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ECOLOGICAL ROLE OF BUDDLEIA *(BUDDLEJA DAVIDII)* IN STREAMBEDS IN TE UREWERA NATIONAL PARK

Summary: Replacement patterns under buddleia *(Buddleja davidii)* groves aged between 2 and 17 years were studied in streambeds in the western Ikawhenua Range and in the upper Waioeka catchment, Te Urewera National Park. Height and basal diameter growth followed an exponential pattern, with rapid early growth (0.5 m/year and 1 cm/year respectively), levelling off after 15 years or more. Intense self-thinning occurred in younger stands. Typical forest floor vegetation was developing within 15 years of colonisation by buddleia. Seedlings of ten indigenous trees and shrubs were widespread under buddleia, with primary colonising species (e.g. *Hebe stricta, Kunzea ericoides)* more common under young stands, and other seral species (e.g. *Pseudopanax arboreus, Melicytus ramiflorus, Aristotelia serrata)* more common under older stands. Buddleia quickly displaces primary native colonisers, herbaceous and woody, where it occurs *en masse,* accelerating successions to forest on fresh alluvium by replacing longer-lived species such as *K. ericoides*. It is a very effective coloniser of new surfaces, and is likely to continue spreading in the Park and persist indefinitely in lowland catchments subject to frequent flooding and alluviation.

Keywords: Buddleia; *Buddleja davidii;* weeds; Te Urewera National Park; alluviation; primary succession.

Introduction

Buddleia *(Buddleja davidii)*[1] is an Asian shrub or small tree (family Buddlejaceae) which is widely grown as an ornamental and is now abundantly naturalised in open or disturbed places in North Island and northern South Island (Webb, Sykes and Garnock-Jones, 1988). Planted earlier in the century as an ornamental near the western and southern peripheries of Te Urewera National Park, it was already widely naturalised in streambeds, on slips and on roadsides in the park by 1977, when concern about its weed status was first voiced by management. An earlier investigation (Williams, 1979) concluded that buddleia largely ousts native species (particularly herbs and subshrubs) occurring early in riverbed successions but that buddleia would itself be replaced by native trees if left undisturbed. The present study assessed replacement patterns under buddleia plants/groves of different ages in streambeds where buddleia is prominent, with a view to quantifying its impact on natural successions and thus its weed status. A comparative study of riverbed successions in catchments where buddleia is absent was beyond the scope of the present investigation.

Study Area

Buddleia was studied in four catchments in the western Ikawhenua Range (Mangahouhi, Te Kopua, Ohutu and Mangamate) and one in the upper Waioeka catchment (Tataweka) (Fig. 1) where it has been widespread for over 10 years (Anon, 1977) and where a range of stands (single plants or small groves) of different ages is present.

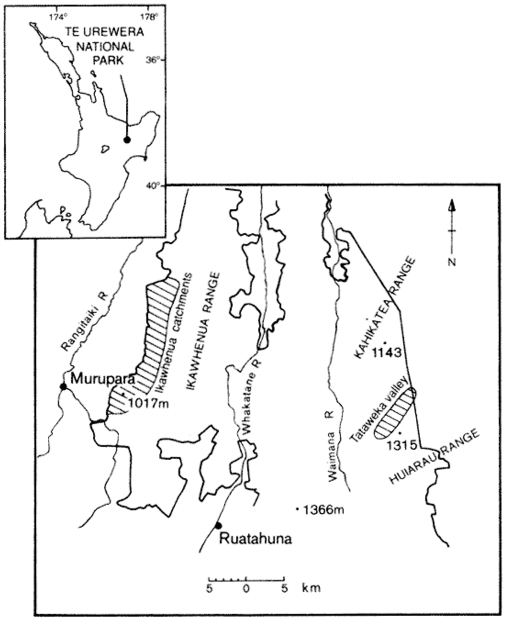

Figure 1; *Location of study areas in Te Urewera National Park.*

[1] Nomenclature follows Allan (1961) and Webb, Sykes and Garnock-Jones (1988) otherwise indicated.

Reconnaissances were also made in three more Ikawhenua catchments (Kopuriki, Horomanga and Opaheru).

The Ikawhenua catchments studied lie at altitudes of about 300-400 m a.s.l. in the Ikawhenua Ecological District (E.D.), Urewera Ecological Region (E.R.) (McEwen, 1987), and are subject to periodic flooding. Soils in streambeds are lithosols and recent soils derived from alluvium composed of mixtures of Kaharoa Ash, Taupo Pumice, older tephras and greywacke (see Vucetich *et al.,* 1960). They have stony sandy upper horizons, are excessively drained and moderately fertile. Periodic flooding and alluvial deposition causes frequent rejuvenation. Climate is mild and moderately humid, with mean annual rainfall of 1400-1600 mm (New Zealand Meterorological Service, 1970) spread over 125-150 days. Mean annual temperature is in the range 10-12.5 ∞C. Strong winds shown a marked southwesterly predominance (Tomlinson, 1976).

Vegetation is fire-induced secondary forest and scrub grading into primary forest dominated by tawa *(Beilschmiedia tawa),* grading into beech-podocarp forest at about 600 m a.s.l. (Nicholls, 1969a). The chief woody colonisers of streambeds in the region are manuka *(Leptospermum scoparium),* kanuka *(Kunzea ericoides* (A. Rich) J. Thompson val. *ericoides)* and tutu *(Coriaria arborea* var. *arborea),* although buddleia is locally prominent.

The upper Tataweka valley lies between the Huiarau and Kahikatea Range at an altitude of about 450 m, in the Waioeka E.D., Raukumara E.R. Soils on the valley floor are lithosols and recent soils derived from alluvium, probably composed of greywacke and tephras, as in the Ikawhenua Range. Climate is cool and humid, with mean annual rainfall probably in excess of 2400 mm/annum (New Zealand Meteorological Service, 1970), spread over 150-175 days. Mean annual temperature is in the range 7.5-10 ∞c. There is a slight predominance of north-westerly winds of all speeds (Tomlinson, 1976). Predominant vegetation is tawa-dominant forest grading into beech-podocarp forest at about 750 m a.s.l. (Nicholls, 1969b).

Methods

Fifty-six temporary 2x2 m plots were systematically placed in the centre of buddleia groves (sometimes under isolated individual plants) of varying ages in streambeds. Age class was initially estimated by canopy height and diameter/range of diameters present. Generally, one plot was placed in each grove. Plot size of 2x2 m was chosen because it approximated the crown area of individual buddleia plants over much of the age range studied, and in some cases only individual plants were available for study. All buddleia plants, overtopping the plot were felled, and basal discs removed. Height and basal diameter of the largest stem of each buddleia were recorded. Presence/absence of woody seedlings ´2.5 cm d.b.h.) was recorded by species in three height classes: <30 cm, 30 cm-l m, >1 m; saplings (2.5-10 cm d.b.h.) were also recorded. Percentage ground cover of bare rock, sand, litter, dicotyledonous herbs, woody seedlings, grasses, sedges, rushes, ferns and mosses was recorded in seven cover abundance classes: 0-10/0, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%. Numbers of buddleia plants per plot were also recorded, and evidence of fresh alluvial deposition since buddleia establishment was obtained by examining substrate profile. Buddleia discs were sanded and aged by counting growth rings, presumed to be annual. In cases where some burial following establishment had occurred, some underestimation of age is likely.

In the absence of long-term permanent plots, data from stands of different ages were treated as indicative of time-series data in individual plots. Height/age and diameter/age functions were fitted for the individual buddleia dataset. Mean buddleia density/plot *vs* age was graphed for pooled age classes. Relationships between ground cover estimates and age of buddleia canopy were tested by non-parametric correlation coefficient. Logistic regressions of occurrence of woody native seedlings and saplings on age of buddleia canopy were derived, and tested by t-test.

Results

Individual Plant Growth

Height growth followed an exponential pattern (r2 = 0.66, P<0.01; Fig. 2), indicating rapid early growth (averaging 0.5 m/year) over the first 10

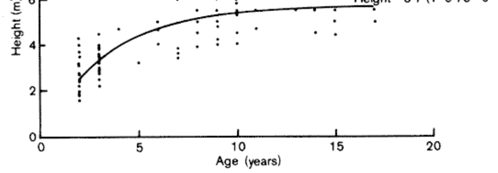

Figure 2: *Height vs age of buddleia in Te Urewera National Park.*

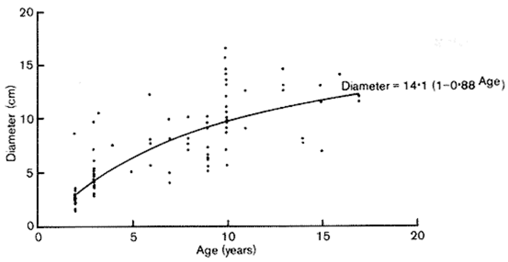

Figure 3: *Basal diameter vs age of buddleia in Te Urewera National Park.*

years, but declining later. Basal diameter growth also followed an exponential pattern (r2 =0.72, p<0.01; Fig. 3), indicating rapid early growth (averaging I cm/year) over the first 10 years, but declining later. Maximum height (averaging 5.7 m) is reached by an average age of about 15 years, though in some instances as early as 7 years (this study; Williams, 1979). Maximum diameter (averaging 14 cm) is predicted by the diameter/age function to be reached by an average age of about 30 years, though in some instances diameters of 14 cm are attained as early as 10 years. The oldest buddleia plant found was 20 years old; pith rot and/or insect attack was noted in this and many other large, old stems. Together with the very brittle nature of buddleia wood, insect and fungal damage cause many larger, older buddleia stems to collapse outward from the centre of the plant under their own weight and that of adjacent plants. Apparent rejuvenation by coppice and epicormic shoots is sometimes evident; they may succeed in prolonging the life of plants substantially.

Stand Density

Intense self-thinning (density-dependent mortality) Occurs over the first few years in buddleia stands (Fig. 4), with stand densities declining from as many as several million plants/hectare in a one

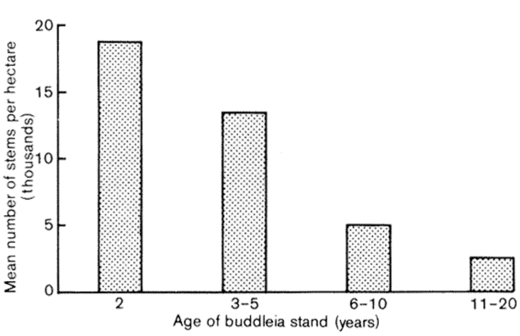

Figure 4: *Mean buddleia density vs age in buddleia stands in Te Urewera National Park.*

year-old population sampled (equivalent density in a 0.5 x 0.5 m plot) to an average of about 13000/ha in 3-5-year-old stands. Williams (1979) noted self-thinning occurring in dense 2 m high (probably 1-2 year old) buddleia stands in the Matahanea catchment 35 km north nor'east of Tataweka. Self-thinning is complete by the time stands are about 10 years old, with mean densities of 2500 plants/hectare.

Ground Cover

Marked differences in composition of ground cover were evident in buddleia stands of different ages (Table I), suggesting changes over time in individual stands. The percentage of exposed gravel and sand declined markedly with age, while woody seedling, sedges (most *Uncinia* species), mosses, ferns and litter all increased with age. These trends indicate the development of typical lowland forest floor vegetation on previously bare new surfaces, within 15 years of colonisation by buddleia.

Table 1: *Correlation coefficients between semi-quantitative estimates of ground cover (see text) and age in buddleia stands of different ages.*

Exposed sand	-0.614**
Exposed gravel	-0.468**
Ferns	0.269*
Litter	0.349**
Mosses	0.417**
Sedges	0.444**
Woody seedlings	0.516**

A large number of dicotyledonous herbs, about half of them adventive, were present in younger buddleia stands, mostly at low frequencies. Some native species *(Gnaphalium* spp, *Raoulia tenuicaulis, Epilobium brunnescens* ssp. *minutiflorum)* were absent from stands over 5 years old, although pennyworts *(Hydrocotyle elongata, H. moschata)* were more common in older (>10 years), rather than younger stands. Most adventive species (e.g. white clover *(Trifolium repens)* and selfheal *(Prunella vulgaris*[a] were absent from stands over 10 years old, although ragwort *(Senecio jacobaea)* and wall lettuce *(Mycelis muralis)* persisted into the oldest stands.

Replacement Patterns

Seedlings and saplings of 28 species of native shrubs and trees were present in plots, although only 10 of these species were widespread. Two relationships between frequency of occurrence and 11-20 age of overtopping buddleia were evident (Table 2, Fig. 5).

Seedlings and saplings of one group, including koromiko *(Hebe stricta* var. *stricta),* kanuka,

Table 2: *Relationships between frequency of occurrence of native seedlings and saplings and age of overtopping buddleia canopy.*

Species	t-value
Decreasers	
Kanuka	-1. 73
Koromiko	-1.45
Tutu	-1.36
Increasers	
Karamu	3.43**
Fivefinger	3.29**
Mahoe	2.89**
Wineberry	2.60*
Lemonwood	2.08*
Lancewood	1.90
Kohuhu	1.93

* significant at p = 0.05
** significant at p = 0.01

manuka and tutu were more common in younger than older stands. The relative scarcity of these species, even in the youngest plots (less than 50% occurrence) and the size of sample meant that results were not statistically significant.

A second group comprises species which were more common in older, rather than younger plots. Karamu *(Coprosma robusta),* five finger *(Pseudopanax arboreus* (Murr.) Philipson), mahoe *(Melicytus ramiflorus* ssp. *ramiflorus),* wineberry *(Aristotelia serrata)* and lemonwood *(Pittosporum eugeniodes)* showed significant increases in frequency with buddleia age, while a number of other species, including kohuhu *(Pittosporum tenuifolium),* lancewood *(Pseudopanax crassifolius),* hangehange *(Geniostoma rupestre* Forst. et Forst. f. var. *ligustrifolium* (Cunn.) Conn), mingimingi *(Leucopogon fascicu/atus* (Forst. f. A. Rich.), *Coprosma grandifolia* Hook. f., pate *(Schefflera digitata)* and putaputaweta *(Carpodetus serratus)* showed similar, but not statistically significant trends.

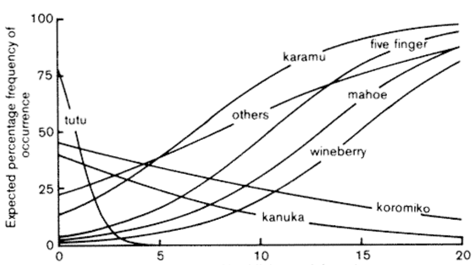

Figure 5: *Expected percentage of plots containing seedlings of native trees and shrubs under buddleia stands of different ages.*

Most species of the second group have the capacity to overtop and outlive buddleia as it collapses with old age. Four years after colonisation, most buddleia stands have seedlings of native species capable of replacing them growing beneath.

Discussion

Although primary successions on alluvium have not been studied in detail in Te Urewera National Park, observations on primary successions on alluvial surfaces of sedimentary origin elsewhere in the country (Wilson, 1976; Dobson, 1979; Wardle, 1980) suggest that successional pathways are linear and depend to some extent on predominant substrate textures. The same is likely to be true of primary successions on alluvuim in the Park. Fine silty sediments tend to be thickly colonised by grasses and dicotyledonous herbs, which resist woody invasion; shrubs tend to appear earlier on coarser gravelly or stony substrates than on silty substrates. Although native species (e.g., *Gnaphalium* ssp., *Raoulia* ssp., *Epilobium* ssp.) are still widespread, herbaceous colonisers of riverbeds in the Park are now predominantly adventive; woody colonisers are still predominantly native (Shaw, 1988), except in catchments where buddleia is prominent.

Substrates under buddleia were predominantly gravelly sand, a texture intermediate between those favouring herbaceous or woody colonisers; silty substrates were not observed in the study areas, where streams are fast-flowing. Owing to its rapid early growth, buddleia quickly supresses herbaceous pioneers where it establishes *en masse* (Williams, 1979); native and adventive herbaceous colonisers occur sparsely under very young buddleia stands, but are generally absent from older ones.

Kanuka commonly occurs early in alluvial successions in Te Urewera National Park (Shaw, 1988), and on sandy substrates on the Manawatu Plains (Esler, 1978) and the Bay of Plenty coast; it occurs in some very young buddleia stands. Although early height growth rates of kanuka on some lowland sites may approach those of buddleia here (G.F. Pardy, pers. comm.), kanuka is quickly outcompeted and eliminated by buddleia. Thus buddleia also quickly usurps the initial native woody phase of successions to forest on fresh alluvium where it establishes *en masse*. The relatively short lifespan of buddleia (probably c. 30 years) compared with kanuka (normally 80-150 years - Burrows, 1973, but occasionally over 300 years - e.g., Druce, 1966) implies that successions to high forest involving buddleia are considerably shorter than those in which kanuka is prominent;

the lifespan of pioneering species is an important determinant of the duration of primary successional pathways (Druce, 1957). Coarse gravelly substrates are often colonised by tutu and koromiko. Like manuka and kanuka, koromiko is outcompeted and eventually largely eliminated by buddleia. Tutu seems to be able to compete with buddleia where the latter establishes at low densities, and mixed young stands of the two species occur in places; they were not sampled in the present study. Tutu has a lifespan more comparable with that of buddleia, about 50 years in the Wellington region (Druce, 1957), so successions involving either or both species may be of comparable duration. At Kowhai Bush, Kaikoura, tutu overtops and supresses buddleia early in riverbed successions (Dobson, 1979); buddleia growth rates there are presumably slower than those of tutu.

Kanuka/manuka stands are commonly invaded by five finger, here as elsewhere, e.g., Kapiti Island (Esler, 1967). Fivefinger also commonly invades buddleia stands, occurring in most of the older samples. Along with mahoe, fivefinger is likely to replace buddleia as it senesces and collapses. Successional sequences with and without buddleia thus converge at this stage; later trends are not clear here and in some other instances (e.g., Kapiti Island - Esler, 1967).

Buddleia stands are occasionally flooded and subject to further depositions of alluvium. Observations suggest that established buddleia plants can survive burial by at least 0.5 m of fine alluvium by producing adventitious roots and shoots on buried or flattened stems. The chief effect of limited burial may be the removal of small native seedlings « 1 m tall), thus prolonging buddleia dominance and setting back the succession.

Buddleia stands on roadsides and landslide scars were not sampled in the present study, but they appear to develop along much the same lines as those in streambeds, Le., invasion and eventual replacement by seral native species. The fate of stands on landslide scars is more difficult to predict, given the inherent instability of many such sites and the heterogeneity of the substrate.

Buddleia has many of the features which characterise successful "weed" species (see Baker, 1974). It matures quickly, being capable of producing seed in its first year of life (Esler, 1988), and produces large quantities of seed, which is tailed for efficient wind and water dispersal. It can recover from storm or flood damage by producing adventitious shoots and roots on buried or flattened stems. Rapid early growth allows it to suppress other species (e.g. kanuka) with overlapping ecological niches, and survive burial during subsequent flooding. Like many weeds, buddleia is an ecological specialist, adapted to its role of colonising new, coarse-textured, nitrogen-deficient surfaces by its drought-tolerant seedlings (Humphries, Jordan and Guarino, 1982) which quickly develop an extensive root system to tap distant water (personal observations, Esler, 1988) and can maintain leaf area in nitrogen-deficient substrates (Humphries and Guarino, 1987). These features, and the success of buddleia in catchments where it has become established, suggest that it will be a permanent component of the Park's flora.

The conclusions of Walker and Chapin (1986) and Walker *et al*. (1986) from their study of primary alluvial successions in Alaska (i.e., that successional pathways are adequately explained by the interaction of stochastic events with life history traits of the dominant species, modified by interactions among species) probably apply here as well. Flooding and alluviation plus seed dispersal determine both the availability of new surfaces, and the extent to which they are colonised by buddleia. Rapid growth and dominance by buddleia evidently facilitate early arrival on the site of seral woody native species like fivefinger, while a relatively short lifespan (c. 30 years) causes its early extinction and replacement by these other species. Detailed study of other aspects of the life history of dominant species (e.g., reproductive biology) would help clarify the processes involved in the succession.

In conclusion, buddleia is one of a suite of woody adventive species which are capable of accelerating successions back to high forest on disturbed sites. In seral scrub on the Port Hills on Banks Peninsula, elder *(Sambucus nigra)* invades broom *(Cytisus scoparius)* and in turn facilitates the development of mahoe forest (Williams, 1983). By quickly displacing longer-lived woody primary native colonisers, buddleia can accelerate the reforestation process in places in streambeds. Further flooding and alluviation can set back the succession or reinitiate it, and on some sites, may be sufficiently frequent and severe to reinitiate the succession often enough to prevent high forest from ever developing. Because of the unstable nature of the habitat, then, buddleia is likely to remain a permanent feature of many catchments where it is already established. In the absence of intervention, it is likely to continue spreading until all suitable habitats within the lowland bioclimatic zone are occupied.

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