Review

The Biology of Australian Weeds 38. *Lonicera japonica* Thunb.

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Name

The genus *Lonicera* L. (syn. *Caprifolium* Mill., *Metalonicera* M.Wang & A.G.Gu, *Xylosteum* Mill., family Caprifoliaceae) includes some 200 species of erect shrubs and twining climbers native to North America (south to Mexico) and Eurasia (south to North Africa, the Himalayas, Java and the Philippines). The genus has been divided into three sections: *Xylosteum* (Mill.) DC. includes species that are upright shrubs, while *Nintooa* (Spach) Maxim. and *Lonicera* are climbing shrubs.

Lonicera japonica Thunb. (syn. *L. aureoreticulata* T.Moore) belongs to section *Nintooa*, and is native to Japan, Taiwan and temperate parts of mainland China. It has been widely distributed to other regions, grown as an ornamental plant particularly for its fragrant blossom as well as for other reasons, and has now become extensively naturalized.

Description

Lonicera japonica (hereafter described by its common name Japanese honeysuckle) is a perennial, woody climber that ascends shrubs and small trees, and also spreads over herbaceous vegetation, forming tangled mats often more than 1 m deep (Figure 1). Its long stems are pubescent when young and generally reddish to purplish brown in colour (Webb *et al.* 1988), twining clockwise around the host and the plant's own stems. In this way it soon builds up a mass of vegetative material that smothers its host in a curtain up to 2 m thick in horizontal plane (Williams *et al.* 1998). This method of climbing limits the plant to hosts with stems less than 15 cm in diameter and prevents it from climbing the trunks of tall trees, although it can use hanging branches, and other lianes. In the presence of support it can reach 7m tall (North America), at least 8 m (Australia) or up to 15 m (New Zealand). Stems are commonly 0.5–2.0 cm in diameter, with major ascendant stems sometimes reaching more than 10 cm. In a greenhouse experiment it was shown that provision of support led to a 15% increase in internode length, a doubling of internode number and a 43% increase in shoot biomass (Schweitzer and Larson 1999). The bark is corky on older stems and becomes shredded, peeling readily. Annual rings are prominent in stem sections.

The lateral runners branch regularly, more so than in most vines (Teramura *et al.* 1991). Such stems may extend 15 m in a single growing season (Little and Somes 1967, 1968). Where stems touch the ground adventitious roots form readily, and in this way expanding vegetative colonies are formed within which few other plants are able to grow. In addition to their ability to root, the runners create new habitat for further cohorts of twining stems. Even in the absence of other support, the result is a dense mat up to 1.5 m deep forming nearly 100% cover. In dense stands of Japanese honeysuckle, such as in open fields and forest margins, the main surface roots are distinguishable from the stems only by the absence of bark. The main roots form an interlaced and twisted mass at or near the soil surface, while root branches and adventitious roots extend down as far as 1 m, and horizontal lengths up to 3 m. Once runners from a single parent plant have established roots, they form individual plants if their above ground parts are severed. Most roots are formed at the nodes, but roots also develop at the end of cuttings or broken stems once a callus has formed (Leatherman 1955).

The ovate to oblong main leaves are commonly 2.5–12.0 cm long by 1.5–6.0 cm wide. Leaves subtending flowers tend to be smaller (Figure 2). The leaves are opposite, simple, pubescent on the lower midrib, shining green on the upper surface and yellowish green below. Leaves on seedlings commonly have deeply lobed margins. Leaves tend to change from deep green to yellow-green with age. Japanese honeysuckle is evergreen in Australia and New Zealand but deciduous in colder parts of North America. In cooler districts its foliage becomes reddish in winter.

Both ascendant and prostrate stems are able to develop flowers and fruits (Figure 2). One peduncle, which bears two foliaceous bracts, is borne in the axil of each

Figure 1. Japanese honeysuckle growing over a shrub and grass on a roadside bank, but not invading pasture beyond (Limeburners Creek near Clarence Town, New South Wales, March 2000).

Figure 2. Specimens of Japanese honeysuckle showing buds, flowers and young fruits (Bostobrick, New South Wales, February 2000).

leaf of a reproductive branch. The paired, sessile, club-shaped floral buds are covered with glandular hairs and are held above the bracts. The flower buds are green when young and turn white before opening (Leatherman 1955). Flowers are in axillary pairs, fragrant, borne on densely hairy peduncles 0.5–2.5 cm long. The bracteoles and calyx lobes are very small and fringed with long hairs. The corolla is 2.0–4.5 cm long, usually white but becoming pale yellow after anthesis, and flushed with pink on the reverse surface. The entire corolla is 2.0–5.0 cm long and the corolla tube is 1.0–3.0 cm long. The lower protruding lip is two-lobed and the upper one four-lobed. The stamens and style are approximately equal in length to the corolla. The stamens are attached to the corolla tube, and the style to a small inferior ovary.

The sessile berries, 0.4–0.7 cm in diameter, are hard and green when immature, and black and soft (even fluid-filled) when ripe. Fruits contain two or three seeds that are approximately 0.2 cm in diameter, ovate to oblong, with a flat to concave inner surface and three ridges on the dorsal surface.

History

Japanese honeysuckle is among plants listed for Alexander Macleay's Garden in Sydney (Stackhouse 1981), which puts its probable introduction between 1820 and 1840. It is one of the most frequently listed plants, appearing in over 75% of catalogues from Melbourne, Adelaide and Sydney nurseries, from 1840 till 1980. It is absent only from specialist fruit tree catalogues or seed catalogues, suggesting that it was not frequently sold in the form of seeds (M. Mulvaney personal communication).

Japanese honeysuckle was first collected growing wild in Australia in November 1919, at Ararat Creek, Narnargoon, Victoria by J.W. Audas, described as 'a garden escape spreading along the creek and possibly in the process of naturalization' (Ewart and Tovey 1920). By 1965 it was noted as being naturalized at Stirling, South Australia (Eichler 1965). In New South Wales, by 1972 it was a 'garden escape, now naturalized in some gullies near coast and Blue Mts where it is spreading and becoming a weed' (Beadle *et al.* 1972). By 1981 it was one of the commonest weeds in Sydney bushland areas (Buchanan 1981). In 1987 its Australian occurrence was described as 'a garden escape near Sydney and in the Blue Mountains in New South Wales, and near Melbourne it has spread into gullies (Auld and Medd 1987).

In New Zealand, Japanese honeysuckle was offered for sale in 1872 (Esler 1988), and in various colour forms is presently offered for sale by five wholesale nurseries (Gaddum 1999). It was first collected in the wild in 1926 (Webb *et al.* 1988). It is assumed to have become naturalized in the Auckland area between 1940 and 1970, though a much earlier date is possible (Esler 1988). In the late 1980s Japanese honeysuckle was described as 'abundantly naturalized in many areas but less common in the southern parts of the South Island' (Webb *et al.* 1988).

The history of Japanese honeysuckle introduction and spread has been well documented in North America, where it is a serious weed (Andrews 1919, Leatherman 1955, Hardt 1986). It was introduced into the USA in 1806, was widely cultivated by the 1860s, and has become 'oppressively established in many parts' (King 1966). However, it did not appear in early floras, and was not noted in the wild until 1882. The first account of its spread was in 1904, and it has now spread over much of the eastern United States from Illinois and Michigan in the north to Florida in the south, and is listed as a pest in several states (F. Campbell personal communication).

Distribution

Japanese honeysuckle is widely grown in gardens in Australia, where the present distribution of wild populations (Figure 3) principally occupies a broad band from Victoria to south-eastern Queensland, with most recorded locations being in moister regions within 200 km of the coast. Outlying populations have been recorded in south-western Western Australia (Hussey *et al.* 1997), the Adelaide Hills of South Australia, Tasmania, and at Paluma near Townsville in tropical Queensland. Six Victorian vegetation types are threatened by Japanese honeysuckle (Carr *et al.* 1992). The most problematic infestations occur in riparian vegetation and wet sclerophyll forest in Victoria, e.g. on the Mornington Peninsula and in Ferntree Gully National Park (Csurhes and Edwards 1998). A survey of alien woody flora in the New England region of northern New South Wales found Japanese honeysuckle to be spreading both in urban habitats and on rural roadsides (Smith 2000).

Japanese honeysuckle has been recognized as a serious weed in New Zealand since the 1960s (Gunning 1964, Auld and Medd 1987), particularly on conservation land (Williams and Timmins 1990). It is

Figure 3. The Australian distribution of Japanese honeysuckle (data from the Biodiversity Information Management Section (Victorian Flora Database), Victoria; Botanic Gardens and State Herbarium of Adelaide; Queensland Herbarium; Australian National Herbarium; Tasmanian Herbarium; National Herbarium of New South Wales; Hussey *et al.* 1997; and specimens collected by the authors).

currently listed as widespread or spreading in all North Island regions except Northland, where it is 'isolated' (Owen 1997), albeit in a wide range of sites (Fromont and King 1992). In Auckland City it is increasing at a moderate rate from an incidence ranked as 'high' in 1970 (Esler 1987). Japanese honeysuckle appears to be most abundant in northern Hawkes Bay across to the Bay of Plenty. It is much less common on the Central Volcanic Plateau and the essentially pastoral landscapes of the southern North Island. In the South Island it is spreading (Owen 1997) in Nelson / Marlborough and Canterbury, where it has been present as widespread but isolated colonies for 30 years (Healy 1969). Although Japanese honeysuckle is widespread in the northern South Island it is uncommon in the south (R.B. Allen, C.J. West personal communication). On the West Coast it is listed only as 'isolated', and it has not yet established in the wild in Southland. Japanese honeysuckle is present in Otago (Allen 1978, Ward and Munro 1989) but has only recently been reported from protected natural areas there.

In North America, Japanese honeysuckle is now an important component of vegetation as far north as Massachusetts, Connecticut, southern New York and Ohio; Long Island and Cape Cod mark its northern limits as a pest (Hardt 1986). It is also widespread in Hawaii (Cronk and Fuller 1995) and in wastelands in parts of southern Chile (P.A. Williams personal observation 1997) and Argentina (Csurhes and Edwards 1998), and is naturalized in southwest Britain (Clapham *et al.* 1962).

Habitat

Climatic requirements

In Australia, Japanese honeysuckle has been collected as high as 1120 m in northern New South Wales, where it withstands an extensive period of frosts each year. In the Blue Mountains, New South Wales it occurs up to 1000 m altitude but is most problematic below 500 m (H. Paterson personal communication). It also occurs, but is not common, in many parts of Tasmania. It reaches maximum abundance in places with a moist, warm temperate climate, as in the Melbourne and Sydney areas. It does not grow widely in tropical regions, but occurs frequently at low altitude sites in north-eastern New South Wales and south-eastern Queensland with a warm temperate-subtropical climate, and has been collected once in tropical Queensland. Its limited distribution in South Australia, although it is generally in cultivation there, is attributed to most areas being too dry to allow it to establish (L. Haegi personal communication).

In New Zealand, Japanese honeysuckle grows from sea level to 743 m, the latter on Rainbow Mountain near Rotorua in the central North Island. A tolerance of cold winter temperatures, demonstrated by its distribution in North America, suggests that its apparent failure to establish in the southern South Island may be more to do with low summer temperatures. Many inland areas of the South Island are probably too dry for Japanese honeysuckle, although it clearly has some capacity to withstand seasonal drought, as evidenced by the abundant stands in inland Hawkes Bay.

Japanese honeysuckle grows up to 1800 m in both open and shaded situations in North America. Growth is limited in northern parts by the death of shoots from frosts, in western parts by inadequate precipitation, and in southern parts possibly by the absence of sufficiently cold temperatures to break seed dormancy (Leatherman 1955). Infestations have reached pest proportions in areas with annual precipitation of at least 1000 mm, mean January (winter) temperatures of at least -1°C, and freezing temperatures on at least 5% of January nights. These conditions are found in areas with a growing season of 217–301 days, whereas it is not a pest in areas with only 135–171 growing days. In Ukraine, Japanese honeysuckle has been noted as growing until the first frosts, its hardiness apparently being due to the shoots lignifying rapidly (Panova 1986).

Substratum

In Australia, Japanese honeysuckle appears tolerant of a wide range of substrates, although its preference for moist gully locations results in its commonly growing on alluvium. In the Blue Mountains, where annual rainfall is around 1000 mm, it grows on sandstone-derived soils only in creeks, gullies and areas affected by increased urban runoff, but on shale-derived soils it can grow without increased runoff (H. Paterson personal communication).

In New Zealand, Japanese honeysuckle grows on a wide range of substrates derived from volcanic, sedimentary, and metamorphic rock types. The most vigorous stands are found on friable moist soils, particularly alluvium and recent colluvium. It is quite tolerant of poor drainage, and can grow in peat bogs and alluvium that is probably saturated for long periods. It rarely establishes on excessively drained and drought-prone sandy or stony soil. It is also tolerant of salt (J. Craw personal communication).

In North America, Japanese honeysuckle grows on a wide range of substrates, from pH 4.0 to 7.9, and spreads most rapidly on soils above pH 6.0 (Leatherman 1955). It grows best on calcareous soils and moist forest soils, as compared to excessively drained sandy soils, where it is limited by moisture availability. Seedling growth is much faster in a well drained fertilized soil than in fine sand (Leatherman 1955). Japanese honeysuckle is one of the few species tolerant of pollution from heavy metals and SO_2 (Caiazza and Quinn 1980).

Plant associations

Japanese honeysuckle is generally associated with vegetation disturbance. It appears not to invade pristine forests, except at sites of local, natural disturbance such as along water courses, but it commonly drapes itself over shrubs and small trees at forest margins, particularly near settlements and beside roads. From such sites its stems spread out across adjoining herbaceous vegetation, forming low, tangled thickets supporting few other plants, sometimes tens of metres across. It commonly infests road verges or gully margins without spreading into adjoining pastures.

In Australia, gullies are commonly mentioned as favoured habitats (e.g. Beadle *et al.* 1972, Auld and Medd 1987, Hussey *et al.* 1997), where Japanese honeysuckle invades vegetation requiring high levels of soil moisture. In the Melbourne area of Victoria, it is a weed in *Eucalyptus ovata* Labill. forest that formerly grew along all minor streams and periodically inundated flats in the region, and may also occur along major streams beneath *E. viminalis* Labill. It commonly grows there with other alien vines or scramblers such as *Galium aparine* L., *Hedera helix* L. and *Rubus discolor* Weihe & Nees (G. Lorimer personal communication). In the Australian Capital Territory its habitats include *Eucalyptus melliodora* A.Cunn. ex Schauer – *E. blakelyi* Maiden woodland close to urban areas, disturbed drainage lines, pine forest, and under *Casuarina cunninghamii* Miq. on river sands, growing with other bird-dispersed alien flora (M. Mulvaney personal communication). In eastern New South Wales it is also commonly seen with other weedy species, growing over alien shrubs and small trees such as *Ligustrum sinense* Lour., *Ligustrum lucidum* L., *Cinnamomum camphora* (L.) J.Presl., and *Pyracantha angustifolia* (Franch.) C.K.Schneid., but also covering native shrubs and sapling eucalypts and probably having significant local impacts on tree regeneration. In the Blue Mountains, Japanese honeysuckle is often associated with *L. sinense,* and it contributes to dense mixed weed 'plumes' which exclude all native vegetation (H. Paterson personal communication). In Tasmania it occurs in heavily disturbed bushland areas and places dominated by other weeds (e.g. *Cotoneaster* spp., *Genista monspessulana* (L.) L.A.S.Johnson, *Passiflora mollissima* (Kunth) L.H.Bailey) but has not been seen in relatively undisturbed bushland (S. Welsh personal communication).

In New Zealand, Japanese honeysuckle has long been recognized as a weed of hedges (Gunning 1964) and now occurs in a wide range of open habitats such as roadsides and wastelands, the margins of wetlands (including coastal wetlands), and communities with some degree of woody cover. Many stands of Japanese honeysuckle have established in the herbaceous or shrubby margins of forest, woodland, and scrub, and then spread into the woody vegetation. In dense forest or scrub, it is often restricted to forming a curtain of growth on the outside margins. Japanese honeysuckle can dominate the understorey and any canopy openings where the forest or scrub is sufficiently open. At Tiritiri Matangi Island near Auckland, replanted native forest has Japanese honeysuckle with stems up to 10 cm diameter and no foliage below the canopy, climbing over parts of the canopy 10–20 m tall (S. Dunning personal communication). Shrublands 4–6 m tall may be completely covered by particularly vigorous stands. Where Japanese honeysuckle grows with otherwise pure stands of *Pteridium esculentum* (G.Forst.) Cockayne, the cover may vary according to the latter's seasonal state. Its extent in these situations is commonly 10% cover over a 20 ha area, and in places is as extensive as 50% cover over 50 ha. The vigorous marginal growth of large stands and the presence of many small outlying patches suggest that Japanese honeysuckle is likely to expand further at many of these sites. In central and eastern North Island areas the main native species most frequently associated with Japanese honeysuckle in vegetation other than wasteland, in rank order, are *Melicytus ramiflorus* J.R. & G.Forst., *Coprosma robusta* Raoul, *Hoheria sexstylosa* Col., *Pittosporum tenuifolium* Sol. ex Gaertn., *Leptospermum scoparium* J.R. & G.Forst., *Pteridium esculentum* and *Pseudopanax arboreus* (Murray) Philipson. The most frequent weeds at the same sites are several species of Convolvulaceae, *Rubus* and *Salix*. It may provide support to other, faster-growing alien vines (e.g. *Ipomoea* spp., *Araujia sericifera* Brot.) (J. Craw personal communication). In combination, these species are suggestive of early secondary vegetation on moist, fertile sites.

In North America, Japanese honeysuckle has spread to old fields, roadsides, fence rows, prairies, sand barrens, and forest openings. In places it is a major component of the third stage of succession in old fields, increasing after fields have been abandoned for four years (Keever 1979). It can invade established woodlands, particularly deciduous woodlands, but is limited by the deep shade of evergreen forest. Woodlands are invaded when natural processes such as storms or Dutch elm disease create canopy openings (Slezak 1976, Thomas 1980). Invasion is particularly successful in moist woodlands and floodplain forests (Andrews 1919, Wistendahl 1958).

Plant/animal relationships

Insect herbivores known to feed on Japanese honeysuckle in North America are primarily indigenous members of the Sphingidae (hawk moths) and Gelechiidae (wax moths). In most parts of Australia and New Zealand there is little evidence for invertebrates feeding on Japanese honeysuckle foliage, but plants in Tasmania have been noted to become heavily infested by aphids (S. Welsh personal communication). Japanese honeysuckle responds rapidly to herbivory by both mammals and insects by allocating resources to stems and leaves. It thus recovers quickly, giving it an advantage over native congeners in North America (Schierenbeck *et al.* 1994).

In New South Wales, cattle, goats and sheep eat it readily, slowing or preventing the plant's spread into pastures. In the Blue Mountains, swamp wallabies which browse *Ligustrum sinense* do not eat Japanese honeysuckle; ringtail possums which build dreys in *L. sinense* and Japanese honeysuckle thickets, and are displaced during clearing, may then be exposed to predators (H. Paterson personal communication).

In New Zealand, Japanese honeysuckle is browsed by a range of mammals, and its expansion at Hawkes Bay may be associated with a decline in feral goat numbers. It spreads rapidly when forest reserves are fenced and animals are excluded. Brushtail possums in captivity nibble the leaves; fruits are also eaten, but are less favoured than fruit of several other weed species (Williams *et al.* 2000).

The flowers produce abundant nectar. At Tiritiri Matangi Island, near Auckland, native birds (stitchbird, bellbird, tui) eagerly consume Japanese honeysuckle nectar (S. Dunning personal communication). Birds of many species feed on its fruits (see below). In Australia, some but not all ripe fruits may be taken, the remainder becoming desiccated on the plants during winter and finally falling to the ground in spring.

Growth and development

Growth rates

Honeysuckle stems of varied sizes were cut near ground level and their growth rings (presumed to be annual) were counted at Barrington (115 m.a.s.l.) and Bostobrick (605 m.a.s.l.) in north-eastern New South Wales, at Black Mountain (650 m.a.s.l.) in the Australian Capital Territory, and several places in New Zealand, mainly in the South Island below 200 m.a.s.l. (Figure 4). Stems reached 4 cm diameter and 12 years of age, with an annual diameter increment ranging from 1.5

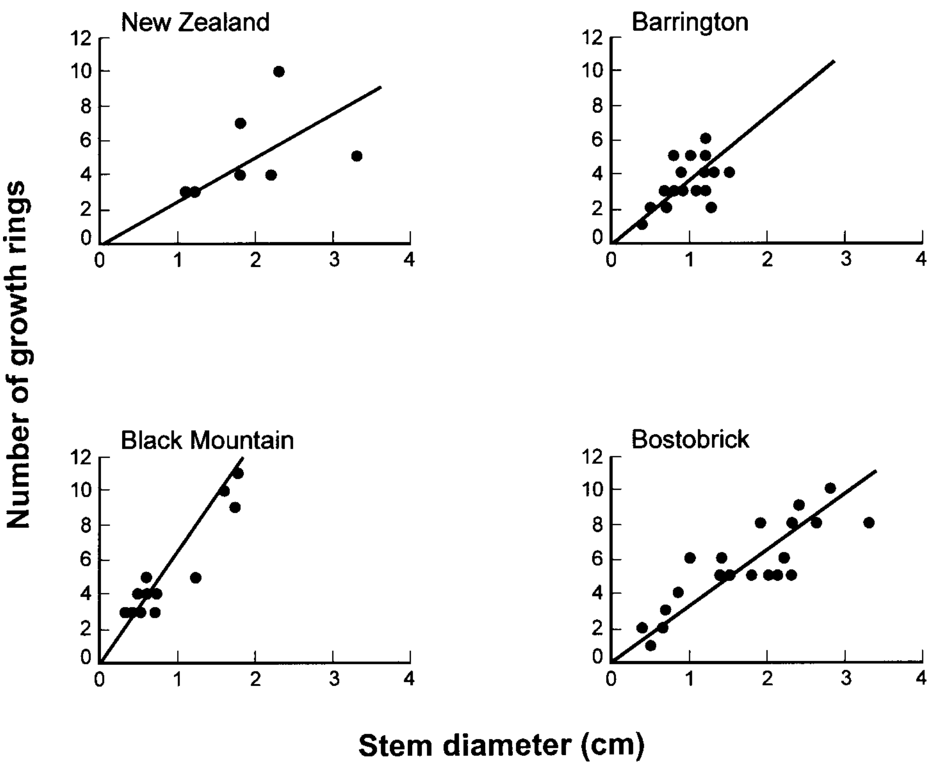

Figure 4. The relationship between age (number of annual growth rings) and size of Japanese honeysuckle stems collected in New Zealand (various sites), at Black Mountain (Australian Capital Territory), and at two sites in New South Wales.

mm to 5.0 mm. Growth rates were faster in the New Zealand and Barrington sites, than in the Australian sites at higher altitudes. These are similar to diameter growth rates of about 1.7 mm per year reported in North America. Here the largest recorded stem was 18 cm diameter but was of unknown age (Leatherman 1955).

Perennation

Japanese honeysuckle shoots become dormant and old leaves may be lost under extremes of cold or dryness. However, leaves are retained over winter in equable conditions where they are capable of growing, or at least fixing carbon, all year round, and shoots may continue growing slowly during winter in these conditions. This is particularly significant during the period of new leaf formation (Schierenbeck and Marshall 1993). In North America, this situation applies from Maryland south (Leatherman 1955), as it probably does throughout the present range of Japanese honeysuckle in Australia and New Zealand.

Physiology and genetics

Several early studies showed Japanese honeysuckle to be able to tolerate heavy shading, but there was a significant inverse relationship between leaf or whole plant dry matter accumulation and light intensity at several levels of shading (Leatherman 1955, Blair *et al.* 1983). Light levels in deciduous North American forests during winter (50–80% of full sun) are well above that required for growth and fruit production of Japanese honeysuckle in these forests (Thomas 1980). Japanese honeysuckle-infested plots divided into density and vigour classes showed that vigour (measured by the number of vegetative runners) was adversely affected by shading to less than 5% of full sunlight, but density was unaffected (Slezak 1976). Few cuttings survived at this level of shading (Leatherman 1955). Similarly in New Zealand, survival, leaf size, and total leaf area of several vines including Japanese honeysuckle declined at relative light intensities below 4%, but survival and growth was still high at 2% light intensity (Baars and Kelly 1996). A light compensation point of 0.9% has been calculated which, together with the aforementioned survival figures, indicates a high degree of shade tolerance, at least for vegetative growth (Robertson *et al.* 1994). However, Japanese honeysuckle cannot grow in the deep shade of intact New Zealand native forest such as podocarp forest.

Studies aimed at predicting the response of Japanese honeysuckle to anticipated increases in atmospheric CO_2 found that the biomass of cuttings after 54 days growth was 135 and 76% greater at 675 and 1000 µL CO_2 L^{-1} respectively, than at 350 µL CO_2 L^{-1} (Sasek and Strain 1991). Morphologically, CO_2 enrichment tripled the number of branches (675 or 1000 µL L^{-1}) and increased total branch length by a factor of six (1000 µL L^{-1}). At the two higher CO_2 concentrations the total leaf area increased by 50%. These responses may increase the competitive ability of Japanese honeysuckle for light, if CO_2 concentrations rise as predicted, and so the vine may become a more serious weed (Sasek and Strain 1991).

Japanese honeysuckle's morphological plasticity in response to support was higher than that of its native North American congener *Lonicera sempervirens* L., in a glasshouse experiment. This was considered to contribute to its ability to occupy more habitats (Schweitzer and Larson 1999). Studies of photosynthesis, stomatal conductance, and water use efficiency found new leaves of Japanese honeysuckle to have significantly higher photosynthetic rates than the emerging leaves of *L. sempervirens* (6.2 vs. 4.4 µmol $m^{-1}s^{-1}$ under the canopy; 4.4 vs. 3.0 µmol $m^{-1}s^{-1}$ in the open) (Schierenbeck and Marshall 1993). Differences in conductance and water use efficiency between species were seldom significant, but Japanese honeysuckle tended to have higher maximum values than *L. sempervirens*. Retention of old leaves by Japanese honeysuckle during new leaf formation (January–March), as well as higher photosynthetic rates in new leaves and relatively high leaf gas exchange (Carter *et al.* 1989), contribute to greater annual carbon gain and also help explain its invasive ability.

Genetic variability within a population can be a means of adaptation to new environments. Levels of allozyme variation in populations of Japanese honeysuckle ($2n = 18$) in the south-eastern United States are no higher than in the congeneric native *L. sempervirens* L. ($2n = 36$). Genetic variability thus appears less important than other life history traits in the relative success of this invasive species (Schierenbeck *et al.* 1995).

Phenology

Japanese honeysuckle flowers for more than half the year. In New Zealand, flowers are present for seven months, from mid-August until April (and occasionally into June) in various parts of the country. In Australia, the flowering period is even longer at warmer sites (Table 1). In northern New South Wales, while a population at Uralla (1010 m.a.s.l.) flowered only from November to April, at lower altitudes at Barrington flowering persisted from October to July. At Bostobrick, a few flowers could be found at all seasons. Even at these sites, however, the main flowering was around December and fruits were not seen until January, with earlier flowers withering without setting any fruit. Ripe fruit was present at all Australian sites from February or March, commonly persisting to July or August, with a few dried fruits still present on some plants in September.

In eastern North America, the flowering period of Japanese honeysuckle is from late April to July and occasionally until November. In those parts of North America where water is limiting, e.g. in southern California, new shoots begin to be formed as soon as the first rains start, or in early spring in other areas (Leatherman 1955). In areas where it is facultatively deciduous, Japanese honeysuckle is one of the first plants to leaf in spring, and in New Jersey leaf production begins when soil temperatures are between 1 and 9°C (Leatherman 1955). In mid-latitude New Zealand, soil temperatures at 10 cm depth are above 5°C even in the coldest months, which would suggest no period of dormancy. This is borne out by the observation near Takaka that stumps cut the previous autumn (March) had shoots up to 20 cm long by early spring (mid-August) (Williams *et al.* 1998).

Observations in North America

Table 1. Floral phenology of Japanese honeysuckle at Wellington, Cobb Valley, and Nelson City, New Zealand in 1996-97; and at Uralla, Barrington and Bostobrick, north-eastern New South Wales, and Black Mountain, Australian Capital Territory, Australia in 1999–2000. (0 = vegetative only, 1 = buds, 2 = flowers, 3 = many flowers, 4 = fruit).

Site	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Wellington			1	1,2	1,3	1,3	1,3	1,3	1,3	3,4	2,4	2,4
Cobb Valley			1	1	1,3	1,3	1,3	1,3	1,3	2		
Nelson City			1	1	1,3	1,3	1,3	1,3	1,3	2		
Uralla		4	4	0	1		1,3	1,3	1,2,4	2,4	2,4	4
Barrington	1,2,4	2,4	0	0	1,2		1,3	1,3	1,2,4	2,4	1,2,4	
Bostobrick		1,2		1,2	1,3		1,3	1,2,4	1,2,4	1,2,4	1,2,4	1,2,4
Black Mt.			0	0	1	1,2	1,3	1,3,4	1,2,4	2,4		0

show that the first floral buds appear approximately one month before flower expansion. They are borne on the current year's growth. Those nearest the base of the current year's growth open first, and flowers continue to bloom at nodes nearer the tip of the branch as the season advances (Leatherman 1955). Vegetative growth may occur at the tip of the branch after floral buds have differentiated, and flower buds have occasionally been observed on this late season vegetative growth (Leatherman 1955). In the Nelson and Wellington areas of New Zealand, the same sequence is common on plants that produce fruit.

Reproduction

Pollination

Flowers open shortly before dusk (Roberts 1979, Miyake and Yahara 1998). They remain white or rose-tinted for only a day or so, and are usually withered by the third day. Nectar secretion begins after the flower is well open, and by the second day half the tube may contain nectar. During different stages of their development the flowers produce at least 13 volatile chemical compounds (Schlotzhauer *et al.* 1996) that are attractive to insects. In Japan, within the plant's native range, pollination happens both at night by hawk moths, and during the day by bees (Miyake and Yahara 1998). There are no observations of pollination in Australia, but in New Zealand bumble bees (*Bombus* spp.) have been observed to prise open flowers to extract the pollen (P.A. Williams personal observation) and native birds visit flowers to feed on nectar (S. Dunning personal communication). Bumble bees have also been noted as being the principal pollinators of Japanese honeysuckle in Britain (Roberts 1979). Cross-pollination in the USA is effected by both insects and hummingbirds (Leatherman 1955). The insects involved include Hymenoptera (*Apis mellifera* L., *Bombus* spp., hornets), Lepidoptera (a hawk moth), and Diptera (syrphid flies).

Seed production and dispersal

Japanese honeysuckle is generally described as producing abundant fruit in North America. In one observation, stems 30 cm long produced an average of 27 flowers, of which 57% produced fruit, i.e. 15.4 fruits per branch (Leatherman 1955). In Australia, limited observations suggest that smaller crops develop (Table 2), although some fruits were formed at all stands we have seen. Fruit production in New Zealand varies. In Auckland fruit production is light (Esler 1988). Near Nelson two large stands produced no fruit in the 1997 autumn despite producing abundant flowers over several months. One of these, located in the Cobb Valley, produced no fruit in 1996 either, yet fruit was produced at a similar latitude in Wellington (Table 2). Very little or no fruit was produced by many stands examined in eastern and central North Island areas in 1997. On the other hand, some other stands produced abundant fruit, in some instances in similar numbers to those recorded in Australia and North America. We have also seen fruiting plants in many scattered localities in the lowlands of the lower North Island and the northern half of the South Island.

Our observations suggest that in many instances fruits are produced most abundantly on side shoots of second-year or older wood, often towards the lower parts of plants. Vigorous young vegetative growth, even on stands that are some years old, often produces abundant flowers which fail to set fruit. The fruits weigh 87.01 ± 4.0 g and comprise 84.0% water. The flesh contains two or three seeds in a mucilaginous pulp that constitutes 64.4% of the dry weight of the fruit (Williams and Karl 1996).

Japanese honeysuckle seeds are dispersed by birds in Victoria (Carr *et al.* 1992) and Western Australia (Hussey *et al.* 1997) while seedlings in a Sydney garden were believed to derive from seeds dispersed by silvereyes (Gannon 1936). Fruit removal has not been observed in northern New South Wales, but the pattern of seedlings around one small isolated stand near Armidale indicates that fruits are taken by small birds, probably silvereyes. The seeds are voided beneath nearby trees or shrubs that provide shelter or other food for these birds. Ten seedlings were found at two places within 50 m of the parent plant, four were found at two places 80 m distant, and a single seedling was located 200 m away. Seedlings also occur sporadically in Armidale city gardens lacking mature individuals of Japanese honeysuckle.

In New Zealand, the fruit is eaten by blackbirds, song thrushes and silvereyes in the Nelson region (Williams and Karl 1996), and by many species of birds at Tiritiri Matangi Island (S. Dunning personal communication). Brushtail possums will also eat the fruits, and some seeds pass through apparently undamaged, although the sample was too small to test the effect of gut passage on germination (Williams *et al.* 2000). Grazing mammals may assist spread by transporting vegetative fragments.

In North America, fruits are eaten by a wide range of birds many of which are native, from turkeys to small passerines. Because of the high water content of the fruit, the seeds pass quickly through birds, including gallinaceous species such as turkey and quail (Handley 1945). The fruits are also eaten by mammals such as deer, but it is not known whether seeds survive passage through the gut.

Germination and development

Japanese honeysuckle seeds require a period of cold temperatures to break dormancy. Germination to a level of 63% was achieved in soil following exposure to temperatures of 5–8°C for 60 days (Leatherman 1955). Germination occurs in spring, as soon as air temperatures exceed 10°C. Germination occurs over a wide temperature range but was greatest at a fluctuating daily range of 18–25°C (Leatherman 1955). The occurrence in Australia of plants in some places unlikely to experience such cold conditions suggests that this germination requirement is not rigid.

Japanese honeysuckle seeds have only a small amount of endosperm, and the cotyledons contain chlorophyll at an early stage. The oval cotyledons are small, foliar, and green. Two true leaves are produced by the time the seedling reaches 3 cm tall. The first true leaves are simple and appear several days after the cotyledons have opened. Seedling leaves are indented, with lobate margins (Buchanan 1981). Tap root development occurs simultaneously with leaf development. After 52 days in full sun, 25% of full sun, and 5% of full sun, seedlings were 6.2, 9.7, and 10.6 cm tall, respectively, and the shoot/root ratio increased from 3.7 to 6.3. Seedlings can reach 30 cm in five months from germination and the first branches appear in this period (Leatherman 1955). Overall, seedling growth is slow for the first two years (Little and Somes 1967). Older seedlings develop several shoots arising from

Table 2. Fruit production on Japanese honeysuckle stems at Whangarei, Kaituna, Hawkes Bay and Wellington, New Zealand, and at Barrington, Black Mountain and Bostobrick, Australia.

Location	Plants (n)	Month / Year	Stem length (cm)	Nodes (n)	Fruits (n)
Whangarei	20	04/97	26.0 ± 7.0	8.1 ± 2.0	4.1 ± 3.1
Kaituna	20	03/97	21.2 ± 8.5	8.2 ± 2.2	14.9 ± 4.2
Hawkes Bay	20	03/97	25.3 ± 9.3	7.7 ± 1.4	11.2 ± 7.1
Wellington	30	03/97	29.1 ± 3.7	9.9 ± 3.7	14.6 ± 1.6
Barrington	30	07/99	45.2 ± 16.6	–	5.8 ± 3.0
Black Mtn	15	01/00	78.7 ± 41.6	–	10.7 ± 4.9
Bostobrick	21	04/00	35.4 ± 11.7	9.6 ± 2.1	6.3 ± 5.7

the original stem base, typically growing out in all directions over the surrounding vegetation.

The rate of development to maturity may be illustrated by an observation of a plant derived from a cutting (but subsequently untended) growing up to smother a *Eucalyptus viminalis* sapling near Armidale, New South Wales. Planted in about 1980, and flowering freely from at least 1985, it was not until 1999 that seedlings were discovered nearby. The parent plant was then destroyed, having reached a height of 3 m (the limit of its support), and spread over surrounding grassland to radial distances of 2–4 m.

Plants grown from cuttings will produce flowers after two years (Leatherman 1955), but there appear to be no studies that have recorded the time to flowering from seed.

Hybrids

No hybrids have been reported, but there are several cultivated forms (Webb *et al.* 1988). The potential of these to produce weedy forms is unknown.

Population dynamics

Despite the literature on growth rates of individual stems, and the frequency of Japanese honeysuckle colonies in various kinds of vegetation in several regions, there appear to be no data on the dynamics of individual populations at any stage of the life-cycle. This may have resulted in part from the growth form of the species, which would make it difficult to establish, for example, seedling survival rates in situations where several individuals were growing in close proximity. Typically there are colonies of differing sizes, suggesting continuing dispersal and recruitment. New colonies appear to be derived both from bird-dispersed seeds, and from garden prunings dumped on roadsides and elsewhere.

Seedlings can sometimes readily be found near parent plants in tableland areas of northern New South Wales. Seedlings are rare in the nearby lower altitude Lismore region (Big Scrub Rainforest Landcare Group 1998), and in the Blue Mountains (H. Paterson personal communication). Similarly, in New Zealand seedlings are rare in the wild. Despite extensive searching we have seldom found one, even in the vicinity of plants producing abundant fruit, and in the presence of other woody seedlings. With few exceptions, young shoots which at first appear to be seedlings, are probably connected to runners from adjacent plants. However, seedlings have been reported from an urban garden in Christchurch (W.R. Sykes personal communication).

Importance

Detrimental

Japanese honeysuckle is a weed of conservation because it impacts upon disturbed native communities, and on attempts to restore them. In Australia, its distribution is generally patchy, but all infestations we have seen appear to be expanding and threatening neighbouring vegetation, except where they are actively controlled or are adjacent to heavily grazed areas.

Most Japanese honeysuckle infestations are in open sites, including forest edges, shrublands, and moist grasslands on floodplains, gullies, or stream banks. These are frequently disturbed places, but Japanese honeysuckle has the potential to invade pristine habitats along water courses, as seen in the Blue Mountains (M. Williams personal communication). We have seen Japanese honeysuckle establishing only close to forest edges or in gaps, but shoots can nevertheless penetrate the shade of relatively dense forest for many metres along the ground or up stems. Some eventually reach the higher light conditions of the canopy where they grow more densely. Like many other alien climbing plants in Australia, Japanese honeysuckle smothers shrubs and small trees, killing or weakening them. Its stems twine around other plants and eventually grow over their crowns, smothering the host. Japanese honeysuckle smothers herbaceous vegetation where support is absent, and probably prevents regeneration of light-demanding trees, including eucalypts.

In Victoria, Japanese honeysuckle threatens heathland, heathy woodland, damp sclerophyll forest, wet sclerophyll forest, riparian vegetation and warm temperate rainforest (Carr *et al.* 1992). In the Melbourne area, along with *Rubus discolor*, it is the worst weed in the *Eucalyptus ovata* forest, and a lesser weed of *E. viminalis* forest and adjoining *E. obliqua* L'Her. or *E. cephalocarpa* Blakely forests (G. Lorimer personal communication).

In the Blue Mountains, Japanese honeysuckle transforms ecosystems along creeks, where it smothers native vegetation and reduces growth and seed production of native shrubs and young trees (H. Paterson personal communication). In the Australian Capital Territory, a 1995 survey showed Japanese honeysuckle in 25 locations, mainly woodland, disturbed drainage lines and pine forests adjoining inner Canberra. In three locations it dominated an area of at least 30 × 30 m (M. Mulvaney personal communication). In Tasmania, it occurs only in heavily disturbed bushland area where its impact is low (S. Welsh personal communication).

The physical impacts of Japanese honeysuckle in New Zealand are similar. In 1995 it was included on the Forest Friendly list of plant species unsuited for planting because of their known weediness (Craw 1994). The most vulnerable conservation values appear to be those associated with open scrub, shrublands, woodlands, and the margins of forests, particularly where these occupy moist alluvial or colluvial sites. Wetland and riparian margins are especially vulnerable. Department of Conservation staff perceive that Japanese honeysuckle has the greatest impact in the lower half of the North Island and Nelson / Marlborough in the South Island, with lesser impacts in the remainder of the country.

In eastern North America, open habitats such as low shrublands may be completely smothered, and several habitat types such as glade communities and ravines are threatened. In forest interiors, particularly those of deciduous forests, Japanese honeysuckle vines cause the collapse of the understorey shrub layer and occasionally small canopy trees, preventing the establishment of new shrub populations. This leads to a simplified forest structure and lower floristic diversity. The secondary effects of these structural changes and floristic simplifications are unknown. It cannot be assumed that processes of natural succession will result in the disappearance of Japanese honeysuckle. Only in situations where it has invaded isolated gaps in otherwise mature and heavily shaded forests is it likely to be controlled by natural processes. In such instances its inability to climb the trunks of mature trees and reduced runner formation under full shade may confine it to the area first invaded (Sather, n.d.).

In oldfield sucessions in New Jersey, Japanese honeysuckle occurred in many vegetative associations, where it often inhibited later successional species (Myster and Pickett 1992). An investigation into both above-ground and below-ground effects of the competitive process, showed that Japanese honeysuckle had a greater effect on the allocation patterns of the host tree than on its photosynthesis (Dillenburg *et al.* 1995). This was mediated through competition between the vine and its host for soil nitrogen (Dillenburg *et al.* 1993a,b).

Japanese honeysuckle affects forestry operations in North America by interfering with site preparation (Little and Somes 1967, 1968) and by occupying intertree spaces in forests managed by selecting individual trees (Cain 1992). It is a particularly serious pest in Virginia apple orchards, where it handicaps cultivation, dries soil, and harbours mice (King 1966).

Many weed species have only a shortterm impact where they are part of the early stages of secondary succession (Williams 1997). While we might imagine that this situation would apply to Japanese honeysuckle at some sites – for example, it may disappear from forest clearings in 30 years – in other communities such as wetlands and shrublands its impact could be more long-lasting. We conclude that Japanese honeysuckle occupies only a fraction of the areas suitable for it, and that it will continue to spread over wide areas of Australia and New Zealand.

Beneficial

Japanese honeysuckle is widely grown for its fragrant blossom, and several cultivars are available. In North America, as well as being widely cultivated as an ornamental plant, it has been used as a road-bank stabilizer, and as food and shelter for wildlife (Handley 1945). It provides valued year-round browse for deer in Alabama, where the use of fertilizers has been recommended to increase its production and quality (Dyess *et al*. 1994). Its extensive spread in eastern USA is attributed to its use as protection of rail and road embankments (King 1966). Japanese honeysuckle is also said to have properties useful in herbal medicine (Van Galen 1995), and it may be of value to apiarists (Roberts 1979).

Weed management

In Australia, Japanese honeysuckle was omitted from some national compilations of significant weeds (e.g. Lamp and Collet 1979, Parsons 1995), but it has since been listed as a potential environmental weed and as a candidate species for preventative control (Csurhes and Edwards 1998). Control attempts have been rather localized, occurring close to urban areas in particular. In the Blue Mountains, Japanese honeysuckle is considered beyond control in many townships where the ratepayers complain about public land infestations invading private lands. However, it has not been declared noxious. Bush regeneration practices there involve simultaneous, integrated treatment of weed trees and Japanese honeysuckle; if only the trees are treated, serious opportunistic regrowth by Japanese honeysuckle occurs (M. Williams personal communication). Initial treatment by physical ripping, herbicide spraying, or scraping and painting of herbicides, followed by intensive secondary hand control, is found to be more efficient than trying to get a total initial kill (H. Paterson personal communication). Hand-pulling is employed for isolated plants and near water courses, and herbicides are used elsewhere (M. Williams personal communication).

Japanese honeysuckle is recognized as a serious threat to at least some of the protected natural areas in nine out of the 13 New Zealand's Department of Conservation conservancies. Despite this, in only five conservancies was any control attempted in 1996/97. Most control was on a small scale: Northland – 0.7% of total conservancy weed control budget; Auckland – one island only; Bay of Plenty – 9%; Tongariro/Taupo – 0.02%; East Coast – <1.0%. It is recognized as being hard to kill, although once an area is cleared new seedlings seldom appear (J. Craw personal communication).

Herbicides

In the Blue Mountains, large Japanese honeysuckle plants are cut or scraped then painted with undiluted glyphosate (360 g L^{-1}) and groundcover with few native plants, away from standing water, is sprayed with triclopyr (1:550). Both of these methods yield good mortality rates (M. Williams personal communication). Spraying with glyphosate at 1:50 has also been found useful (H. Paterson personal communication). In the Lismore area, spraying glyphosate at 1:100 dilution with penetrant, and cutting, scraping and painting stumps at swollen nodes with undiluted glyphosate, are recommended (Big Scrub Rainforest Landcare Group 1998). However, in the Blue Mountains the latter technique has been found to lead to resprouting (H. Paterson personal communication).

A test by DuPont (Australia) in western Victoria using 10 g Brush-Off® (metsulfuron-methyl) and 200 mL Roundup® (glyphosate) with 100 mL Pulse® (penetrant) per 100 L water eradicated 0.5 ha of Japanese honeysuckle, and provided a better result than any rate of metsulfuron-methyl applied alone (D. Matthews personal communication). At Warrandyte State Park, Victoria, a mixture of 1% triclopyr and glyphosate was found to reduce live foliage of Japanese honeysuckle by at least 90%; application was most effective during active growth when leaves are fresh and soft (G. Jameson personal communication).

In New Zealand, glyphosate, triclopyr plus picloram, clopyralid and metsulfuron-methyl all gave an initial high kill of Japanese honeysuckle. Although the results for chemical effectiveness were obscured by differences in soils between the sites, very little regrowth had occurred from the glyphosate and metsulfuron-methyl plots one year after a single spraying (Williams *et al*. 1998). Clopyralid has been found to be a particularly effective herbicide for Japanese honeysuckle at Hawkes Bay (G. Prickett personal communication). At Tiritiri Matangi Island the most effective control, without also killing grass, has been achieved using a spray comprising 10 g Escort® (metsulfuron-methyl) with 20 mL Pulse penetrant in 20 L water (S. Dunning personal communication).

Several chemicals have been tested for control of Japanese honeysuckle in North America. There is great variability among test results because of variability in season and rates of application, the geographical area in which research was conducted, and the duration of the research. The treatments trialed in North America are summarized as follows by Sather (n.d.). Glyphosate is the chemical of preference because it provides an opportunity to treat Japanese honeysuckle in the autumn after deciduous species have lost their leaves. Application of a 2% solution of glyphosate in autumn provides effective control. A follow-up treatment is recommended for plants that may have been missed in the first application. There does not appear to be any advantage to combining glyphosate with more persistent chemicals; tests of spring applications of glyphosate with dicamba, picloram, and triclopyr all gave poor results (Weber 1982). In field tests, amitrole gave better second year results than glyphosate (McClemore 1982), but results with amitrole in other tests were variable (Brender 1961, Shipman 1962, Little and Somes 1968).

A mid-August application of glyphosate at a rate of 2.2 kg ha^{-1} controlled 83% of actively growing Japanese honeysuckle in North Carolina (Yonce and Skroch 1989). Regehr and Frey (1988) found that glyphosate at 5.4 g L^{-1} (1.5% v/v) applied in winter (December) to Japanese honeysuckle growing on a fence killed the vines and eliminated most regrowth from basal and subterranean buds 28 months after treatment, without significantly damaging adjacent trees. Other chemicals reported as being effective against Japanese honeysuckle include: bromacil (Romney *et al*. 1976); DPX 5648 with diuron (Weber 1982); DPX 5648 with hexazinone (Weber 1982); hexazinone (Romney *et al*. 1976); picloram (Little and Somes 1967, Weber 1982) and picloram with 2,4-D amine (Miller 1985, McClemore 1982).

Chemicals that have given extremely variable results, result in top damage only, require pretreatment, or are reported to give poor results include: amitrole (Brender 1961, Shipman 1962, Little and Somes 1968); aminotriazole (Brender 1961); atrazine (Fitzgerald and Seldon 1973); dicamba (Little and Somes 1967, 1968, Weber 1982); 2,4-D (Shipman 1962; Little and Somes 1967, 1968); DPX 5648 (Weber 1982); fenac (Little and Somes 1967, 1968); fenuron (Little and Somes 1967, 1968); oryzalin (Bowman 1983); simazine (Fitzgerald and Seldon 1973); sulfometuron (Michael 1985); and triclopyr (Weber 1982).

Other treatments

The ineffectiveness of attempting to control Japanese honeysuckle by physical methods is illustrated by mowing experiments in the USA. Plants cut 5 cm above ground produced an even cover 20 cm tall after two months and 60 cm tall two years later. Both the original plants and cut runners resprouted and, after a second treatment, the yield of Japanese honeysuckle was greater than on control plots (Stransky 1984). These data suggest that consistent mowing on edges, such as along trails, might increase the number of stems, but could keep the length of runners under control and prevent vegetative invasion of adjoining areas (Sather, n.d.).

Grazing will help control, but not destroy, established stands of Japanese honeysuckle. It seems logical to assume that the effects of grazing would be similar to, but less predictable than, the effect of mowing (Brender 1961, Sather n.d.). However, at some Australian roadside sites, Japanese honeysuckle has vigorously colonized the ungrazed road verge grassland, but has not spread through the fence into adjacent cattle pasture (Figure 1), showing that consistent grazing pressure has the potential to slow or halt the plant's vegetative spread. On Tiritiri Matangi Island, a sheep-grazed paddock adjacent to an area badly infested by Japanese honeysuckle remains clear of the weed (S. Dunning personal communication).

Hand-pulling of Japanese honeysuckle has been tried on Tiritiri Matangi Island and found to be ineffective both in terms of effort expended and degree of control, with new plants regenerating from small fragments (S. Dunning personal communication). Hand-pulling in experimental plots at Takaka in the lower Cobb Valley, and in mainly native vegetation at Porirua, Wellington (V. Froude personal communication), also resulted in rapid regrowth from remaining stems. No Japanese honeysuckle seedlings were observed in plots cleared by hand pulling at Takaka (Williams *et al.* 1998).

Fire is sometimes recommended for Japanese honeysuckle control in America (Barden and Matthews 1980). In Australia, it has been found in the Blue Mountains that high intensity fires can significantly reduce infestations, but fires of moderate intensity lead to subsequent resprouting (H. Paterson personal communication). Japanese honeysuckle appears to be an opportunistic user of ash-bed nutrition in burned, formerly heavily disturbed areas (M. Williams personal communication).

Biological control with invertebrates has been mooted as a possible management option for Japanese honeysuckle (P. Syrett personal communication). There are likely to be agents that would be effective against it. However, Japanese honeysuckle appears to be mainly of conservation concern, so there would be no other sector with which to share the high development costs of a biological control program. Further, there may be limited conservation benefit in reducing the vigour of the weed where it poses no immediate conservation threat. More investigation is required to determine the part biological control can play in the management of Japanese honeysuckle.

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