, DC, 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"; it was assumed that seed recipients would report back to SPI regarding success or failure with the plants. Indeed, the first introduction of Amur honeysuckle in the United States resulted from a Plant Introduction Experiment where seeds were sent from Washington, DC, to the New York Botanical Garden. The results of this first introduction are not known, but almost certainly it was successful, considering the ease with which the species can be propagated.

Records from SPI indicate that Amur honeysuckle was imported from foreign countries and released at least seven times from 1898 to 1927 (Figure 3). These plants or seeds originated at botanical gardens in Great Britain or were introduced from Manchuria by agricultural explorers working for USDA. Thus it is clear that Amur honeysuckle as now naturalized in the United States represents a variety of genotypes, but the specific geographic range over which these genotypes were collected is not known. The seven introductions that occurred from 1898 to 1927 represent a minimal number because imported honeysuckles were often not identified to species. This introduction effort was successful: In 1931, the species was available from at least eight commercial nurseries throughout the United States (Farrington 1931).

The Soil Conservation Service

From the 1960s to 1984 (Figure 3), the USDA Soil Conservation Service (SCS; now known as the Natural Resource Conservation Service) sponsored a program to develop improved cultivars of Amur honeysuckle. Five introductions occurred during this period. These plants were intended to be used by property owners or others to achieve the traditional SCS goals (soil stabilization and reclamation), to improve habitat for birds, and to serve ornamental functions in landscape plantings. The consistently high flower and fruit production of Amur honeysuckle suited it well for wildlife habitat improvement. Although Amur honeysuckle was not shown to be unique in terms of soil stabilization, ease of mechanical seed harvest (Belcher and Hamer 1982) and high survivability of seedlings after cold storage (Gaffney and Belcher 1978) facilitated plant distribution and establishment in large reclamation projects.

From plants already naturalized in various parts of the United States, genotypes were selected for more abundant fruit production, propagated vegetatively, and then cultivated in seed production blocks at various plant materials centers around the country (Sharp and Belcher 1981). Occasionally SCS would germinate seeds and make seedlings available to other government agencies involved in reclamation work. More commonly, however, seeds were made available by request to commercial nurseries, and the resulting plants were sold to private individuals. The most successful of these cultivars, called Rem-Red, is still recommended by SCS (Lorenz et al. 1989) and is commercially available.

Escape

The tendency of Amur honeysuckle to reproduce and spread beyond the point of initial planting was first recorded in archives of the Morton Arboretum near Chicago in the mid-1920s.³ In spite of this early warning, the Morton Arboretum was still touting the virtues of the plant more than a decade later (Kammerer 1939). Evidence of naturalized populations did not begin to appear until the late 1950s, and it continued to

³Floyd A. Swink, 1994, personal communication. Morton Arboretum, Lisle, IL.

be reported through the early 1970s (Braun 1961, Dirr 1977, Pringle 1973). These initial reports were harbingers of the invasion to come. For example, Lucy Braun (1961), in her book on Ohio woody plants, noted 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 34 Ohio counties (Trisel and Gorchov 1994).

The relatively long time period between first introduction (1898) and widespread escape (1950s) for Amur honeysuckle is common among biological invasions (Mack 1985). The delay may be explained in terms of life-history traits and the mode of introduction. First, Amur honeysuckle is a long-lived woody plant that does not produce fruit until shrubs are three to five years old. Therefore, the rate of population increase relative to an annual plant would be expected to be slow. Second, introduction of Amur honevsuckle would typically occur as a result of a few individuals placed in landscape plantings. Foci for subsequent spread would be limited compared with annual weeds, which often contaminate crop seed and are thereby widely distributed (Mack 1985).

Amur honeysuckle has been intensively cultivated in Europe longer than in the United States with no reported naturalization. Fruit production by the species seems to be less regular and abundant in at least western Europe than it is in eastern North America. Although the first report of flowering of Amur honeysuckle in eastern Europe (St. Petersburg in 1883; Regel 1884) mentioned the "sanguineous" fruit, early western European notes included data on flowers only (e.g., Belgium [Anonymous 1909], France [Mottet 1907], Germany [Purpus 1900], and Great Britain [Anonymous 1907]) or remarked on lack of fruit development (e.g., Germany [Dippel 1889]). Not until approximately two decades after the shrub's introduction into England were the fruits described in British horticultural literature (e.g., Anonymous 1917). Even as late as 1934 in England (Anonymous 1934), the merits of



Figure 3. Pathways and dates of Amur honeysuckle introduction to Europe and North America. SCS = release of improved cultivars by the US Department of Agriculture Soil Conservation Service.

the plant as a fruiting shrub were said to be not well known, although "in warm seasons and on certain soils" fruiting could be abundant. Western European regions apparently lack the environmental correspondence that exists between 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 achieved some critical level of importance in local plant communities (e.g., McClain and Anderson 1990, Yost et al. 1991). Bird dispersal of Amur honeysuckle seeds was assumed by some earlier publications (e.g., Dirr 1977), but it was only in 1983 (Ingold and Craycraft 1983) that seeds were collected from the guts of birds. Williams et al. (1992) found that small mammals consumed some seeds of Amur honeysuckle, but the low consumption rates were not likely to limit seed availability. Dominance

of forest understories and open sites by Amur honeysuckle prompted research to estimate net primary production. Results from the northern Kentucky region indicated that opengrown populations were more productive than forest-grown populations. Net primary production of dense open-grown thickets (maximal production 1350 g • $m^{-2} \bullet yr^{-1}$) approached that of entire woodland communities (Whittaker 1975), suggesting that Amur honeysuckle has a large impact on the carbon and nutrient budgets of invaded sites (Luken 1988). Open-grown shrubs readily resprout and reestablish growth when clipped annually, but forest-grown shrubs cannot sustain this stress (Luken and Mattimiro 1991), suggesting that carbon gain in shaded habitats is relatively restricted.

The success of Amur honeysuckle throughout a wide range of habitats and light environments logically leads to research that focuses on the life-history traits, the expression of these traits in various environments,

and the importance of preadaptation. In its original, eastern Asiatic range, Amur honeysuckle naturally thrives in frequently disturbed habitats. For example, during 1994, one of us (JOL) found Amur honeysuckle growing almost exclusively in thin, low-elevation woodlands and floodplain forests of northeastern China. Evolution in these habitats would presumably favor traits commonly found among early successional, colonizing species (Bazzaz 1986). Indeed, Amur honeysuckle has high reproductive output (Luken and Mattimiro 1991), its seeds are efficiently dispersed by birds (Ingold and Craycraft 1983), its morphology and physiology are relatively plastic in response to changing light availability (Luken 1988, Luken et al. 1995, in press), and its tissues are readily replaced when lost or damaged (Luken and Mattimiro 1991).

With these traits in place, genetic reorganization was not necessary; the primary limiting factors for population spread were probably distribution efficiency and competitive pressure. Distribution was widespread and efficient through SPI and then commercial nurseries; competitive pressures were relaxed in the largely urban and urban-fringe environments where long histories of human disturbance have created vacant niches and abundant bare ground (e.g., Yost et al. 1991).

The major limitation to growth and population spread of Amur honeysuckle is light availability operating at the seedling stage. Seeds are released in a nondormant condition (Luken and Goessling 1995). In the field, seed germination and seedling establishment may occur year-round with a distinct pulse during relatively warm, wet periods in winter and early spring.4 However, seedling growth in forests is severely curtailed by low light conditions; increase in growth occurs up to full sun conditions (Luken et al. 1995). Production of long shoots, the primary mechanism that allows seedlings to reach increased height and improved light environments, is also limited by low light conditions (Luken et al. in press). As such,

Amur honeysuckle is moderately shade intolerant; adult shrubs are not likely to show self-replacement unless disturbances radically improve light availability.

Although much is now known about the autecology of Amur honeysuckle, no definitive study has yet been done to determine if invasion by the species is directly linked to local extinction of native plants (see however Luken 1990, Trisel and Gorchov 1994). However, in response to Amur honeysuckle's spread and increasing importance in various plant communities, the Illinois Department of Conservation adopted a policy in 1989 that no uses of Amur honeysuckle are acceptable in that state (Harty 1993). Furthermore, many prescriptions are now available for eliminating this species from natural areas (Nyboer 1992).

Lessons for the future

Considering the varied functions that scientists strive to develop in plants and the different values that people hold regarding nature preservation, it is not surprising to observe conflicts when resource-management policies emerge. For example, at the same time that SCS was releasing cultivars of Amur honeysuckle for conservation plantings and horticulturists were recommending the species as an ornamental, various botanists were decrying its weedy tendencies. Furthermore, Amur honeysuckle and many other nonindigenous plants (e.g., crownvetch, Coronilla varia) are currently seeded and planted across large areas of land, while managers of parks and natural areas attempt to control these species and actively pursue an indigenous-species-only policy. Clearly, the arena is set for innovative, multidisciplinary policies that can be applied to nonindigenous plant species already firmly established as components of regional floras and to future introductions that could homogenize regional floras even further.

Sound science should be the basis of any attempt to remove or control plant species. Specifically, if the term *weed* is borrowed from agriculture and then applied to plants growing

in natural communities, then a demonstration of negative impact on the management goal (e.g., establishment of presettlement conditions, preserving rare species, maximizing species diversity, and maintaining patch dynamics) in natural communities is required. Contrary to agricultural systems where weed impact can be measured in terms of impact on 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 (i.e., population, community, or ecosystem). Still, such studies can be done (e.g., Vitousek 1986) and can be much simplified if prioritized management goals are known at the start of research.

A special problem is posed by resource-management policies in natural areas and preserves that call for indigenous species only. Origins of this policy can be traced to the formative years of our national park system when management goals were established by scientists and park administrators (Grinnell and Storer 1916, McClelland 1993). Generally, the concept of successfully preserved nature that emerged from the national parks was one that used pre-Colombian conditions as the benchmark. This benchmark framed ecological systems as assemblages of native species that were balanced, stable, and free of human influence (Luken 1994). Achievement and maintenance of the pre-Colombian benchmark becomes increasingly difficult if not impossible because historical disturbance regimens no longer operate and the background of available species is changed (Hobbs and Huenneke 1992).

Within a new paradigm for conservation that recognizes the dynamic nature of all ecological systems (Pickett et al. 1992), nonindigenous plants would not be eliminated from biological communities simply because of their historical absence. Instead, they would be evaluated based on their functional roles in ecological processes. Hobbs and Huenneke (1992) rightfully pointed out that management activities aimed at modifying certain ecological processes (e.g., pre-

⁴James O. Luken and Linda Kuddes, 1995, unpublished data.

scribed burning to stimulate seed germination of indigenous species) may indeed facilitate invasion by nonindigenous plants. As such, resource managers may need to choose from a menu of conservation goals; some of these goals may call for inclusion of nonindigenous species, while others may call for elimination of these species (Hobbs and Huenneke 1992).

Increased efforts should be devoted to the study of emerging interactions between indigenous and nonindigenous species and to the functional roles that nonindigenous species now play in biological communities with long histories of human influence. For example, Schiffman (1994) found that endangered indigenous giant kangaroo rats (Dipodomys ingens) in California grasslands facilitated colonization and dispersal of nonindigenous plants; indeed, "eradication of [these] exotic plants would probably have a significant negative impact on populations of this endangered species" (Schiffman 1994, p. 534). Amur honeysuckle 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 (e.g., nutrient retention, carbon storage, and animal habitat improvement) are served by Amur honeysuckle in the absence of indigenous species or when niches are unfilled (e.g., Whelan and Dilger 1992, Woods 1993). Assessing the function of nonindigenous species in urban landscapes and surrounding areas is likely to require largescale research that is now conducted mostly in pristine systems.

Finally, careful examination of life-history traits associated with the thousands of plants accidentally or intentionally introduced, coupled with an analysis of when, where, and if the species have become naturalized, would be a useful exercise (Reichard and Hamilton 1994). Such an analysis would likely have some predictive or regulatory value when new introductions are proposed or when new cultivars are being developed (Ruesink et al. 1995). That attention should be focused on seed production and seed germination is

suggested by the case of Amur honeysuckle, by a previous survey of plants that eventually became problem weeds (Forcella 1985), and by a rating system for management of nonindigenous plants already established (Hiebert and Stubbendieck 1993). Specifically, species with high and consistent seed output, poorly developed seed dormancy, rapid germination, and ability to germinate at low temperatures and low light may be most likely to spread rapidly across a wide range of habitats. Of course, these life-history traits must be examined also within the context of environmental conditions common to the most frequently invaded systems. Considering the small number of introduced horticultural species and cultivars that have naturalized and eventually become components of our regional floras, the goal of such a screening process would not be to eliminate plant introduction but would be to reduce the risk of future problems.

Conclusions

Urban sprawl in the United States is likely to continue to push parks, nature reserves, and natural areas into closer and closer association with people, streets, houses, and gardens. The mostly nonindigenous floras of urban areas are also likely to be brought into closer association with nature reserves where native species are valued. To avoid problems with escape, plant scientists introducing or developing cultivars for ornamental or conservation use should screen potential candidates for life-history traits that increase naturalization ability. In the case of nonindigenous plants now well established in natural areas, resource managers should develop preservation goals and then assess whether nonindigenous plants are serving valuable ecological functions before resorting to wholesale plant-control measures.

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