Vegetation recovery in rural kahikatea (*Dacrycarpus dacrydioides*) forest fragments in the Waikato region, New Zealand, following retirement from grazing

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Abstract: Vegetation was sampled in kahikatea (*Dacrycarpus dacrydioides*)-dominant forest fragments having different recovery periods since grazing ceased in the Waikato region, North Island, New Zealand. Changes in vegetation were modeled against recovery periods ranging from 0–74 y and in relation to position within fragment (edge or interior). Indigenous plant species richness increased and adventive plant species (mostly pasture herbs) richness declined with increasing recovery period; small tree and sapling density and seedling ground cover increased. Fragment edges had higher adventive species richness, lower basal area, more established seedlings, lower litter cover and higher grass ground cover, than interior plots. Some indigenous species (e.g. *Laurelia novaezealandiae* and *Myrsine australis*) increased with recovery period while some adventive species (e.g. *Solanum pseudocapsicum*) declined. The relative basal area of *Alectryon excelsus* increased significantly with recovery period at edges, and that of *Melicytus ramiflorus* everywhere. Twenty years represents a turning point in the recovery period, with the end of the loss phase of adventive pasture species, the start of the re-establishment phase of indigenous ground layer and understorey species, and significant recovery of population structures of major species. In relatively non-weedy rural environments, retirement from grazing may be sufficient to ensure a return to near-natural states in 40–50 y.

Keywords: grazing; chronosequence; fragmentation; biodiversity

Introduction

Retirement of forest fragments from grazing is becoming increasingly common in rural New Zealand, as elsewhere (e.g. Australia; Spooner et al., 2002), with growing awareness of their importance as reservoirs of indigenous biodiversity and their integral contribution to the uniqueness of the landscapes in which they occur. Forest fragments dominated by the indigenous tree species kahikatea (Dacrycarpus dacrydioides) occupy 0.2% of the dairy landscape of the middle Waikato region (Burns et al., 2000). Most are smaller than 1 ha and have arisen via secondary succession since widespread land development for agriculture c. 125 years ago. Such fragments are the sole reservoirs of indigenous biodiversity remaining in parts of the region and represent the only prospects for its survival. As in much of the world (Saunders et al., 1991), the conservation of regional biotas here depends entirely on the retention and management of remnants. Although valued by farmers for stock shelter, their ecological intactness has been widely compromised by grazing and their long-term survival is uncertain.

Fragmentation and the consequences for biodiversity of creating 'islands' of different sizes have been the focus of much research (e.g. Saunders et al., 1991). Results are often difficult to interpret, however, because habitat loss and habitat fragmentation per se, i.e. the breaking apart of habitat after habitat loss, have often been confused (Fahrig 2003). Habitat loss has large, consistently negative effects on biodiversity whereas fragmentation has much weaker effects on biodiversity that are at least as likely to be positive as negative. Fragmentation alters the physical (e.g. microclimate, hydrological) and biological environments of fragments, and grazing has been an almost inevitable corollary of forest fragmentation in pastoral landscapes in New Zealand. Esler (1978) qualitatively described a degradation sequence in forest fragments of different composition in the Manawatu region but there have been no quantitative studies of the impacts of grazing, nor of recovery from it. Fragments are particularly susceptible to weed invasion (Timmins and Williams, 1991), and interactions between retirement from grazing and the abundance of invasive weeds are of particular concern for managers and the maintenance of indigenous biodiversity.

In the absence of long-term permanent plots, the best way of measuring vegetation change over time (Burrows, 1990), one can use a chronosequence of sites in which all factors apart from time are standardised. A 'space-for-time' study was undertaken on a single soil type widespread in the region and the one most typically associated with *Dacrycarpus* forest and under similar climate. The objective of our study was to determine patterns of vegetation recovery after retirement from grazing.

Study Areas

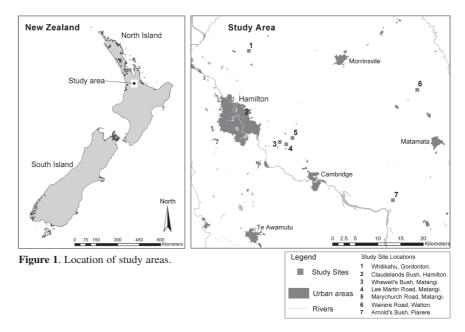
Seven forest fragments ranging in area from 1.2 to 9.9 ha were sampled in five localities in the Waikato Ecological Region, North Island (Fig. 1). Altitudes range from 20–100 m a.s.l. Climate in the region is warm-temperate and humid with a mean annual rainfall of 1200–1600 mm, falling mostly in winter. Mean annual temperature is ~13°C, with a January (midsummer) mean of ~18°C and a July (midwinter) mean of ~8°C (New Zealand Meteorological Service, 1985). Ground frosts occur on average of ~60 days annum⁻¹. All fragments are on Te Kowhai silt loam, a Gley Recent soil derived from rhyolitic tephra (Hewitt, 1992). Apart from Claudelands Bush in Hamilton City, all are in rural dairying landscapes.

Before European settlement and subsequent widespread clearance in the late 19th century, the lowlands of the Waikato region supported a mosaic of forest, shrublands, and wetland vegetation (Clarkson

et al., 2002). In present-day secondary forest remnants on damp valley floors, abundant Dacycarpus dacrydioides (kahikatea, white pine), frequent Laurelia novaezelandiae (pukatea), less frequent Alectryon excelsus (titoki), Beilschmiedia tawa (tawa), and occasional Elaeocarpus hookerianus (pokaka), Dacrydium cupressinum (rimu, red pine), Prumnopitys taxifolia (matai, black pine) and Podocarpus totara (totara), form a canopy at ~25 m. *Melicytus ramiflorus* (mahoe), Hedycarya arborea (porokaiwhiri, pigeonwood), Streblus heterophyllus (milk tree, turepo) and Schefflera digitata (pate) form a scattered subcanopy at ~8 m. The understorey contains a rich variety of divaricating shrubs, typically Melicytus micranthus (small-leaved mahoe), Melicope simplex (poataniwha), Coprosma areolata, and C. rotundifolia.

Population structures of *Dacrycarpus* comprise two groups of trees, a small cohort of larger trees (100–200 cm d.b.h.) 200–500 years old that are survivors from the earlier forest, and a much larger cohort of smaller trees (30–90 cm d.b.h.) 80–120 years old (Burns *et al.*, 2000). All fragments are secondary and artefacts of widespread clearing of earlier forest some 100–120 years ago, although some such as Claudelands Bush incorporate relict stands of old-growth forest. Given a typical lifespan of 450 years in *Dacrycarpus* (Enright and Ogden, 1995) and the relative youth of the stands, canopies are likely to remain dominated by *Dacrycarpus* for at least another three centuries.

Introduced possums (*Trichosurus vulpecula*) have probably been present throughout since the mid-1950s (Cowan, 1990). Apart from domestic stock in fragments



still being grazed, large introduced mammals are absent.

All localities have been subject to modified drainage, so hydrological processes have undoubtedly been altered at all of them. Planting of early successional indigenous species has been undertaken at the edges of three fragments. Additional wind protection has been engineered and substantial weed control undertaken at Claudelands Bush, and restoration of the water table at Whewell's Bush.

Methods

Data collection

Potential study stands were located on soil and vegetation maps of the region and then visited to determine fencing history. Te Kowhai silt loam was identified as the most representative soil type under Dacrycarpus stands. In total, seven forest fragments with known fencing histories (determined from local knowledge) on this soil type were located, in five localities (Hamilton, Gordonton, Matangi, Walton, and Piarere) in the Waikato region (Appendix 1). In each fragment, four 20×20 m plots were located under closed canopy, two at the edges (one at the northern end, one at the southern end), and two in the interior, 20 m apart on a N-S axis. In the smallest fragments, only 2 plots were sampled, one at the northern end and one in then interior. In each plot, all vascular species were recorded and all trees (>10 cm d.b.h.) tagged and measured for species and d.b.h.. A 10×10 m permanently marked subplot was nested within each plot in which all saplings (2.5–10 cm d.b.h.) were measured for d.b.h., and all established seedlings (>15 cm high, <2.5 cm d.b.h.) were recorded by species. Cover of herbaceous species (including ferns, sedges, grasses, and lianes) was recorded semi-quantitatively in the subplot by species in seven classes: <1, 2–5, 6– 25, 26–50, 51–75, 76–95, >96%. Other ground cover components (e.g. litter, coarse woody debris, bare soil) were recorded semi-quantitatively in the same classes. Four 1×1 m plots were located within each subplot, one at each corner, in which all ephemeral seedlings (<15 cm high) were recorded by species.

Analysis

A range of variables, indigenous species richness (number per 0.04 ha), adventive species richness (number per 0.04 ha), basal area, large tree density, small tree density, sapling density, established seedling density, ephemeral seedling density, cover of coarse woody debris, litter, exposed roots, ferns, sedges, grasses, and lianes, was tested against site, position within fragment (edge or interior), recovery period (time since retirement from grazing), and grazing history (period for which grazed before fencing).

Preliminary analysis showed that results were strongly influenced by the Hamilton site because its recovery period (74 years) was almost twice as long any other (39 years). Being an urban rather than rural site, it is also atypical for reasons unrelated to recovery period. To lessen its influence, the recovery period variable was log-transformed. This still gives the recovery period effect a sensible biological interpretation because it implies that sites differing by the same percentage recovery period will have the same vegetation change.

Rather than the square-root transformation often used to counter the higher variability of higher parameter values but for which there is no simple biological interpretation, points were weighted in inverse proportion to their mean. This is equivalent to assuming that their distribution is proportional to a Poisson, with the net effect that the fitted line is less affected by one or two high values.

Some variables (e.g. recovery period, grazing history) varied between sites, others (e.g. position) within sites. Therefore, estimates have standard errors that vary depending on the extent to which they depend on comparisons between rather than within sites. A linear mixed-effect model, implemented in S-Plus 6 for Windows (1999; MathSoft Inc., Seattle), correctly allowed for these two levels of variability. Interactions between variables were tested, but there was rarely any evidence of any effect. Where there was, the effect was described separately for edge and interior plots.

Results

Vascular flora and species richness

A total of 98 indigenous and 56 adventive vascular plant species were recorded in *Dacrycarpus* fragments. Most adventive species were pasture grasses and herbs and were confined to the edges of more recently fenced fragments. Despite some confounding factors, for example, the situation of the oldest fenced remnant in an urban area and hence proximity to major seed sources of weeds, two patterns of presence/absence in relation to recovery period are discernible. One group of species, predominantly adventive and including most of the dicotyledonous herbs recorded, occurred only in fragments fenced for <15 years. Another group, entirely indigenous and comprised largely of terrestrial ferns and relatively shade-tolerant understorey shrubs, was largely or wholly confined to remnants fenced for >25 years. The occurrence of the remaining vascular indigenous species showed no clear relationship with recovery period.

Indigenous species richness increased significantly (P < 0.01) with recovery period (time since retirement from grazing), with species richness increasing by 3.3

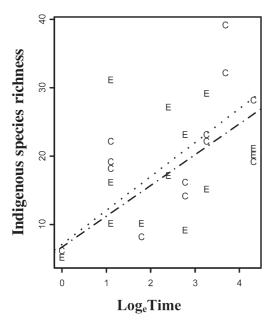


Figure 2. Change in indigenous plant species richness with time (years) since fencing in *Dacrycarpus* forest fragments in the Waikato. Dotted line = centre plots; dot-dash line = edge plots; C = centre plot; E = edge plot.

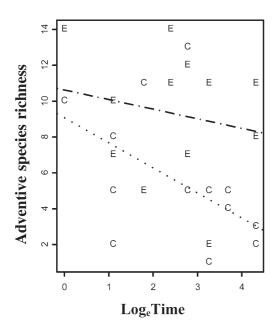


Figure 3. Change in adventive plant species richness with time (years) since fencing in *Dacrycarpus* forest fragments in the Waikato. Dotted line = centre plots; dot-dash line = edge plots; C = centre plot; E = edge plot.

(± 1.1) species per year for every doubling of the recovery period (Fig. 2). It did not differ between edge and interior plots. Adventive species richness decreased significantly (P < 0.05) with recovery period, with species richness decreasing by 0.7 (± 0.5) species per year for every doubling of the recovery period (Fig. 3). It also differed significantly (P < 0.01) between edge and interior plots, with edge plots having an average of 3.8 (± 1.3) more species than interior plots.

Basal area

Mean plot basal area was 92.2 m² ha⁻¹. Basal area did not change with recovery period but did differ between edge and interior plots, with edge plots averaging 14 (±6) m² ha⁻¹ less than interior plots.

Density

The density of small trees and saplings increased significantly (P < 0.05) with recovery period, small trees increasing by 23 (± 11) ha⁻¹ with each doubling of recovery period and saplings by 46 (± 13) ha⁻¹. No effect of plot position was evident.

Established seedling density did not change with recovery period but tended to be higher (P < 0.1) in edge by 6100 (± 6) ha⁻¹ than interior plots. No effects were evident with ephemeral seedlings.

Relative density and relative dominance (basal area)

The relative densities of Laurelia novaezealandiae and Myrsine australis (mapou) increased significantly (P < 0.05) with recovery period while those of the adventive Solanum pseudocapsicum (Jerusalem cherry) declined significantly (P < 0.01). The relative basal area of Alectryon excelsus increased significantly in edge plots (P < 0.05) and of Melicytus ramiflorus in both interior and edge plots (P = 0.05) with recovery period.

Ground cover

Seedling cover tended (P < 0.1) to increase, by an average of $0.6(\pm 0.3)\%$ for each doubling of the recovery period. Grass cover was significantly (P < 0.05) higher in edge than interior plots, decreasing by an average of $3.3(\pm 3.4)\%$ in edge plots for each doubling of recovery period, and increasing by an average of $0.4(\pm 3.2)\%$ in interior plots. Liane cover tended to increase (P < 0.1) with recovery period, by $0.9(\pm 0.5)\%$ with each doubling of recovery period. Litter cover did not change with recovery period but tended (P < 0.1) to be lower (by an average of $12(\pm 6)\%$) in edge than interior plots. No effects were evident in ground cover of coarse woody debris, exposed roots, sedges, or ferns.

Table 1. Population structures—mean density (stems ha^{-1}) of small trees (10–30cm d.b.h.), saplings (2.5–10 cm d.b.h.), and established seedlings (>15 cm high, <2.5 cm d.b.h.)—of major canopy species in *Dacrycarpus* fragments in the Waikato fenced for varying lengths of time (recovery period in years). X = absent from the fragment. Present = present outside plots.

Species	Size class	Wairere (0)	Wairere (1)	Marychurch (2)	Lee Martin (5)	Arnold's Bush (10)	Whitikahu (15)	Whewell's Bush (25)	Arnold's Bush (39)	Claudeland's Bush (74)
Dacrycarpus										
dacrydioides	saplings	12.5	X	X	12.5	X	12.5	6.3	X	6.3
	seedlings	X	X	X	X	X	25	6.3	X	6.3
Laurelia	· ·									
novaezealandiae	trees	X	X	12.5	Present	X	Present	Present	X	6.3
	saplings	X	X		X	X	X	43.8	X	6.3
	seedlings	X	X	18.8	Present	X	Present	400	X	1637.5
Alectryon	· ·									
excelsus	trees	X	X	Present	Present		12.5	Present	X	68.8
	saplings	X	X	X	X		Present	Present	X	Present
	seedlings	X	X	Present	75	62.5	1243.8	193.8	Present	12.5
Beilschmiedia										
tawa	trees	X	X	93.8	25	Present	18.8	37.5	Present	68.8
	saplings	X	X	Present	X	X	Present	Present	Present	12.5
	seedlings	X	X	50	62.5	Present	12.5	18.8	Present	87.5

Table 2. Population structures—mean density (stems ha^{-1}) of small trees (10–30cm d.b.h.), saplings (2.5–10 cm d.b.h.), and established seedlings (>15 cm high, <2.5 cm d.b.h.)—of major subcanopy species in *Dacrycarpus* fragments in the Waikato fenced for varying lengths of time (recovery period in years). X = absent from the fragment. Present = present outside plots.

Species	Size class	Wairere (0)	Wairere (1)	Marychurch (2)	Lee Martin (5)	Arnold's Bush (10)	Whitikahu (15)	Whewell's Bush (25)	Arnold's Bush (39)	Claudeland's Bush (74)
Melicytus										
ramiflorus	trees	X	X	6.3	X	Present	Present	12.5	12.5	37.5
	saplings	X	X	Present	X	Present	25	87.5	25	206.3
	seedlings	X	X	X	X	X	X	Present	Present	Present
Hedycarya	· ·									
arborea	trees	X	X	X	X	X	X	X	X	X
	saplings	X	X	X	Present	Present	X	X	Present	Present
	seedlings	X	X	12.5	12.5	X	X	X	37.5	Present

Population structures of major canopy and subcanopy species

Population structures (size-class distributions) of major canopy (Table 1) and subcanopy (Table 2) species show a general pattern of increasing frequency and abundance of seedlings and saplings with recovery period. Established seedlings of most major species were present in fragments fenced for at least 2 years; saplings of most major species were present in fragments fenced for at least 15 years.

Discussion

The results of our study enable us to predict how *Dacrycarpus* forest fragments (Fig. 4) are likely to recover from grazing in relatively weed-free rural environments. After fencing, i.e. retirement from grazing by domestic stock, the number of indigenous

species present steadily increases, while the much smaller number of adventive species slowly decreases. Other fragments nearby, and larger forest tracts in the region are possible sources of this recovery, but the relative importance of each is unknown and requires further investigation.

After some 20 years the adventive species originally present, predominantly herbaceous pasture plants, will have mostly disappeared, having been shaded out or out-competed by taller indigenous species (Fig. 5). At the same time, a variety of indigenous terrestrial ferns and relatively shade-tolerant understorey shrubs will begin to re-appear. Numbers of saplings in the understorey increase steadily while small trees in the subcanopy increase slowly. Some indigenous species, e.g. the tall canopy tree *Laurelia novaezelandiae* and the small subcanopy trees *Myrsine australis* and *Streblus heterophyllus*, become steadily more numerous. Others, e.g. the large subcanopy tree



Figure 4. Long-grazed understorey of a *Dacrycarpus* forest fragment at Puketaha, Waikato region, showing absence of ground layer, understorey, and subcanopy.

Melicytus ramiflorus and, at the edge, the tall canopy tree Alectryon excelsus, become increasingly important in terms of the biomass of the forest. If present, some weeds, e.g. the tall shrub Berberis glaucocarpa (barberry), persist regardless of time since fencing, while others decline. On the ground, the cover of small indigenous seedlings and lianes increases slowly. At the edge, predominantly adventive grass cover declines rapidly while inside, the cover of indigenous grasses and litter increases more slowly. A group of terrestrial ferns and relatively shade-tolerant understorey shrubs was largely or wholly confined to remnants fenced for 25 years or more, providing a suite of 'indicator' species that confirm ecosystem recovery is progressing satisfactorily.

Major canopy and subcanopy species in these fragments comprise a mixture of relatively shade-intolerant (*Dacrycarpus*, *Laurelia*, *Alectryon*) and tolerant (*Beilschmiedia*, *Melicytus*, *Hedycarya*) species. Regeneration strategies range from mass replacement after major disturbance (e.g. *Dacrycarpus*; Wardle, 1974) through to small group or single-tree replacement (e.g. *Beilschmiedia*; Knowles and Beveridge, 1982). Within 15 years of fencing, however, population structures of canopy species have begun to show significant recovery from grazing, with juvenile trees (saplings) of most major species present.

Basal areas are high by New Zealand standards (see Ogden, 1983), and the lack of any recovery effect indicates that it has already reached a steady state in stands 100–120 years old. Burns *et al.* (2000) found even higher basal areas (mean 101 m² ha⁻¹) in a



Figure 5. Understorey of Whewell's Bush, Matangi, Waikato Region, a Dacrycarpus forest fragment fenced for 25 years, showing recovery of ground layer, understorey, and subcanopy.

comparable suite of stands in the same region. The high basal areas of *Dacrycarpus* stands may reflect generally elevated light levels resulting from the high edge:area ratios compared with larger forest tracts. Differences between grazed and ungrazed forests are also evident in another quantitative study of indigenous forest degradation through grazing at Whatawhata (unpubl. data). As in our study, indigenous species richness was lower, adventive species richness higher, and sapling density lower in grazed than in ungrazed forest. Grazed edge plots differed more in composition from intact forest than interior plots. Broadly similar results have been described from grassy woodlands in New South Wales, where indigenous tree recruitment was more common, indigenous perennial cover higher, and adventive annual cover lower 2-4 years after fencing (Spooner et al., 2002).

The original flora of this forest type can be gauged from forest with comparable soils and climates that has never been grazed. White Pine Bush, a 4 ha remnant in the eastern Bay of Plenty that has never been grazed, had 121 vascular indigenous species some 45 years after fragmentation (Smale, 1984). This is only 20% more species than the total recorded in long-grazed fragments here. Thus, despite grazing histories of 50-100 years or more, a remarkable proportion of the original indigenous vascular flora survives in these remnants. For instance, fully two-thirds of the total indigenous species complement was present in the combined fragments fenced for 5 years or less, or still grazed. On the one hand, this proportion is somewhat misleading because in the absence of effective regeneration, many canopy and subcanopy species will inevitably disappear when the existing mature survivors of the original forest die (see Esler, 1978) and the number will decline. On the other, the survival of substantial numbers of species—and the reestablishment after fencing of lost species—are cause for optimism in the sense that with the simple remedial measure of fencing, even long-grazed fragments evidently have the potential for self-restoration. A high proportion of the original indigenous flora evidently survived some 50 years of grazing in Claudelands Bush, one-third of which was lost long after grazing had ceased. The lost species were mostly understorey shrubs and terrestrial ferns, the component lost by grazing in our study; prolonged smothering by the adventive herb Tradescantia fluminensis (wandering jew) and lowering of the water table may have been responsible (Whaley *et al.*, 1997).

Three major threats to the integrity of *Dacrycarpus* forest fragments on gleyed alluvial soils are perceived. Hydrological regimes have been widely altered, but the impacts remain unclear. Forest remnants on extensively grazed hill country elsewhere in the Waikato region show greatly elevated levels of

phosphorus in the soils beneath them, resulting from a long history of aerial topdressing with phosphatic fertilisers (Stevenson 2004); a similar situation probably applies in our fragments.

The other major shadow on the horizon is invasive weeds. The only widespread threatening weed was Ligustrum sinense (Chinese privet), present in every fragment in this study although typically only as seedlings. The species invaded a mixed hardwood forest in northeastern North America and, over 20 years, severely reduced ground-layer herbaceous species and almost completely suppressed regeneration of canopy trees (Merriam and Feil, 2002). Its potential for disrupting ecological processes in New Zealand forest is unknown, but Esler (1988) lists it as a secondary threatening weed in the Auckland region. It is moderately shade-tolerant and itself casts dense shade that may inhibit other species.

Apart from ubiquitous *L. sinense*, the most threatening weeds of forest remnants were largely absent from the fragments in this study. *Tradescantia fluminensis*, a major invasive herbaceous weed suppressing regeneration (Kelly and Skipworth, 1984) on moist, fertile alluvial soils of the kind here, was the predominant ground cover in much of Claudelands Bush for several decades before it was largely removed some 20 years ago (Whaley *et al.*, 1997). *Hedera helix* (ivy) is abundant at one edge of Arnold's Bush, Piarere, and appears to be actively spreading. The widespread presence of such weeds might well alter the recovery pathway described here.

Conclusions

A surprisingly large number of indigenous species survive in long-grazed *Dacrycarpus* fragments in rural landscapes, and with the simple remedial measure of fencing, many lost species re-establish. Thus these fragments evidently have the potential for self-restoration. Twenty years represents a turning point in the recovery period, with the end of the loss phase of adventive pasture species, the start of the re-establishment phase of indigenous ground layer and understorey species, and significant recovery of population structures of major species. In the absence of threatening weeds, retirement from grazing by means of fencing may alone be sufficient to ensure a return to near-natural states in 40–50 years.

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Appendix 1. Study sites of Dacrycarpus-dominant rural forest fragments in the Waikato Basin, New Zealand

Site	No. plots	Grid reference	Soil type	Area (ha)	Recovery period (time since retirement from grazing (years)	Additional Management
Wairere Rd, Walton	2	T14/502844	Te Kowhai s.l.	2.4	0 (currently grazed)	None
Wairere Rd, Walton	2	T14/502844	Te Kowhai s.l.	2.4	1	None
Marychurch Rd, Matangi	4	S14/227738	Te Kowhai s.l.	3.1	2	None
Lee Martin Rd, Matangi	2	S14/213724	Te Kowhai s.l.	1.2	5	None
Arnold's Bush, Piarere	2	T15/448601	Te Kowhai s.l. and Horotiu s.l.	3.8	10	None
Whitikahu Rd, Gordonton	4	S14/131930	Te Kowhai s.l. Brown phase	2.0	15	Edge planting
Whewell's Bush, Matangi	4	S14/199729	Te Kowhai s.l.	9.9	25	Edge planting, water table manipulation
Arnold's Bush, Piarere	2	T15/448601	Te Kowhai s.l. and Horotiu s.l.	3.8	39	None
Claudelands Bush, Hamilton	4	\$14/120783	Te Kowhai s.l.	5.2	74	Edge planting, windbreak, weed control