

Biology and ecology of Japanese honeysuckle (*Lonicera japonica*) and its impacts in New Zealand

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Abstract

The world literature on Japanese honeysuckle (*Lonicera japonica*), and observations made throughout New Zealand on its history of introduction and spread, biology, ecology, and impacts, are summarised. Japanese honeysuckle does not fruit regularly in all areas of New Zealand but, once established, colonies can become extensive, e.g. 50 percent cover over an area of 50 ha. It is present throughout New Zealand, but particularly in the North Island. It is spreading in a wide range of scrub, wetlands, and other low-statured communities, and in damaged forests. Japanese honeysuckle is underestimated as a weed, but it is likely to be highly detrimental to conservation values.

1. Introduction

Japanese honeysuckle (*Lonicera japonica*) has been recognised as a weed of conservation land in New Zealand for at least a decade (Williams & Timmins 1990). It is present in most Department of Conservation (DOC) conservancies (Owen 1997). The potential impacts of Japanese honeysuckle are often underestimated because of an apparent slow rate of spread, while in other areas, e.g. northern Hawkes Bay, concern has been raised about its rapid spread (G.Y. Walls, pers. comm. 1996). This concern prompted a literature review and an investigation into what is known about Japanese honeysuckle in New Zealand generally.

2. Methods

International literature was searched and the information available about Japanese honeysuckle from New Zealand sources was compiled. All the DOC field centres and other sources within DOC were solicited for information. During ten days in March 1997 we visited many North Island areas where Japanese honeysuckle is conspicuous on conservation land. We travelled from Wellington through the Wairarapa to Palmerston North, Hawkes Bay, through the Urewera to the Rotorua area, around the Bay of Plenty, then south through the central North Island. We also made observations on Japanese honeysuckle in the course of other fieldwork in Northland, the Waikato, Nelson/Marlborough, the West Coast, and Canterbury. Most of these observations, particularly in the North Island, were made in March-April to maximise the probability of determining whether populations were fruiting.

At most sites visited during the main North Island study, brief notes were taken in a systematic manner on the composition of the vegetation being impacted on, the nature and extent of the Japanese honeysuckle infestation, and the reproductive stages of Japanese honeysuckle (Appendix, Section 7.1). Observations on flowering and fruiting phenology were made at regular intervals at two sites in the Nelson region and one in Wellington City, and less intensive observations were made by colleagues elsewhere.

3. Results and discussion

The results are presented using a format similar to that adopted for biological floras. Summaries from the literature (mainly from North America) and our original observations are mostly interwoven, although in a few sections they are presented separately.

3.1 TAXONOMY

Lonicera japonica Thunb., family Caprifoliaceae

Standard common name: Japanese honeysuckle

Other names: Chinese honeysuckle (USA.)

3.2 DESCRIPTION

Japanese honeysuckle is a perennial, trailing or climbing woody vine with tangled stems that are pubescent when young and generally reddish to purplish brown in colour (Webb et al. 1988). The bark is corky on older stems and becomes shredded, peeling readily. Stems are often 1-5 cm in diameter, many reaching 10 cm diameter on old plants. Annual rings are prominent in stem sections. (See also Section 3.6, Morphology.)

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. The leaves are opposite, simple, pubescent on the lower midrib, shining green on the upper surface, and yellowish green below. Leaves tend to change from a deep blue-green to yellow-green with age. Japanese honeysuckle is evergreen in New Zealand but deciduous in colder parts of North America.

Flowers are in axillary pairs, fragrant, with peduncles 0.5-2.5 cm long that are densely hairy. 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 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 1.0-3.0 cm. 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, 4.0–7.0 cm in diameter, are hard and green when immature and black when ripe. The 2 or 3 seeds are approx. 0.2 cm in diameter, ovate to oblong, with a flat to concave inner surface and with three ridges on the back.

3.3 HISTORY AND DISTRIBUTION

New Zealand

Japanese honeysuckle was offered for sale in 1872 in New Zealand (Esler 1988), and was first collected in the wild here in 1926 (Webb et al. 1988). It is assumed to have become naturalised in the Auckland area between 1940 and 1970. At the time of the preparation of *Flora of New Zealand* Vol. 4 (Webb et al. 1988) Japanese honeysuckle was described as “abundantly naturalised in many areas but less common in the southern parts of the South Island”. Ten years later this generalisation still holds. Japanese honeysuckle is widespread in the northern South Island but uncommon in the south (R.B. Allen, C.J. West, pers. comm. 1997). In 1995 it was included on the Forest Friendly list of plants unsuited for planting because of its known weediness (Craw 1994).

Japanese honeysuckle is currently listed as “widespread” or “spreading” in all North Island conservancies except Northland, where it is “isolated” (Owen 1997), albeit in a wide range of sites (Fromont & King 1992). In Auckland City it is increasing at a moderate rate from an incidence ranked as “medium” in 1970 (Esler 1988). 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). On the West Coast it is listed only as “isolated”, and has not yet established in the wild in Southland. Japanese honeysuckle is present in Otago (Allen 1978; Ward & Munro 1989) but has only recently been reported from protected natural areas there.

Rest of the world

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). It was introduced into the USA in 1806, and was widely cultivated by the 1860s. 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, pers. comm. 1996). It was widely cultivated in North America as an ornamental plant, as a road-bank stabiliser, and as food and shelter for wildlife (Handley 1945).

Japanese honeysuckle is widespread in other parts of the world, i.e. Hawaii (Cronk & Fuller 1995); the southern parts of Australia through New South Wales and Victoria, where it is regarded as a very serious threat to native vegetation (Carr et al. 1992); and in wastelands in parts of Southern Chile (P.A. Williams, pers. obs. 1997).

3.4 HABITAT

Climatic requirements

Japanese honeysuckle grows up to 1800 m above sea level (asl) 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 100 cm, 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 New Zealand, Japanese honeysuckle grows from sea level to 743 m asl, 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 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 (Appendix, Section 7.1).

Substrate

In North America, Japanese honeysuckle grows on a wide range of substrates from pH 4.0 to 7.9 and spreads most rapidly in soils above pH 6.0 (Leatherman 1955). It grows best on calcareous soils and moist forest soils, compared with excessively drained sandy soils, where it is limited by moisture availability. Seedling growth is much faster (30 cm vs. 9 cm) in a well drained fertilised soil than in fine sand (Leatherman 1955). Japanese honeysuckle is one of the few species tolerant of pollution from heavy metals and sulphur dioxide (Caiazza & Quinn 1980).

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.

Plant communities

Japanese honeysuckle is generally associated with disturbance, and has spread to old fields, roadsides, fence rows, prairies, sand barrens, and forest openings

in North America. 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). Japanese honeysuckle can invade established woodlands, particularly deciduous woodlands, but is limited by the deep shade of evergreen forest. Such woodlands are invaded when natural processes such as storms or Dutch elm disease create canopy openings (Thomas 1980; Slezak 1976). Invasion is particularly successful in moist woodlands and floodplain forests (Andrews 1919; Wistendahl 1958).

In New Zealand, Japanese honeysuckle 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. It has long been recognised as a weed of hedges in New Zealand (Gunning 1964). 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. Shrublands 4–6 m tall may be completely covered by particularly vigorous stands. Where Japanese honeysuckle grows with otherwise pure stands of bracken (*Pteridium esculentum*) the cover may vary according to the seasonal state of the bracken. Its extent in these situations is commonly 10 percent cover over a 20 ha area, and in places is as extensive as 50 percent 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 (Appendix, Section 7.1).

In central and eastern North Island areas the main native species most frequently associated with Japanese honeysuckle in vegetation other than wasteland are, in rank order, mahoe (*Melicytus ramiflorus*), karamu (*Coprosma robusta*), lacebark (*Hoberia sexstylosa*), kohuhu (*Pittosporum tenuifolium*), manuka (*Leptospermum scoparium*), bracken (*Pteridium esculentum*), and fivefinger (*Pseudopanax arboreus*). The most frequent weeds at the same sites are several species of Convolvulaceae, blackberry (*Rubus* species), and willows (*Salix* species). In combination, these species are suggestive of early secondary vegetation on moist, fertile sites.

3.5 PLANT AND 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). Nothing is known of the invertebrates associated with Japanese honeysuckle in New Zealand, apart from the observation that bumble bees (*Bombus* spp.) prise open flowers to extract the pollen (P.A. Williams, pers. obs.). Japanese honeysuckle responds rapidly to herbivory by both mammals and insects by allocating resources to stems and leaves and so it recovers quickly, which gives it an advantage over native congeners (Schierenbeck et al. 1994).

Japanese honeysuckle is browsed by a range of mammals, and its expansion in Hawkes Bay may be associated with a decline in feral goat numbers. It spreads rapidly when forest reserves are fenced and animals are excluded. Possums (*Trichosurus vulpecula*) in captivity nibble the leaves. The fruits are eaten, but are less favoured than fruit of several other weed species (Williams & Karl, unpubl. data).

3.6 MORPHOLOGY

Japanese honeysuckle universally produces long stems that twine 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 2.0 m thick on a horizontal plane (Williams & Timmins 1998). This method of climbing limits the plant to hosts with stems less than 15 cm in diameter and prevents it from climbing the boles of tall trees. It can utilise hanging branches and other lianes to the same effect. In the presence of supporting foliage and other vines it can reach 7 m tall (North America), or 15 m in New Zealand (Appendix, Section 7.1). The lateral runners branch regularly, more so than in most vines (Temamura et al. 1991), and produce roots at the nodes where they contact the ground. Such stems may extend 15 m from the original point of contact in a single growing season (Little 1961). In addition to their ability to root, the runners create new habitat for further cohorts of twining stems. Even in the absence of supporting woody vegetation, the result is a dense matt up to 1.5 m deep forming 100 percent cover.

Stems are commonly 0.5–2.0 cm in diameter. At one site in North America stems of 1–2 cm diameter were 5–12 years old, and at another site stems of 1.0–1.5 cm diameter were 4–9 years old. The thickest recorded stem, 18 cm in diameter, was of unknown age (Leatherman 1955).

Seven stems from mostly northern South Island localities were cut near ground level. Stems 2–3 cm in diameter are likely to have between 4 and 10 years of rings which is assumed to equate to their age in years (Table 1). Maximum size is larger for a given age, and growth rates are therefore faster, than those reported in North America.

TABLE 1. RELATIONSHIP BETWEEN STEM DIAMETER AND INFERRED AGE OF *LONICERA JAPONICA* IN NEW ZEALAND.

Location	Diameter (cm)	No. of rings
Motueka	1.1	3
Cobb Valley	1.2	3
Motueka	1.8	4
Rotorua	1.8	7
Cobb Valley	2.2	4
Morere Springs	2.3	10
Cobb Valley	3.3	5

In dense stands of Japanese honeysuckle, such as those in open fields and forest margins, the main surfaceroots 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 a metre, and horizontal lengths up to 3 m (Leatherman 1955). Once runners from a single parent plant have established roots, they will resprout as separate 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 oval cotyledons are small, foliar, and green. The first true leaves, which appear several days after the cotyledons have opened, are simple. The first adult leaves are indented. Taproot development occurs simultaneously with leaf development. After 52 days in full sun, 25 percent of full sun, and 5 percent 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 5 months from germination and the first branches appear in this period (Leatherman 1955). Overall, seedling growth is slow for the first two years (Little & Somes 1967).

Perennation

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

3.7 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 percent of full sun) are well above the level 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 of less than 5 percent 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 percent, but survival and growth were still high at 2 percent light intensity (Baars & Kelly 1996). A light compensation point of 0.9 was calculated and, together with the aforementioned survival figures, indicates a high degree of shade tolerance, at least for vegetative growth (Robertson et al. 1994).

Studies aimed at predicting the response of Japanese honeysuckle to anticipated increases in atmospheric carbon dioxide found that the biomass of cuttings after 54 days growth was 135 percent and 76 percent greater at 675 and 1000 $\mu\text{l CO}_2/\text{litre}$, respectively, than at 350 $\mu\text{l CO}_2/\text{litre}$ (Sasek & Strain 1991). Morphologically, CO_2 enrichment tripled the number of branches (675 or 1000 $\mu\text{l/litre}$) and increased total branch length by a factor of six (1000 $\mu\text{l/litre}$). At the two higher CO_2 concentrations the total leaf area increased by 50 percent. 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 & Strain 1992). There is no information to suggest that the situation would be different in New Zealand.

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 a native North American species, *Lonicera sempervirens* (6.2 vs. 4.4 mmol/m/s under the canopy; 4.4 vs. 3.0 mmol/m/s in the open) (Schierenbeck & 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 help explain its invasive ability.

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

3.8 PHENOLOGY

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 it 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 & Timmins, in prep.).

In North America, the first floral buds appear approximately one month before flower expansion. They are borne on the current year's growth. One peduncle which bears two foliaceous bracts is borne in the axil of each leaf of a reproductive branch. The paired, sessile, club-shaped floral buds are covered with glandular hairs and are above the bracts. The flower buds are green when young and turn white before opening. Those nearest the base of the current year's growth open first, and flowers continue to bloom at nodes near the tip of the branch as the season advances (Leatherman 1955). In North America, 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, this sequence is common on plants that produce fruit.

In eastern North America, the flowering period of Japanese honeysuckle is from late April to July and occasionally until November. In New Zealand, flowers are

present from mid August until April (and occasionally through into June) in various parts of the country - a period of seven months in both countries.

3.9 REPRODUCTION

Floral biology

Flowers can be produced from cuttings after two years (Leatherman 1955), but there appear to be no studies that have recorded the time to flowering from seed. Flowers 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. Cross-pollination is effected by insects and hummingbirds in the USA (Leatherman 1955). Insects involved include Hymenoptera (*Apis mellifera*, *Bombus* spp., and hornets), Lepidoptera (a hawk moth), and Diptera (syrphid flies). All these groups are present in New Zealand, although hawk moths are more common in the north (R. Toft, pers. comm. 1997).

Seed production and dispersal

Japanese honeysuckle is generally described as producing abundant fruit in North America. For example, stems 30 cm long produced an average of 27 flowers, of which 57 percent produced fruit, i.e. 15.4 fruits per branch (Leatherman 1955). Fruit production in New Zealand has been recorded as light, sufficiently so to limit the weed potential in the Auckland area (Esler 1988). Similarly, near Nelson, two large stands produced no fruit in the 1997 autumn despite producing abundant flowers over several months (Table 2). The Cobb Valley stand produced no fruit in 1996 either, although 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, other stands produced abundant fruit, in some instances in very similar numbers - about 15 per stem (Table 3) - to those recorded from North America. We have also seen fruiting plants in many scattered localities in the lowlands of the lower North Island (Appendix, Section 7.1) and the northern half of the South Island.

Our observations suggest that in many instances fruit is produced most abundantly on side shoots of second-year or older wood, often towards the

TABLE 2. FLORAL PHENOLOGY OF *LONICERA JAPONICA* AT WELLINGTON, COBB VALLEY, AND NELSON CITY OVER 1996-97.

Site	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Wellington	0,1	1,2	1,3	1,3	1,3	1,3	1,3	3,4	2,4	2,4
Cobb Valley	0,1	1	1,3	1,3	1,3	1,3	1,3	2
Nelson City	0,1	1	1,3	1,3	1,3	1,3	1,3	2

0, vegetative only; 1, buds; 2, flowers; 3, many flowers; 4 fruit

TABLE 3. FRUIT PRODUCTION ON *LONICERA JAPONICA* STEMS.

Location	Plants(n)	Month/Year	Stem length(cm)	Nodes(n)	Fruits(n)
Whangarei	20	04/97	26. ± 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
Hawke's 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

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 grams and contain 84.0 percent water. The flesh contains 2 or 3 seeds in a mucilaginous pulp which constitutes 64.4 percent of the dry weight of the fruit (Williams & Karl 1996).

In North America, fruits are eaten by a wide range of birds, from turkeys down to small passerines, many of which are native. 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). Japanese honeysuckle fruits are also eaten by mammals such as deer, but it is not known whether seeds pass through the gut.

In New Zealand, the fruit is eaten by blackbirds, thrushes, and silvereyes in the Nelson region (Williams & Karl 1996). Possums will eat the fruits, some of which pass through apparently undamaged, although the sample was too small to test the effect of gut passage (P.A. Williams and B.J. Karl, unpubl. data).

Seed germination

Data on seed germination are equivocal. Data in Leatherman (1955) show 63 percent germination in soil after no stratification treatment, following storage at 4–16°C. Yet the conclusion was that Japanese honeysuckle seeds require a period of cold temperatures to break dormancy, and this may be achieved by exposure to temperatures of 5–8°C for 60 days. Germination then occurs in spring, as soon as air temperatures reach above 10°C. Germination occurs over a wide temperature range but was greatest at a fluctuating daily range of 18–25°C (Leatherman 1955).

Japanese honeysuckle seedlings have only a small amount of endosperm, and the cotyledons contain chlorophyll at an early stage. Two true leaves are produced by the time the seedling reaches 3 cm tall. The shoot develops more rapidly than the root during early stages. After 52 days, shoot lengths were 6.2 cm and 10.6 cm respectively for plants grown outside in the sun or in shade, and their root/shoot ratios were 3.7 and 6.4, respectively (Leatherman 1955).

3.10 POPULATION DYNAMICS

Despite the considerable literature on growth rates of individual stems, and the frequency of Japanese honeysuckle colonies in several kinds of vegetation, there appear to be no data on the dynamics of individual populations at any stage of the life-cycle. This results 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.

Seedlings appear to be extraordinarily uncommon in the wild in New Zealand. Despite extensive searching we have seldom found one in the wild, even in the vicinity of plants producing abundant fruit and in the presence of other woody seedlings, including those of *Muehlenbeckia australis*. With possibly a few exceptions, all young shoots which appear to be seedlings are probably connected to runners from adjacent plants. Seedlings have been reported from an urban garden in Christchurch (W.R. Sykes, pers. comm.1997).

3.11 ECOLOGICAL IMPACT

North America

Japanese honeysuckle stems twine around other plants and eventually grow over their crowns, with the result that the hosts are completely smothered. Open habitats such as low shrublands may be completely smothered, and in eastern North America, several habitat types such as glade communities and ravines are threatened. However, it is not able to climb tall trees with thick stems. In forest interiors, particularly of deciduous forests, the 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 boles of mature trees and reduced runner formation under full shade may confine it to the area first invaded (Sather, undated).

An investigation into the precise nature of the competitive process, examining both above-ground and below-ground effects, showed that Japanese honeysuckle had a greater effect on the actual allocation patterns of the host tree than on its photosynthesis (Dillenburg et al. 1995), and 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 & Somes 1967, 1968) and by occupying inter-tree spaces in forests managed by selecting individual trees (Cain 1992).

New Zealand

The physical impacts of Japanese honeysuckle in New Zealand are very similar to those described above for North America. The conservation values most vulnerable 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 also vulnerable.

The perception of DOC conservancy staff of the impact of Japanese honeysuckle on sites of high conservation value can be summarised as five decreasing orders (Owen 1997, and a more recent survey):

- (4) known to be affecting conservation sites: all the North Island except Nelson/Marlborough;
- (3) present, but only suspected of affecting conservation sites: Northland and Auckland;
- (2) present, not affecting conservation sites, but considered to have potential to impact: West Coast and Southland;
- (1) present, but effects not identified: Canterbury;
- (0) not considered to have potential for impacts.

From our own opportunistic observations, primarily from roadsides, made over the last two years, we concur with these rankings. Japanese honeysuckle is very abundant in northern Hawke's Bay, Gisborne, Rotorua, Bay of Plenty, parts of the Waikato and Taupo basins, and in the hilly parts of the Wellington region. It is also abundant in the Wanganui and Taranaki regions (C. Ogle, pers. comm. 1996). It is considered a problem but is probably less abundant in the western Waikato (J. Roxburgh, pers. comm. 1996).

Overall, Japanese honeysuckle is associated with the hilly landscapes where there are untrimmed roadsides and unattended land and associated areas of shrubbery, scrub, and forest remnants. In the districts where it is even moderately abundant, its distribution is highly patchy, i.e. there are frequently large and conspicuous colonies separated by many kilometres. These patches are often closely associated with human settlements such as small villages, schools, and even individual farmhouses. This distribution pattern is consistent with a plant that is initially distributed by humans, with occasional secondary spread, principally by birds and possibly by other animals. Grazing mammals may also assist spread by transporting vegetative fragments. This secondary dispersal is slow, as evidenced by the infrequency of seedlings. Once established, individual patches develop primarily by vegetative spread. The pattern also suggests that the reason that some large areas of habitat suitable for Japanese honeysuckle are at present not infested is simply because it has not arrived there yet.

Many weed species have only a short-term 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 its impact could be more long-term.

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 New Zealand. For example, in the vicinity of Lake Taupo it is confined to a few well established localities, but can be expected to spread slowly to the large areas of similar habitat throughout the Taupo catchment. If this occurs, riparian woodlands and scrub, and wetland margins in particular, will be heavily impacted.

3.12 WEED MANAGEMENT

Japanese honeysuckle is recognised as a serious threat to at least some protected natural areas in 70 percent of 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 (Tiritiri Matangi Island), Bay of Plenty (9%), Tongariro/Taupo (0.02%), and East Coast (<1.0%).

Physical methods

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 as measured by dry matter was greater than on control plots (Stransky 1984). These data suggest that repeated consistent mowing in edge situations such as along trails might increase the number of stems but could keep the length of runners under control, thus preventing vegetative invasion of adjoining areas (Sather, undated).

Grazing will help control, but not destroy Japanese honeysuckle, and it seems logical that the effects of grazing would be similar to, but less predictable than, the effect of mowing (Brender 1961; Sather, undated).

Hand pulling Japanese honeysuckle has been tried on Tiritiri Matangi Island and in experimental plots, but resulted only in rapid regrowth from the remaining stems. No Japanese honeysuckle seedlings were observed in plots cleared by hand pulling at Takaka (Williams & Timmins 1998).

Herbicides

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 summarised as follows by Sather (undated).

Glyphosate (Roundup) 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 in combining it with more persistent chemicals, and 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 are variable (Brender 1961; Shipman 1962; Little & Somes 1968).

Other chemicals that have been reported as 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 & Somes 1967; Weber 1982) and picloram with 2,4-D amine (Miller 1985; McClemore 1982).

Chemicals that have given extremely variable results, or have resulted in top damage only, or required pretreatment, or are reported to have given poor results include: amitrole (Brender 1961; Shipman 1962; Little & Somes 1968); aminotriazole (Brender 1961); atrazine (Fitzgerald & Seldon 1973); dicamba (Little & Somes 1967, 1968; Weber 1982); dicamba with 2,4-D (Prine & Starr 1972); 2,4-D (Shipman 1962; Little & Somes 1967, 1968); DPX 5648 (Weber 1982); fenac (Little 1961); fenuron (Little 1961); oryzalin (Bowman 1983); simadine (Fitzgerald & Seldon 1973); sulfometuron (Michael 1985); and triclopyr (Weber 1982).

Roundup (glyphosate), Grazon (triclopyr), Versatil (clopyralid), and Escort (metasulphuron) all gave an initial high kill of Japanese honeysuckle, and although the results for chemical effectiveness were obscured by differences in soils between the sites, very little regrowth had occurred from the Roundup and Escort plots one year after a single spraying (Williams & Timmins 1998). Versatil has been found to be a particularly effective spray for Japanese honeysuckle in Hawkes Bay (G. Prickett, pers.comm. 1996).

Biological control

Biological control with invertebrates has been mooted as a possible management option for Japanese honeysuckle (P. Syrett, pers. comm. 1996), but is unlikely to provide the hoped-for solution. The distribution of Japanese honeysuckle in dispersed clumps would make it difficult for any control agent to disperse and successfully attack all populations. Japanese honeysuckle seems to be mainly of conservation concern, which means that there would be no other industry with which to share the high development costs of a biological control programme.

Control strategy

Given Japanese honeysuckle's capacity for rapid expansion by vegetative growth, but more limited ability to establish new populations, there is the potential to control any new population in a catchment or conservancy as soon as it appears. Already it is too late to apply this strategy, on a conservancy basis at least, in most North Island conservancies. In contrast, over much of the South Island the possibility still exists to mount a weed-led campaign before that option is lost. Over some of its North Island range this approach could still be applied on a catchment basis. In most conservancies, however, Japanese honeysuckle should be controlled only as part of a site-led programme (Williams 1997) because it is too well established in areas with low conservation values.

4. Conclusions

Japanese honeysuckle is a deceptive weed. It is a plant most people are familiar with, yet, because it has such appealing flowers and fragrance, and because it

impacts mostly on shrublands and lower statured vegetation, its weed potential in New Zealand has been underestimated. This results partly from its slow rate of establishing new populations; new plants establish rarely, in comparison with old man's beard, for example, yet once they become entrenched they can quickly spread over large areas. As with most weed invasions, the damage caused is very difficult to define precisely. It is perhaps not a problem beyond the initial stages of forest successions, but in communities of lower stature, especially open-canopied forest and the few remaining wetlands, its impacts could be severe. While it is present almost throughout New Zealand, Japanese honeysuckle is still expanding quite rapidly in many areas, and its full distribution and impact on conservation land have yet to become apparent.

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7. Appendix

7.1 SITE FACTORS AND VEGETATION ASSOCIATED

No.	Locality	Grid	Alt. (m.asl)	Physiography & vegetation	Dimensions & area	Main species	JHS cover %
1	Plimmerton Taupo swamp (a)	R26 676 148	20	Stream banks scrub, forest, vineland	100m x 10m 0.1 ha	<i>Salix</i> spp., <i>Populus</i> spp., <i>Coprosma robusta</i> , <i>Muehlenbeckia australis</i> , JHS	20
2	Plimmerton Taupo swamp (b)	R26 676 142	20	swamp flaxland, vineland	50m x 10m 0.05 ha	<i>Rubus</i> sp., <i>Pbormium tenax</i> , <i>Cortaderia fulvida</i> , <i>Pteridium esculentum</i> , <i>Cytisus scoparius</i> , JHS	40
3	Pauatahanui Pauatahanui inlet	R26 703 096	1	banks, vineland, scrub	1km x 5m 0.5 ha	<i>Rubus</i> sp., <i>Ulex europaeus</i> , JHS	80
4	Woodville Pahiatua Hill (a)	T24 467 743	200	bluffs and toe- slopes forest, scrub, vineland	500m x 15m 0.75 ha	<i>Beilschmiedia tawa</i> , <i>Alectryon excelsus</i> , <i>Hoheria sexstylosa</i> , <i>Podocarpus ballii</i> , <i>Muehlenbeckia australis</i> , <i>Convolvulus arvensis</i> , JHS	20
5	Woodville Pahiatua Hill (b)	T24 467 743	200	low terrace woodland, vineland	50m x 50m 0.25 ha	<i>Sophora tetrapetala</i> , <i>Beilschmiedia tawa</i> , <i>Rubus</i> sp., JHS	25
6	E. Pahiatua Ngaturi bridge	T24 578 778	100	scarp forest,scrub	1km x 150m 15 ha	<i>Sophora tetrapetala</i> , <i>Podocarpus ballii</i> , <i>Kunzea ericoides</i> , JHS	15
7	E. Pahiatua Makuri township	T24 645 702	100	scarp vineland	100m x 100m 1.0 ha	<i>Rubus</i> sp., <i>Convolvulus arvensis</i> , JHS	80
8	Huntermville Silver Hope	S22 259 350	250	poorly drained terrace forest	100m x 100m 1.0 ha	<i>Dacrycarpus dacrydioides</i> , <i>Beilschmiedia tawa</i> , <i>Melicytus ramiflorus</i> , <i>Pseudopanax arboreus</i> , <i>Schefflera digitata</i> , <i>Pteridium esculentum</i> , <i>Muehlenbeckia australis</i> , JHS	15
9	Huntermville Bruce park	S22 259 349	250	Bluff scrub	100m x 50m 0.5 ha	<i>Coprosma robusta</i> , <i>Melicytus ramiflorus</i> , <i>Acer pseudoplatanus</i> , <i>Hoheria sexstylosa</i> , JHS	10

WITH JAPANESE HONEYSUCKLE (JHS) IN NEW ZEALAND

Distribution	Adjacent vegetation	Max. ht (m)	Phenology	Other weeds	Prognosis	Comments
marginal	<i>Salix</i> spp. forest	3	fl.few fr.few	<i>Paraserianthes lophantha</i> , <i>Senecio angulatus</i> , <i>Convolvulus arvensis</i>	Spread restricted by water	
marginal	<i>Pbormium tenax</i>	3	fl.few fr. none	<i>Rubus fruticosus</i> <i>Convolvulus arvensis</i>	Expansion likely	
marginal	saltmarsh flat	1.5	fr.none fl.none	<i>Vinca major</i> , <i>Rubus fruticosus</i> , <i>Ulex europaeus</i>	No change likely, restricted by saltmarsh	
marginal & dispersed	similar to main	8	fl. few fr. none	<i>Convolvulus arvensis</i> , <i>Leycesteria formosa</i> , <i>Rubus</i> sp.	Expansion through forest likely	
marginal & dispersed	as for main species, plus <i>Alectryon excelsus</i> , <i>Hoberia sexstylosa</i>	15	fl. none fr.none	<i>Rubus fruticosus</i> , <i>Salix</i> spp., <i>Tradescantia fluminensis</i>	Expansion through forest likely	
marginal & dispersed	as for main species, without JHS	6	fl. none fr. ?	<i>Clematis vitalba</i> , <i>Acer pseudoplatanus</i> , <i>Ulex europaeus</i> , <i>Convolvulus arvensis</i> , <i>Rubus fruticosus</i> , <i>P. lophantha</i> , <i>Salix</i> sp., <i>Cytisus scoparius</i>	Expansion likely	
marginal	<i>Acer pseudoplatanus</i> forest	8	fl.none fr.none	<i>Convolvulus arvensis</i> , <i>Acer pseudoplatanus</i> , <i>Euonymus</i>	Little change likely deep into forest	Runners extend
dispersed & marginal	similar tall forest	15	fl.none fr.none	<i>Salix</i> spp., <i>P. lophantha</i> , <i>Crocsmia x crocosmifolia</i> , <i>Convolvulus arvensis</i> , <i>Cobaea scandens</i> , <i>Rubus fruticosus</i> , <i>Hedera helix</i> , <i>Selaginella kraussiana</i>	Expansion likely	
dispersed	similar scrub with some tall trees	15	fl.none fr.none	<i>Cobaea scandens</i> , <i>Rubus fruticosus</i> , <i>Vinca major</i> , <i>Convolvulus arvensis</i>	Spreading	

No.	Locality	Grid	Alt. (m.asl)	Physiography & vegetation	Dimensions & area	Main species	JHS cover %
10	Hunterville Simpsons	T22 320 418	300	terrace treeland	n.a.	<i>Dacrycarpus dacrydioides</i> , <i>Pseudopanax crassifolius</i> , <i>Hoberia sexstylosa</i> , <i>Pittosporum tenuifolium</i>	0
11	Manawatu Shannons Ridge	T24 456 953	240	ridge, scrub and low forest	50m x 10m 0.5 ha	<i>Melicytus ramiflorus</i> , <i>Hoberia sexstylosa</i> , <i>Pseudopanax crassifolius</i> , <i>Beilschmiedia tawa</i> , JHS	20
12	Manawatu Gorge (general areas)	T24 45- 96-	100	hill slopes and bluffs, mixed scrub	1km x 200m 20 ha	<i>Melicytus ramiflorus</i> , <i>Brachyglottis repanda</i> , <i>Cordyline australis</i> , <i>Phormium cookianum</i> , <i>Pittosporum tenuifolium</i> , <i>Hoberia sexstylosa</i> , <i>Muehlenbeckia australis</i> , JHS	10
13	Manawatu Gorge (south side)	T24 459 957	150	hill slope low forest	50m x 50m 0.25 ha	<i>Leptospermum scoparium</i> , <i>Melicytus ramiflorus</i> , <i>Pittosporum tenuifolium</i> , <i>Brachyglottis repanda</i> <i>Geniostoma ligustrifolia</i> , JHS	50
14	Manawatu Gorge Balance Bridge	T24 494 925	100	terrace low forest	50m x 20m 0.10 ha	<i>Melicytus ramiflorus</i> , <i>Alectryon excelsus</i> , <i>Pittosporum eugenioides</i> , <i>Hoberia sexstylosa</i> , <i>Muehlenbeckia australis</i> , <i>Dacrydium dacrydioides</i> <i>Beilschmiedia tawa</i> , JHS	10
15	Hawkes Bay Lake Tutira	V20 456 138	200	road side lake edge	1km x 40m 4.0 ha	<i>Rubus fruticosus</i> , <i>Salix babylonica</i> , <i>Typha orientalis</i> , <i>Cordyline australis</i> <i>Pseudopanax arboreus</i>	80
16	Hawkes Bay Morere Springs (a)	X19 251 352	180	hill slope shrub-vine land	1km x 0.5km 50.0 ha	Revegetation plantings of <i>Leptospermum scoparium</i> , <i>Coprosma robusta</i> , <i>Rubus fruticosus</i> , JHS	50
17	Hawkes Bay Morere Springs (b)	X19 253 352	100	hill slope forest	1km x 0.5km 50.0 ha	<i>Melicytus ramiflorus</i> , <i>Pseudopanax arboreus</i> , <i>Rhopalostylis sapida</i> , JHS	< 1.0

Distribution	Adjacent vegetation	Max. ht (m)	Phenology	Other weeds	Prognosis	Comments
was marginal	similar	12	fl.none fr.?	<i>Cobea scandens, Leycesteria formosa, Convolvulus arvensis, Hedera helix, Euonymus europaeus, Berberis darwinii, Crataegus monogyna, Buddleja davidii</i>	Controlled	Proof of successful control
marginal	similar	3	fl.none fr.none	<i>Cytisus scoparius, Rubus fruticosus</i>	Spreading slowly	Not spread for 5 years
marginal and dispersed	similar	15	fl.few fr.few	<i>Clematis vitalba, Cytisus scoparius, Chamaecytisus palmensis, Salix spp., Vinca major, Senecio mikantoides, Passiflora mollissima, Convolvulaceae Agapantha orientalis</i>	Spreading	Notes relate to extensive infestations at entrance to the gorge
dispersed	similar	8	fl.none fr.few	none	Spreading	Encouraged by ground instability and occasional fire
dispersed	similar	5	fl. none fr. few	<i>Chamaecytisus palmensis, Convolvulaceae, Crocosmia x crocosmifolia, Tradescantia fluminensis, Vinca major</i>	Spreading	Associated with rubbish dumping
marginal	limited by lake	5	fl.few fr.none	<i>Robinia pseudoacacia, Tradescantia fluminensis, Ulmus x hollandica, Passiflora mollissima, Vinca major, Leycesteria formosa, Hedera helix, Pinus radiata, Chamaecytisus palmensis, Rubus fruticosus, Salix spp., Convolvulaceae</i>	Spreading	
dispersed	forest (see next site)	6	fl.few fr. some	<i>Rubus fruticosus, Salix sp., Cotoneaster sp.</i>	Spreading	Friable ash/mudstone soils
dispersed	similar	5	fl.none fr.none	<i>Tradescantia fluminensis</i>	Spreading	

No.	Locality	Grid	Alt. (m.asl)	Physiography & vegetation	Dimensions & area	Main species	JHS cover %
18	Whataroa Te Raupo (a)	W18 829 564	180	scarp and toe-slope treeland, vineland	500m x 250m 12.5 ha fr.?	<i>Sophora tetraptera</i> , <i>Dacrycarpus dacrydioides</i> , <i>Podocarpus ballii</i> , <i>Pseudopanax arboreus</i> , <i>Pittosporum tenuifolium</i> , <i>Alectryon excelsus</i> , <i>Coriaria arborea</i> , JHS	30
19	Whataroa Te Raupo (b)	W18 829 564	180	hill slopes, forest, vineland	1km x 400m 40 ha	<i>Sophora tetraptera</i> , <i>Hoberia sexstylosa</i> , <i>Melicytus ramiflorus</i> , <i>Pittosporum tenuifolium</i> , JHS	10
20	Rotorua Tarawera landing	U16 057 274	310	Roadside bank and hill slope scrub, low forest vineland	50m x 50m 0.25 ha	<i>Melicytus ramiflorus</i> , <i>Pseudopanax arboreus</i> , <i>Leptospermum scoparium</i> , <i>Coriaria arborea</i> , JHS	80
21	Lake Tarawera Te Wairoa stream	U16 056 272	300	Scarp, toe-slopes lake margin scrub, treeland, vineland	1km x 300m 30 ha	<i>Cyathea medullaris</i> , <i>Ulex europaeus</i> , <i>Pittosporum tenuifolium</i> , <i>Coprosma robusta</i> , <i>Coriaria arborea</i> , wetland species, JHS	50
22	Rainbow Mountain	U16 063 149	743	hill slopes forest and scrub	100m x 25m	<i>Weinmannia racemosa</i>	<1
23	Kaituna Lagoon	U14 074 773	10	plain forest, treeland, vineland	1km x 500m 50 ha	<i>Dacrycarpus dacrydioides</i> <i>Melicytus ramiflorus</i> , JHS	30
24	Matata Awatarariki stream	V15 396 617	20	gully, bluffs scrub, vineland	1km x 200m 20 ha	<i>Melicytus ramiflorus</i> , <i>Pseudopanax arboreus</i> , <i>Coprosma robusta</i> , <i>Coriaria arborea</i> , <i>Rubus fruticosus</i> <i>Leptospermum scoparium</i> , <i>Cyathea medullaris</i> , JHS	15
25	Otariki Braemar Rd wetland	V15 37- 51-	60	wetland, shrubland, rushland	0.5km x 100m 5 ha	<i>Leptospermum scoparium</i> , <i>Pbormium tenax</i> , <i>Baumea rubiginosa</i> , <i>Gleichenia circinata</i> <i>Coprosma tenuicaulis</i> , <i>Cordyline australis</i> , <i>Blechnum</i> sp., JHS	1
26	Lake Taupo Tauranga - Taupo river	T18 615 506	400	treeland scrub shrubland	1.0km x 100m 10 ha	<i>Sophora microphylla</i> , <i>Kunzea ericoides</i> , <i>Coprosma robusta</i> , <i>Pittosporum tenuifolium</i> , <i>Pteridium esculentum</i> , <i>Melicystus ramiflorus</i> , JHS	80
27	Northland Kaihu Valley	P07 755 017	100	shrubland	100 m x 30 m 0.3 ha	<i>Leptospermum scoparium</i> , <i>Pteridium esculentum</i> , <i>Podocarpus ballii</i> <i>Coprosma robusta</i> ., JHS	20

Distribution	Adjacent vegetation	Max. ht (m)	Phenology	Other weeds	Prognosis	Comments
dispersed	similar	12	fl.few	<i>Rubus fruticosus</i> , <i>Salix fragilis</i> , <i>Pinus radiata</i>	Spreading	A dramatic example, control no longer possible
dispersed & marginal	similar	15	fl.few fr.much	<i>Rubus fruticosus</i> , <i>Berberis darwinii</i> , <i>Cytisus scoparius</i>	Spreading	Tallest trees beyond reach, light pools vulnerable
dispersed & marginal	similar	10	fl.few fr.much	<i>Rubus fruticosus</i> , <i>Teline monspessulana</i> , <i>Ulex europaeus</i> , <i>Buddleija davidii</i> , <i>Erica lusitanica</i>	Spreading	
dispersed	similar	8	fl.few fr.some	<i>Salix</i> spp., <i>Racosperma mearnsii</i> , <i>Clematis vitalba</i>	Spreading	Much <i>C. vitalba</i> previously on site eliminated
marginal	similar	8	fl.few fr.none	<i>Cotoneaster</i> spp., <i>Erica lusitanica</i> , <i>Berberis darwinii</i> , <i>Salix fragilis</i> , <i>Cytisus scoparius</i> , <i>Pinus</i> spp. (5)	May spread slowly	
dispersed	pasture	8	fl.many fr.much	<i>Ligustrum sinense</i> , <i>Calystegia</i> sp., <i>Berberis glaucocarpa</i> , <i>Rubus fruticosus</i> , <i>Salix cinerea</i>	Spreading within forest patch	JHS causing major disruption to stand regeneration
marginal	<i>Metrosideros excelsa</i> forest	6	fl.few fr.much	<i>Ulex europaeus</i> <i>Cortaderia</i> spp., <i>Paraserianthes lophantha</i> , <i>Pyracantha</i> sp., <i>Salix cinerea</i> , <i>Ligustrum sinense</i> , <i>Rubus fruticosus</i>	Not expected to spread	
marginal & dispersed	similar	4	fl.few fr.some	<i>Rubus fruticosus</i> , <i>Salix cinerea</i> , <i>Calystegia</i> sp.	Spreading through wetland	Rooting at every node in swamp
marginal & dispersed	similar	12	fl.few fr.few	<i>Rubus fruticosus</i> <i>Calystegia</i> sp., <i>Salix cinerea</i> , <i>Populus</i> sp.	Spreading in catchment	
marginal	farmland	7	fl.none fr.some	<i>Ulex europaeus</i>	Very slow spread	