

Japanese Honeysuckle (*Lonicera japonica*) as an Invasive Species; History, Ecology, and Context

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Japanese honeysuckle (*Lonicera japonica*) was introduced outside of Asia in the early 19th century and is now invasive to varying degrees on every continent, except Antarctica, and many archipelagos. The basic ecology and life history of Japanese honeysuckle are well known and described here; however, research needs on the underlying causes of the voracity and subsequent ecological impacts of this species are many. Virtually all ecological experimentation with Japanese honeysuckle has been conducted in the southeastern U.S., thus more data are needed in other regions, particularly South America and Africa. Although Japanese honeysuckle is naturalized in many areas where it has been introduced, there still may be hope for the control of local infestations and its further spread in areas that have a fairly recent introduction history. Japanese honeysuckle may be secure throughout much of its introduced range, but land management principles that discourage its use and public education to prevent further dispersal are recommended strongly.

Keywords honeysuckle, invasive, succession, nonnative, genetics, life history, ecology

NATURAL HISTORY AND INTRODUCTION HISTORY

The blame for the introduction of Japanese honeysuckle (*Lonicera japonica* Thunb.) as a horticultural specimen outside of Asia can be placed with a 19th century gardener and collector for Kew Gardens, William Kerr, who brought it and a number of other cultivars from China in 1806. Although a specific date is not available, Japanese honeysuckle was introduced to North America early the same century; the first North American herbarium record is from a Kentucky cultivar collected in 1842 (Gray Herbarium). Perhaps more blame should be placed with George R. Hall, a physician and plant breeder who introduced a vigorous and popular variety to the U.S. in 1862 that has been since named Hall's honeysuckle (*L. japonica* var. *halliana*). Alas, attractive and fragrant flowers destined Japanese honeysuckle to be a valued cultivar, and hardy growth characteristics and a long-flowering period the harbingers of a garden escapee. Japanese

honeysuckle was first noted as an escape from cultivation along the Potomac River in 1882 (U.S. National Herbarium), and with the further assistance of dispersal via animals, ornamental cultivation, and plantings for wildlife forage and bank stabilization, it has become naturalized in many temperate, subtropical, and tropical zones throughout the world.

In its native range, Japanese honeysuckle occurs in thickets in the hills of Japan, Korea, and eastern China (Ohwi, 1965). Data on the current distribution, ecology, physiology, and phenotypic plasticity of Japanese honeysuckle indicate that it likely will continue to spread and become a serious pest where minimal conditions for growth are present. It prefers well-drained forest soils of pH 6.1 to 7.9 but has been found invasive in areas where the soil pH values are 4.0 and 8.0. Japanese honeysuckle is considered a lower-end facultative wetland indicator by the USFWS (1988) and often occurs along wetland areas, but not in poorly drained, permanently saturated soils. It will thrive in sandy soils as long as there is available moisture. In addition to a tolerance to heavy metals and SO₂, a lack of soil organic matter and low mineral composition do not appear to have a major effect on Japanese honeysuckle (Caiazza and Quinn, 1980). Generally, it thrives in areas where the mean annual precipitation is 1000 mm and mean winter temperatures are at least –1°C, but there are many exceptions (see below). Japanese honeysuckle is killed by temperatures of ≤–10°C; above-ground portions may be killed above this temperature, but the plants will resprout from the roots. Its distribution appears to be limited only by drought, temperatures required for seed stratification, and heavy frost. In areas where temperatures are not suitable for seed stratification, it will spread via vegetative propagation (Leatherman, 1955).

Current Distribution Outside of Asia

Four decades ago, Leatherman (1955) estimated the latitudinal limits of Japanese honeysuckle to be 31 to 38°N, but based on current distribution data these limits can be extended to 45°N to 45°S, although only at higher altitudes in subtropical and tropical regions. Its current naturalized distribution includes major

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portions of North America, Mediterranean and Central Europe, southern Britain, North Africa, South Africa, Australia, New Zealand, the Philippine Islands, the Hawaiian and other Pacific Islands, and most recently Central and South America. Of these introductions, little is known about the distribution or degree of invasiveness of Japanese honeysuckle in Africa.

North America

In North America, Japanese honeysuckle is present in 42 states and Puerto Rico but naturalized primarily from Illinois, Missouri, Arkansas, and Louisiana east to the Atlantic. In the northeast, its limits are Massachusetts, Connecticut, New York (Hardt, 1986), and southern Ontario (CWS, 1993). In the southeastern U.S., it is common along fence rows and in mid-successional disturbed areas, and it thrives on the well-drained moist soils in woodlands and bottomlands (Radford *et al.*, 1968). Japanese honeysuckle is generally absent from coarse sands and poor peat soils (Jackson, 1974), and its distribution is limited on the xeric, sandy soils of the coastal plain of North Carolina, South Carolina, Georgia, Alabama, Northern Florida, Mississippi, and Louisiana. It is generally not found above 360 m in its northeastern distribution of the U.S. nor above 1500 m in the Appalachian Mountains. In Arkansas, it is not found above 840 m in the Ozark Mountains, but it is abundant at 850 m in the Ouachita Mountains (Leatherman, 1955).

Japanese honeysuckle has become a pest in drier parts of the North America under local conditions where there is irrigation. It has become well-established along many riparian corridors and human-made waterways throughout the western states but particularly in California, Arizona, Oregon, and Texas. It is generally not found above 1000 m in California (Hickman, 1993). In New Mexico it can be found in areas with adequate soil moisture from 1350 to 2100 m. Despite predictions that it would not establish in alkaline soils, it has been found well-established in riparian areas of Utah where the soil pH is 8.0 (Gray Herbarium).

Although it is considered a widespread, naturalized pest, Japanese honeysuckle is widely available throughout the U.S. and is still planted as a cultivar in areas without a heavy frost. As recently as 1994 it has been recommended by wildlife managers for use as forage and cover (Dyess *et al.*, 1994).

Pacific Islands

Japanese honeysuckle occurs throughout the Pacific Islands (Nuzzo, 1996) and is commonly known in the Cook Islands as pitate papa'ā and mangamangā rima, and in Hawai'i as ma'u ke and honekakala (Space and Flynn, 2000). It was planted historically in the Hawaiian Islands for bank stabilization and still is planted widely as an ornamental. The first naturalized collection of Japanese honeysuckle was made in Hawai'i in 1951 and it is now a management problem on Kauai, Oahu, East Maui, and the island of Hawai'i. In Fiji, it has naturalized in some areas to about 850 m (Smith, 2001). The habitats in Hawai'i and other Pacific Islands in which Japanese honeysuckle is found are cool, mesic-to-wet areas where the annual precipitation ranges from

760 to 3000 mm and elevationally from sea level to 1200 m (Motooka *et al.*, 2002; Starr *et al.*, 2003).

Australia/New Zealand

It is unclear when Japanese honeysuckle was introduced to Australia, but it is listed in over 75% of the catalogues from Australian nurseries from 1840 to 1980, thus likely it was introduced between 1820 and 1840. It was first reported as a garden escape in Australia in 1919 and was naturalized in Stirling, South Australia by 1965 (Eichler, 1965), New South Wales by 1972 (Beadle *et al.*, 1972), and the Sydney bushland by 1980 (Buchanan, 1981).

Carr *et al.* (1992) called Japanese honeysuckle a serious threat to native vegetation in southern Australia through New South Wales and Victoria. It is considered one of the worst invaders of native *Eucalyptus ovata* forests in the Melbourne area (Williams *et al.*, 2001); however, as in most areas where it occurs, it is most problematic in the riparian communities of Australia (Csurhes and Edward, 1998). Australian infestations are the worst at low elevations, but it occurs up to 1120 m in New South Wales. In Victoria, Japanese honeysuckle threatens a variety of habitats, specifically heathlands, heathy woodland, damp sclerophyllous forests, wet sclerophyllous forests, riparian vegetation, and warm temperate rainforests (Carr *et al.*, 1992). In Tasmania, it thrives in the warm, moist temperate climates but does not appear to be too aggressive in the tropical areas (Williams and Timmins, 1997).

Japanese honeysuckle was first reported as escaped from cultivation in New Zealand in 1926 and now occurs throughout the country from sea level to 743 m. Although it is uncommon at the southern end of the South Island, it is widespread throughout the northern end of the South Island and the entire North Island (Williams *et al.*, 2001). Habitats in which Japanese honeysuckle are particularly aggressive include open scrub, shrublands, woodlands, and forest margins, especially where there are moist alluvial soils. It is a particular concern on the southern half of the North Island, where growing conditions are most ideal.

Central and South America

Japanese honeysuckle is becoming naturalized at higher elevations throughout Central and South America, as substantiated by a number of herbarium reports from El Salvador, Guatemala, Honduras, Columbia, and Panama (Starr *et al.*, 2003). The first collection of Japanese honeysuckle in Brazil was reported in the Rio Grande do Sul region in 1940. By 1989, it was commonly reported from Rio Grande do Sul and from 1150 to 1200 m in the Rio de Janeiro area (New York Botanical Garden Herbarium). Japanese honeysuckle has become a management problem in the understory of *Populus deltoides* plantations near the Parana River in Argentina (Vicari-Ricardo *et al.*, 1996), and throughout southern Argentina and Chile (Csurhes and Edwards, 1998; Pauchard and Alaback, 2004). It is one of many species that pose a serious threat to the flora of the Juan Fernandez Islands, a Chilean National Park and IUCN

Biosphere Reserve (Swenson *et al.*, 1997; Dirnböck *et al.*, 2003).

Description

Japanese honeysuckle is a high-twining or trailing perennial that may climb well into the arboreal canopy or densely cover the ground surface. The green, herbaceous, pubescent stems quickly become densely tangled during growth, mature to reddish-brown, become woody and nonpubescent, and eventually develop a shredded, peeling bark.

A summary of the physical characteristics of Japanese honeysuckle as provided by Hickman (1993), Wagner *et al.* (1999), and Leatherman (1955) is as follows. Throughout its distribution, the leaf phenology of Japanese honeysuckle ranges from facultatively deciduous in the colder parts of its range to evergreen in warmer regions. The leaves are sparsely pubescent, ovate or oblong in shape, 3.0 to 8.0 cm long, 1.0 to 3.5 cm wide, and opposite or sometimes three to the node. The leaf margins are entire except for the new leaves, which frequently can be lobed. Petioles are 0.4 to 1.0 cm long and pubescent. The flowers are fragrant with a two-lipped corolla 2.0 to 4.5 cm long that is glandular-pubescent on the outside, white or sometimes pink on the first day, and yellow on the second day. The calyx is fused to the inferior ovary and covered with glandular-pubescent. Flowers occur in pairs on single peduncles 0.5 to 2.5 cm long in upper leaf axils and are subtended by bracts 1.0 to 2.0 cm long. Stamens are attached and approximately equal or slightly exerted to the corolla tube. The style is equal or slightly exerted to the corolla tube, and the stigma glandular-pubescent and receptive during and after anthesis. The fruits are sessile, globose, or subglobose-to-oval berries (sometimes flat to concave on the inner surface) that are purple-black at maturity and 6.0 to 7.0 mm in diameter. The seeds are brown-black, 2 to 3 mm in length, ovate to oblong, flattened, concave on the inner surfaces, and have an average weight of 3.8 mg per seed. Seed number ranges from 1 to 16 per fruit with a mean of 5.9.

Systematics

The genus *Lonicera*, named by Linnaeus after the 16th century German naturalist and physician, Adam Lonitzer (Bailey, 1949), is composed of roughly 180 species and is found in the traditional Caprifoliaceae. Although recent molecular phylogenetic studies have determined that the traditional Caprifoliaceae is nonmonophyletic, nuclear and chloroplast data strongly support the retention of *Lonicera*, which appears to be most closely related to the taxa *Hepacodium*, *Leycesteria*, *Symphoricarpos*, and *Triosteum* (Donoghue *et al.*, 2003).

Lonicera is divided into two subgenera, *Lonicera* and *Chamecerasus*, the latter of which contains *L. japonica*. There are no known natural or artificial hybrids between subgenera of *Lonicera* (Sax and Kribs, 1930). *Lonicera japonica* ($x = 9$, $2n = 18$; Sax and Kribs, 1930; Leatherman, 1955), later dubbed *Japanese honeysuckle*, was collected and named by Carl Thunberg in 1784 during the course of his work on the *Flora*

Japonica. Classification of Japanese honeysuckle within the subgenus *Chamecerasus* is based on the twining growth habit and flower occurrence in axillary pairs; in section *Nintooa* based on evergreen/semievergreen leaves, toothed calyx, two-lipped corolla, and black fruit; and in subsection *Volubilis* based on the presence of fragrant volatile chemicals and a spurless corolla (Rehder, 1940). There are four named varieties; *L. japonica* var. *halliana* (Dipp.) Nichols, the most common yellow form; *L. japonica* var. *chinensis* (Wats.) with red flowers and glabrous leaves; *L. japonica* var. *repens* with white or purple-tinged flowers, leaves mostly glabrous, and purple veins on leaves; and *L. japonica* var. *aureo-reticulata* (T. Moore) Nichols with yellow-veined, smaller leaves that are now known to be caused by a virus (Rehder, 1940).

There are at least twelve horticultural varieties of Japanese honeysuckle available for purchase through the internet, dubiously named “elegant creeper,” “Hall’s prolific,” “cream cascade,” and “mint crisp.” One variety, “Interold Dart’s World,” admittedly attractive with deep green leaves and a corolla that is purple-crimson on the outside and cream on the inside, is patented. The most popular and widely available cultivar, however, is *L. japonica* “Halliana” or Hall’s honeysuckle. No known naturally occurring inter- or intraspecific hybrids of Japanese honeysuckle have been reported; however, the species is quite variable, and some overlap between the varieties may reflect gene flow.

Genetic diversity within Japanese honeysuckle as measured by allozyme variation in ten populations in the southeastern U.S. is similar to that in other species with similar life history traits (perennial, early-to-mid-successional, and obligately outcrossing; Hamrick *et al.*, 1992). Percent polymorphic loci (P_s) = 75%, mean alleles per polymorphic locus (A_{ps}) = 2.28, and total genetic diversity (H_t) = 0.216 (Schierenbeck *et al.*, 1995). The proportion of total diversity among populations (G_{st}) for Japanese honeysuckle (0.092), is comparable to the G_{st} values found in other long-lived species (0.084) and is consistent with the prediction that this species has large outbreeding populations. Although species and population levels of genetic variability in Japanese honeysuckle are high, they may still reflect genetic sampling, immigration, and subsequent persistence of a subset of the variation present in its home range. Even with the likelihood of multiple introductions of Japanese honeysuckle (Mack, 1991), the levels of variation found in the southeastern U.S. may be lower than variation in its native range because of founder effects. A broader (greater regional sampling) more in depth (more local sampling with more variable molecular markers) study is recommended to measure the distribution of genetic variation between the native and introduced ranges.

LIFE HISTORY CHARACTERISTICS

Japanese honeysuckle demonstrates phenotypic plasticity for leaf phenology, plant architecture, and response to herbivory, all of which contribute to its success as an invader in a wide

range of habitats (Schierenbeck, 1992). However, because there is no quantitative genetic experimentation with Japanese honeysuckle, little can be concluded about the genetic or environmental basis of variability described below (Pigliucci, 2003).

Stem elongation in established plants of Japanese honeysuckle begins when soil temperatures range between 3 and 8°C. Vegetative growth is dependent upon site conditions, but with available light and moisture seedlings can grow 30 cm in length five months from germination (Leatherman, 1955). Young plants begin to build a vegetative blanket by twining clockwise around host plants and their own stems, a phenomenon that has been demonstrated to aid in its clonal mobility (Larson, 2000). The presence of a support will increase internode length by 15%, double the internode number, and result in a 43% increase in shoot biomass (Schweitzer and Larson, 1999). Without support in open fields, Japanese honeysuckle will form mats up to 1.5 m deep with 100% cover (Hardt, 1986). New ramets will establish via stems that come in contact with the ground and root adventitiously. The growth of well-rooted stems ranges from 105 to 226 cm over five months (mean = 163 ± 6.5 cm), with 2.0 ± 0.6 branches per stem, and a mean of 59.3 ± 3.9 leaves per stem. Branches are 2 to 60 cm long (mean = 12 ± 4 cm) and the mean number of leaves per branch of 19 ± 8 (Leatherman, 1955). If Japanese honeysuckle is in the presence of support stems less than 15 cm in diameter, it can reach heights of 15 m (Williams *et al.*, 2001). The maximum recorded stem diameter for Japanese honeysuckle is 18 cm for a plant of unknown age (Williams and Timmins, 1997). Root depth generally reaches 30 to 50 cm with available soil moisture and up to 102 cm on dry sites; lateral extension from the root crown has been measured to 2.5 m (Brender, 1961).

Throughout most of its native and introduced range, Japanese honeysuckle is evergreen or semievergreen; however, it is facultatively deciduous in response to cold or drought. In the drier portions of its range, *e.g.*, the southwestern U.S. and parts of Australia, the plants retain few leaves during the dry season, and new leaf formation begins with seasonal rainfall. In the colder portions of its range, leaves begin to form when soil temperatures reach 1 to 9°C (Leatherman, 1955).

Disturbance produces light gaps, and since light interception is dependent directly on leaf area, the phenological and allocations patterns of Japanese honeysuckle allow it to aggressively exploit such gaps (Schierenbeck, 1992). Leaf sizes demonstrate phenotypic plasticity, ranging from 7.8 ± 0.7 cm² in full sun to 10.7 ± 0.6 cm² in shade. The ability of Japanese honeysuckle to maintain higher specific leaf areas than native species in a variety of light environments enables it to capitalize on a broad spectrum of changes both diurnally and seasonally. In addition, its ability to climb or not climb allows the placement of plant modules that take full advantage of local conditions and ultimately increase fitness (Schweitzer and Larson, 1999). A comparison of Japanese honeysuckle with native vines in New Zealand found a higher degree of shade tolerance and more rapid growth in high-light environments than native species with similar ecological requirements (Baars and Kelly, 1996).

Flowering in Japanese honeysuckle has been observed to begin within a year after germination (K. Schierenbeck, personal observation), but most flowering begins in the second year (Leatherman, 1955). A mature stem 30 cm long will produce a mean of 27 flowers, and without controlling for pollination 57% of the flowers will produce fruit that contain between one and ten seeds (Leatherman, 1955). Under ideal growing conditions, the flowering period lasts for eight months.

In both the northern and southern hemisphere, fruit and seed dispersal is performed by a wide range of birds (*e.g.*, silvereyes, song thrushes, blackbirds, turkeys, and passerines) and mammals (*e.g.*, brushtail possums, rodents, and ungulates; Handley, 1945; Carr *et al.*, 1992; Hussey *et al.*, 1997; Williams and Karl, 1996). Local dispersal appears to be primarily vegetative, but this has not been verified via genetic studies of clone size.

Fresh seeds of Japanese honeysuckle are dormant and require stratification of 5 to 8°C for 60 days. Germination begins at temperatures of approximately 10°C but is greatest from 18 to 25°C (Leatherman, 1955). The seeds contain small amounts of carbohydrates and do not appear to have a long viability. Under dry storage, day conditions of 25°C and 15°C nights for 6 months, seeds retain a viability of 47% (Hidayati *et al.*, 2000). After three years, Japanese honeysuckle has a seed viability of 1 to 3% and thus relies on dispersal just before or following disturbance (Shelton *et al.*, 2002). Seedling survival with adequate moisture is 60% in 2% full sun and 100% at 3% full sun (Baars and Kelly, 1996). The first true leaves range from entire to lobed.

PHYSIOLOGICAL ECOLOGY

Comparison between native and nonnative species has been suggested as a method by which to identify those physiological characteristics important to the invasion process (Pattison *et al.*, 1998). However, a review of 79 of these comparisons indicated that caution should be applied in the analysis of such studies (Daehler, 2003). For example, differences in relative growth rates initially may appear to be due to higher photosynthetic rates, when in fact there are alternative explanations. Japanese honeysuckle provides such an example, as greater carbon gain in comparison to a native congener is better explained by a difference in leaf phenology rather than photosynthesis rates.

An examination of monthly diurnal measurements of photosynthesis, conductance, and transpiration of Japanese honeysuckle and its native congener, woodbine or coral honeysuckle (*L. sempervirens*), for one year in two light environments found that annual carbon gain for Japanese honeysuckle was much greater (Schierenbeck and Marshall, 1993). New leaves of Japanese honeysuckle have higher photosynthetic rates than coral honeysuckle under the forest canopy (6.2 *versus* 4.4 μmol m⁻¹s⁻¹, respectively) and in the open (4.4 *versus* 3.0 μmol m⁻¹s⁻¹). Although there is no significant difference in photosynthetic rates between species in February and March, the earlier onset of growth and persistence of Japanese honeysuckle leaves contributes to the greater overall carbon gain. For example, in January the respective measurements for Japanese honeysuckle

and coral honeysuckle were 3.46 and 2.98 $\mu\text{mol m}^{-1}\text{s}^{-1}$, but total leaf areas were 299 versus 64 cm^2 and result in total carbon fixation of 100.69 versus 18.47 mmol C month^{-1} . The retention of Japanese honeysuckle leaves throughout the winter months in otherwise deciduous forests can be seen throughout a range of habitats.

A number of authors found the light compensation point for Japanese honeysuckle is 0.9% (Sasek and Strain, 1990; Schierenbeck and Marshall, 1993; Robertson *et al.*, 1994). It can tolerate heavy shading to less than 5%, but as shading increases it will produce fewer leaves and vegetative runners (Slezak, 1976). Survival, leaf size, and total leaf area will decline at light intensities below 4%, but it will germinate and survive to 2% (Baars and Kelly, 1996). Deeply shaded, undisturbed native podocarp forests of New Zealand appear to be resistant to Japanese honeysuckle invasion (Williams *et al.*, 2001).

High transpiration rates are consistent with the inability of Japanese honeysuckle to tolerate drought conditions (Leatherman, 1955; Schierenbeck, 1992). There are no stomates on the heavily cutinized upper epidermis for either sun or shade leaves. However, the average number of stomates on the lower epidermis of sun leaves is 404 ± 34 , and on shade leaves is 226 ± 32 (Leatherman, 1955).

Sasek and Strain (1990) found that, compared to a control level of 350 $\mu\text{l CO}_2 \text{l}^{-1}$, under increased CO_2 concentrations the growth of Japanese honeysuckle will increase 135% at 675 $\mu\text{l CO}_2 \text{l}^{-1}$ and 74% at 1000 $\mu\text{l CO}_2 \text{l}^{-1}$. In both treatments, the number of branches tripled after 54 days of growth and the total leaf area increased by 50%. Similarly, Belote *et al.* (2003) found above-ground net primary productivity was consistently 2.5 to 3.3 times greater for Japanese honeysuckle under elevated CO_2 concentrations of 550 ppm than ambient CO_2 . There is little doubt that Japanese honeysuckle will respond favorably to increasing atmospheric CO_2 levels (Dukes, 2000) and support the prediction that with increased global warming its range will expand (Sasek and Strain, 1990).

FIRE ECOLOGY

Japanese honeysuckle is considered an important species in the disruption of fire regimes throughout the eastern U.S. (Richburg *et al.*, 2002) and survives all but the most severe fires by resprouting from below-ground stems (Barden and Matthews, 1980; Faulkner *et al.*, 1989). Although a number of studies indicate that the biomass of Japanese honeysuckle is significantly reduced due to fire, it will recover quickly and can remain the dominant species even after two years of fire treatment (Anderson and Schwegman, 1971, 1991; Barden and Matthews, 1980; Cain *et al.*, 1998). Under ideal growing conditions, Japanese honeysuckle will show strong post-fire recovery after one month (Faulkner *et al.*, 1989). In an experiment that was burned and subsequently ignored for 11 years, the cover of Japanese honeysuckle was four times that of preburn levels (Schwegman and Anderson, 1986).

Fire may be an effective control method, but only after repeated burning over an undetermined number of years. A twenty-three-year study in longleaf pine forests did show Japanese honeysuckle control in plots that were burned every two years in winter, spring, and summer. The percent cover of Japanese honeysuckle for each treatment was 16.05% for no burn, 0% for winter burn, 1.2% for spring burn, and 0% for summer burn (Kush *et al.*, 2000). Fire treatment at five-year intervals has been suggested as method for control, but it will not eliminate it (Stransky, 1984).

In areas of fire suppression, Japanese honeysuckle competes effectively for light gaps, establishes below-ground biomass, and consequently is hypothesized to promote the growth of other shade-tolerant species (Richburg *et al.*, 2002). Although research on the specific role of Japanese honeysuckle in fire and succession is lacking, there is little doubt that it is encouraged by fire suppression.

COMMUNITY ECOLOGY

General

Occurrences of Japanese honeysuckle often begin with humans through its use as roadside stabilizer or ornamental and are consistent with the hypothesis that human dispersal is important not only as a primary but also a secondary mechanism in the naturalization process (Kowarik, 2003). Further dispersal into surrounding plant communities is facilitated by birds and small mammals and vegetative spread.

Data on the role of Japanese honeysuckle in plant communities is primarily from the southeastern U.S., where it has been naturalized the longest. Japanese honeysuckle is found in most plant associations in the southeastern and east-central U.S., *e.g.*, *Quercus* spp. pine associations, stands of northern white cedar (*Thuja occidentalis*), white pine (*Pinus strobus*), red pine (*P. resinosa*), pitch pine (*P. rigida*), loblolly pine (*P. taeda*), all Piedmont alluvial forests, upland swamp communities, black-jack oak (*Quercus marilandica*) woodlands, maritime shrub thickets, old fields in various stages of succession, and mixed hardwood stands. Japanese honeysuckle is found only occasionally in stands of spruce (*Picea* spp.), fir (*Abies* spp.), or coastal pine barrens (Jackson, 1974). It is ubiquitous through the bottomland pine and riverbottom forests of the Carolinas and is present in every forest age class.

Individuals of Japanese honeysuckle scattered throughout the coastal plain and Piedmont habitats of the southeastern U.S. suggest there is continued recruitment. Stands of individuals of varying size are also present, although it is not clear if this is due to seed dispersal or vegetative propagation. Percent cover of Japanese honeysuckle ranges from 6% in young stands to 100% in mid-successional forests (Oosting, 1942). Genetic studies of ramet and genet growth are needed to determine the recruitment history of the species, particularly with varying climatic regimes.

Japanese honeysuckle has been identified as a successful competitor and a contributor to reduced species diversity in

many plant communities (Oosting, 1942; Davison and Forman, 1982; Bell *et al.*, 1988). It alters vegetative structure in deciduous forests and ensures its continued dominance through the suppression of juvenile individuals and the reproductive inhibition of associated species (Thomas, 1980; Friedland and Smith, 1982; Nyboer, 1990). Through root competition, Japanese honeysuckle affects a significant reduction on leaf photosynthetic capacity, nitrogen-use efficiency, and biomass allocation patterns of American sweetgum (*Liquidambar styraciflua*) saplings (Dillenburg *et al.*, 1993a, 1993b). The need for extra support that it places on host plants can increase the stem-to-leaf ratios of the host plants (Friedland and Smith, 1982). In a study of ten old fields followed over 31 years of succession, Japanese honeysuckle was significantly involved in many negative associations and played a major role in the inhibition of later successional species (Myser and Pickett, 1992). Even with heavy grazing from wildlife, it remains dominant in many mid-successional communities (Oosting, 1942; Leatherman, 1955).

Japanese honeysuckle will grow in full sun and full shade but it prefers light gaps, forest margins, old fields, and disturbed areas with light and moisture (Keever, 1979; Robertson *et al.*, 1994). Once established, it will spread rapidly by layering on roadcuts, abandoned fields, fences, woodlots, and crevices of natural or artificial stone walls (Leatherman, 1955). Japanese honeysuckle responds well to the light gaps provided by storm disturbance in the deciduous woodlands and floodplain forests of the southeastern U.S. Ten years after hurricane caused avalanches in the Blue Ridge Mountains, Japanese honeysuckle had the highest relative cover and frequency of any species (Hull and Scott, 1982). Light gaps allow the rapidly growing Japanese honeysuckle to cover understory shrubs or establishing canopy trees; thinning for forest management simply allows it to have the advantage over other species (Peitz *et al.*, 1999). Although mature intact oak-hickory and pine forests appear to be somewhat resilient, Japanese honeysuckle is often found lurking in the understory and will respond positively to most disturbances (Lang and Forman, 1978; Slezak, 1976). It has been found in the understory of an old-growth oak forest thought to be undisturbed for more than 250 years (Shear *et al.*, 1997).

Although community ecological data on Japanese honeysuckle outside of North America are only beginning to accumulate, there is evidence that it is threatening populations of the endangered and endemic na'ena'e (*Dubautia latifolia*) in Hawai'i (Starr *et al.*, 2003). In Australia, there is evidence that Japanese honeysuckle is displacing the flora that provides important habitat for marsupial ringtail possums (Williams *et al.*, 2001).

Natural Pests

Remarkably, there are no known pests or diseases that cause serious harm to Japanese honeysuckle (Gilman, 1999). Some disease-producing organisms have been observed on Japanese honeysuckle, but they don't appear to cause

much damage. These include the fungi, *Corticium koleroga*, *Phoma mariae*, *Polyporus dichrous*, *Rhytisma lonicericola*, and *Erysiphe polygoni* (Wescott, 1950), and the crown gall bacteria (*Pseudomonas tumefaciens*; Leatherman, 1955). Insect larva of the hornworm (*Haemorrhagia diffinis*), bumblebee hawkmoths (sphingidae), and skippers and darters (hesperiidae) have been observed eating the leaves of Japanese honeysuckle but not in large numbers. Aphids (Homopterans) are observed in the warmer regions of its range, but they do not appear to seriously damage the plants (Williams *et al.*, 2001). In regions where there are seasonal fluctuations in climate, peak leaf expansion for Japanese honeysuckle occurs in the late fall, late winter, and early spring, and thus its leaf phenology mediates the effects of herbivory by completing leaf formation prior to most insect activity.

Under combined herbivory from mammals and insects, Japanese honeysuckle has a substantial advantage over native congeners. The comparison of growth and biomass allocation patterns across three herbivory treatments found that unlike its native congener, coral honeysuckle, Japanese honeysuckle has a compensatory response to herbivory and greater biomass allocation to leaves than in nonherbivory treatments (Schierenbeck *et al.*, 1994). Leaf phenology (Harrington *et al.*, 1989) and flexible allocation patterns in response to herbivory have been found to play key role in the spread and persistence of an invasive species.

Pollination

The pollinators of Japanese honeysuckle are consistent throughout both the introduced and home range and include small birds, bees, and hornets (hymenoptera, *Apis mellifera*, *Bombus* spp., *Vespa* spp., *Vespa* spp.), hawkmoths and waxmoths (lepidoptera, sphingidae, gelechiidae), and syrphid flies (diptera; Leatherman, 1955; Schierenbeck *et al.*, 1994; Williams and Timmins, 1997). Pollination is facilitated by the dusk-opening flowers and provides the plant with the advantage of both nocturnal and diurnal pollinators (Miyake and Yahara, 1998). Scholtzhauer *et al.* (1996) found 13 volatile chemical compounds present in Japanese honeysuckle nectar that are attractive to insects.

Flowering period is affected by the interrelationship of latitude and elevation, but under ideal conditions, *e.g.*, Australia, New Zealand, and the southeastern U.S., Japanese honeysuckle will flower for 7 to 8 months (Leatherman, 1955; Schierenbeck, 1992; Williams *et al.*, 2001). Fruit set begins with corolla abscission and it takes about 60 days for the fruit to mature. Fruit set occurs during, and continues throughout and past, the flowering season. Seed set in Japanese honeysuckle is limited by obligate outcrossing; 17.4% of naturally pollinated flowers in Arkansas formed fruit, whereas 78% of hand-pollinated flowers formed fruit (Larson *et al.*, 2003). The lack of effective pollinators is hypothesized to be responsible for the great variability in seed set observed in Hawai'i, New Zealand, and Australia, but data are lacking (Starr *et al.*, 2003).

Dispersal

The fruits of Japanese honeysuckle provide a dependable source of protein and nutrients for and the seeds are distributed by birds and small mammals wherever it occurs (Miller and Miller, 1989). Japanese honeysuckle fruits have been observed being eaten by wild turkeys, bobwhites, mockingbirds, white-throated sparrows, white-crowned sparrows, slate-colored juncos, American robins, purple finches, goldfinches, bluebirds, pine grosbeaks, hermit thrushes, and house finches in North America (Martin *et al.*, 1951; Handley, 1945). The native stitchbirds, bellbirds, and tuis of Tiritiri Matangi Island near Auckland, New Zealand also have been observed consuming the fruits (Williams *et al.*, 2001). Stomach analyses of robins confirm Japanese honeysuckle as a part of its diet, and there is anecdotal evidence that bobwhites and other gallinaceous birds pass viable seed.

ECONOMIC IMPACTS OF CONTROL

Japanese honeysuckle continues to have economic importance as a popular cultivar, wildlife forage, and nectar source for apiaries (Roberts, 1979). Historically, throughout the southeastern U.S., it was used extensively for wildlife forage and shelter (Handley, 1945), as well as railroad and roadbank stabilization (Leatherman, 1955). The continued use of Japanese honeysuckle for wildlife habitat and diet may create some conflict between the goals of wildlife managers and invasive species control efforts. Japanese honeysuckle is well-ensconced as an important browse species for white-tailed deer throughout the eastern and southeastern U.S. It can account for 49.4% of the year-round diet of white-tailed deer in these areas and provides them with an important source of crude protein, calcium, phosphorous, and digestive dry matter (Sheldon and Causey, 1974). As recently as 10 years ago, the literature contained recommendations on how to increase the production and quality of Japanese honeysuckle as forage (Dyess *et al.*, 1994). Despite its use for the benefit of wildlife in managed systems, Japanese honeysuckle also presents serious problems in forests and orchards through water competition, the provision of rodent habitat, and the general interference of farming operations (King, 1966; Little and Somes, 1967, 1968).

There is evidence that Japanese honeysuckle has been used medicinally since the Tang dynasty in 659 AD (Turner and Wasson, 1997), and it continues to be a popular component of herbal teas in Guangdong, Hong Kong, and Macao (Hu, 1997). Only the flowers are used, as the fruits are poisonous, and the leaves can be poisonous in large quantities (Hu, 1997). The Pharmacopoeia Commission of the People's Republic of China (1995) and the U.S. Agricultural Research Service list a number of chemical compounds contained by Japanese honeysuckle that are effective as antiseptic, antidiarrheal, and anticarcinogenic compounds. Japanese honeysuckle has been used historically as an antidiarrheal agent by members of the Hilltribe in Thailand, and experimentation found that extracts of the Japanese honeysuckle do, in fact, have an

inhibitory effect against the diarrheal bacteria, *Bacillus cereus* and *Staphylococcus aureus* (Kernsaphai, 1998). Despite the historical use of Japanese honeysuckle for medicinal purposes, it is not "Generally recognized as Safe" by the U.S. Food and Drug Administration and thus is not approved for use as food or medicine in the U.S. Because Japanese honeysuckle is naturalized throughout much of the U.S., restriction of its sale or import as an herb would have little or no economic impact.

Governmental control of the distribution and sale of Japanese honeysuckle is limited. It is listed neither on the U.S. 2003 State Noxious-Weed Seed List nor as a Federal Noxious Weed. Although it is listed as an invasive species by many organizations and government agencies, in the U.S. the sale of Japanese honeysuckle is prohibited only in Illinois. In New Zealand the intentional sale, propagation, or distribution of Japanese honeysuckle is prohibited (Starr *et al.*, 2003).

Although the bane of the existence of natural area managers, the popularity of Japanese honeysuckle as a cultivar and browse species may lead to difficulties in convincing the public that it should be eradicated, controlled, or its sale discontinued. The pleasant fragrance and attractive flowers are often associated with childhood memories, and "honeysuckle" is referenced with sentimentalism in many stories and poems.

CONTROL

No treatise on a nonnative, invasive species would be complete without some instruction on how to get rid of it, and many brave individuals have tried to eradicate Japanese honeysuckle infestations. Much of the work on Japanese honeysuckle control is located in the "gray" literature (*i.e.*, government pamphlets, regional publications) and, presumably due to difficulties associated with access, a number of experiments have been repeated over the last three decades. Although site conditions and the quality of experimentation are widely variable, there are consistencies that emerge for the control of Japanese honeysuckle. It is clear that the removal of Japanese honeysuckle requires a combination fire or manual removal, chemical treatment, and a large amount of perseverance.

The most effective treatments for the control of Japanese honeysuckle are applied during periods of active growth. Although there is much variability of treatment effectiveness due to habitat conditions, in all locations it is important that treatment be continued until there is eradication and the site subsequently checked periodically for new propagules. Hand-pulling of Japanese honeysuckle will only work with very young plants (Evans, 1982); with older plants in open fields, discing or burning followed by repeated herbicide treatment of the resprouts is the best strategy (Motooka *et al.*, 2002). Above-ground mowing has been found to be ineffective and encourages regrowth (Stransky, 1984).

The use of low intensity or even moderately hot fires only encourages resprouting of Japanese honeysuckle. An attempt to control Japanese honeysuckle with fire alone in the understory of a stand of loblolly pine resulted in 14% cover after one year

on treated plots (90% in control plots) and 52% cover after three years (98% in control plots) (Bramlett *et al.*, 1991). Nyboer (1992) found that fire followed by herbicide application of new shoots was effective for control. In areas where Japanese honeysuckle is the dominant species and the occurrence of other species is not an issue, high intensity fires are effective for control (Cacek, 1998).

The evergreen-to-semievergreen habit in some climates allows the use of foliar herbicides in deciduous forests without effecting nontarget organisms. A review of a number of herbicide treatments found that a combination of 10 g metsulfuron-methyl, 200 ml glyphosate, and 100 ml penetrant per 100 l H₂O provided best control (Williams *et al.*, 2001). Fegehr and Frey (1988) found 5.4 g l⁻¹ glyphosphate applied in winter along a fence row was still effective 28 months after application. In areas where herbicide use is not an option, the repeated removal of aboveground material is important to prevent re-establishment and spread.

SUMMARY

Japanese honeysuckle is recognized as a serious problem on many archipelagos and every continent except Antarctica. Mack *et al.* (2002) emphasize the economic and ecological importance of screening out the world's worst weeds before they become a problem. Could scientists have predicted that Japanese honeysuckle was destined to become one of the world's worst weeds? There is little doubt, had William Kerr been conscious and concerned with the introduction of invasive species, he would have preferred to enjoy Japanese honeysuckle in Asia exclusively. The Risk Assessment System designed by Daehler *et al.* (2004) for Hawai'i easily identifies Japanese honeysuckle as a high-risk species. The "ideal weed characteristics" (*sensu* Baker, 1974; Bazzaz, 1979; Newsome and Noble, 1986) that apply to Japanese honeysuckle are rapid growth rate, long period of carbon gain, perennial habit, sexual reproduction, vigorous vegetative propagation, animal-dispersed seeds, no known pests, survival and reproduction in $\geq 2\%$ to full sun, wide soil pH tolerance, a compensatory response to herbivory, and a long flowering period. The weaknesses of Japanese honeysuckle as an invader are trivial by comparison but include a limited tolerance to drought, the need for seed stratification, a need for obligate outcrossing, limited seed viability after one year, and a susceptibility to temperatures below -10°C (Schierenbeck, 1992). In the face of increased CO₂ levels, data provided by Sasek and Strain (1988) and Belote *et al.* (2003) demonstrate that Japanese honeysuckle will continue to increase its advantage over the many native species with which it occurs.

Research needs on the underlying causes of the voracity and subsequent ecological impacts of Japanese honeysuckle are many. Virtually all of the ecological experimentation with Japanese honeysuckle has been conducted in the southeastern U.S., and thus much more data are needed in other regions, particularly the tropics; *e.g.*, what is the potential for it to disrupt

successional processes in tropical ecosystems, and how much variation is there in the need for seed stratification? The work on the genetic variation of Japanese honeysuckle is limited to one study, and possible research questions in this area include the following: What is the asexual rate of spread from a single genotype? Are some genotypes more fit than others, *i.e.*, what are the paternal and maternal contributions of sexually reproducing individuals? What is the genetic basis of the ability to survive under a wide variety of habitat conditions? Is there gene flow between the different varieties of Japanese honeysuckle, and what role might this have on the evolution of its invasive ability?

Although Japanese honeysuckle is naturalized many areas where it has been introduced, there may still be hope for the control of local infestations in areas that have a fairly recent introduction history, *e.g.*, the Juan Fernandez Islands, and Central and South America. The future of Japanese honeysuckle throughout much of its introduced range may be secure, but through further experimentation, land management principles that discourage its growth and spread, and public education, local control and eradication are possible.

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