

Successional processes induced by fires on the northern offshore islands of New Zealand

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Abstract: Major trends in forest successions following fires are identified for northern offshore islands of New Zealand. Data are from the author's observations over several decades, and published descriptions. Islands studied extend from the Cavalli group in the north to the Aldermen group in the south. Their original vegetation was largely destroyed by human-induced fires. Successions that followed were dominated for several centuries by pohutukawa (*Metrosideros excelsa*) or, for a shorter time, by kanuka (*Kunzea ericoides*). Compared with other seral species, pohutukawa retards the rate at which a diverse community can develop. This should be recognised when restoring an island that has lost most of its woody vegetation.

Keywords: fires; burrowing petrels; *Rattus exulans*; succession; wind-driven salt.

Introduction

It is clear from archaeological and botanical evidence that vegetation on all the large and many small northern offshore islands of New Zealand was burnt during Maori occupation or visitation. Archaeological evidence for human settlement and fires includes storage pits, stone-faced terraces, defended sites (pā) and shell middens (Hayward, 1986). Botanical evidence includes: abundant pioneer plants that establish after fires, particularly pohutukawa (*Metrosideros excelsa*), kanuka (*Kunzea ericoides*), manuka (*Leptospermum scoparium*) and bracken (*Pteridium esculentum*); other species characteristic of fire-induced vegetation on the Northland mainland, e.g. akepiro (*Olearia furfuracea*) and mapou (*Myrsine australis*); and the widespread occurrence of charcoal in island soils. Charcoal, however, decreases with continuing weathering and petrel-burrowing.

This study identifies major fire-induced successions affecting northern islands. Data are derived from my observations over 50 years, and published studies. Trends described have taken place largely in the presence of kiore (*Rattus exulans*), but usually in the absence of other mammals. Understanding successional processes is essential for effective management of these islands whether this involves protection or restoration.

Islands included in this study are the Cavalli group southwards to the Poor Knights and Hen and Chicken groups, Cuvier Island, the lowland/coastal section of Little Barrier Island, the Mercury and Ohinau

groups and the Aldermen Islands (Fig. 1, Appendix 1). I have excluded islands smaller than 15 ha because burrowing seabirds frequently dominate vegetation on smaller islands. Great Barrier Island and inner islands of the Hauraki Gulf (e.g. Waiheke, Ponui, Rakino, Noises, and Rangitoto islands) were excluded because Rangitoto Island is dominated by successions following volcanic eruptions, and both Great Barrier Island and the inner islands of Hauraki Gulf are greatly modified by people. The Three Kings and Kermadec islands were also excluded because of their very distinctive biotas.

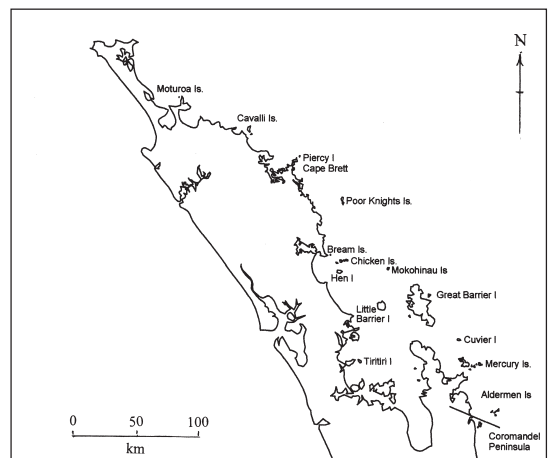


Figure 1. Northern offshore islands included in the study.

The northern islands have warm humid summers, mild winters and mean annual rainfall between 900 and 1500 mm with winter maxima. Island vegetation may have been burned by people for a variety of reasons including clearing to promote bracken or cultivate kumara, creation of settlements, defense sites and sea views to detect invaders, the creation of charcoal to condition soil for crops (author's observations), easier access to seabird burrows (Sir Robert Falla, *pers. comm.*), and accidental fires. Dodson *et al.* (1988) found charcoal indicating natural fires at Paranoa, near Cape Reinga, that pre-dated human influence. As droughts commonly affect these islands, some burning by lightning-induced fires is possible.

Methods

Identifying successional trends

Successional changes were described from qualitative observations supplemented with data from permanent plots, vegetation mapping, and stand comparisons. Within permanent sample plots, all size-classes of tree species were counted or measured periodically. Permanent plot data are limited by the short time-spans between samplings, the small number of plots established in the time available, and by the possibility that not all vegetation types are represented in plot samples.

Some data are derived from vegetation maps. All or part of an island was mapped and re-mapped using many small samples (Atkinson, 1985). Sampling was systematic rather than random in order to cover all major site types. Representativeness may be achieved but the time frame is often too short to detect change.

Other data are derived from comparisons of stands of apparently differing age on similar sites. When a long time-span is covered, a sequence may be identified. Care is needed to ensure that topographically and geologically equivalent sites are compared.

Differences in trunk diameter (d.b.h.) between species in a mixed stand are not, by themselves, reliable for detecting successional change; d.b.h. data should be coupled with estimates of crown diameters and tree heights (relative to canopy height) of the species being compared. Confusion can arise between a self-replicating species and one that is gradually infiltrating, even when trees are accurately aged (Ogden, 1985a).

Rates and mechanisms driving succession

Although it is sometimes difficult to determine the factors that initiate successions, this is usually not the case for fires. Characteristic plant species, and sometimes soil charcoal, often provide direct evidence

for fires. However, factors determining which species replace the primary immigrants that follow a fire, and in what order, are often difficult to identify. It becomes a matter of observing as many replacement situations as possible, forming a hypothesis, and testing it with further observation or experiment.

Data on rates of succession can be derived where dates for some fires are known. Estimates of tree ages from counts of annual growth rings were not obtained because pohutukawa and kanuka woods are too hard for extracting long increment cores. Opportunities to obtain cross-sections from trunks were few and, when obtained, older growth rings were sometimes destroyed by heart-rot fungi.

Without a measurable baseline, the amount of successional change cannot be assessed. I use canopy composition as a baseline for measuring change with "canopy" defined as the layer or layers formed by the uppermost plant crowns or their parts (Atkinson, 1962, 1985; Atkinson *et al.*, 1968). A canopy tree is defined as one having half or more of its crown exposed to the sky when viewed from the ground along a line-of-sight at right angles to the slope (Atkinson, 1962).

Understorey changes may be highly significant for future composition, including that of the canopy. Where a species is spreading through the understorey and likely to contribute to a future canopy, this can be indicated within a symbolic description (see below). This judgement depends on knowledge that the species contributes to canopies in similar environments elsewhere.

Atkinson (1985) derived a range of symbols that provide a convenient means to indicate vegetation structural and compositional features. I have used these extensively in this paper, and so the symbols are listed and defined in Table 1. Quantitative criteria for distinguishing forest, scrub and shrubland are given in Atkinson (1985).

Results

Successional trends vary between islands, but consistent patterns can be recognised with successions that follow fires. Other identifiable processes relate to the development of pohutukawa:kanuka successions, and the manuka:bracken successions.

Succession following fire

Wind-dispersed primary immigrants

Following fire, vegetation is dominated by five pioneer species that, with one exception, have abundant small seeds or spores dispersed by wind; pohutukawa, kanuka, manuka, bracken and bird-dispersed flax (*Phormium*

Table 1. Symbols describing structural and compositional features of vegetation as used in the text and for Table 2 descriptions of successional trends in forest or scrub.

Symbol	Description
A-B-C forest	Species A exceeds Species B in % cover which exceeds Species C in % cover within a single-layered forest canopy
A/B/C forest	Species A overtops Species B which overtops Species C in a three-layered forest canopy <i>but the three species may be in any order of % cover</i>
A//B forest	Species A forms a single-layered forest canopy above an understorey formed by Species B
A-B//C or A/B//C forest	Species C is in the understorey in both cases
A-B//C → A-B/C → A-B-C	Three stages in a successional trend
A::B forest	Discrete stands of species A and B grow side by side to form a mosaic pattern rather than mixtures of A and B

tenax). Establishment patterns of these species are partly site dependent, and are governed by the timing of seed germination, the persistence of seed banks, and tolerance of wind-carried salt. For example, pohutukawa seeds usually germinate close to the time of seed-fall in summer, whereas manuka maintains a seed-bank in old capsules. Manuka seeds germinate at almost any time if high temperatures or fires open the capsules. However kanuka capsules are smaller and easily destroyed by fire, giving manuka an advantage when both grow together (Esler and Astridge, 1974). Kanuka seed-banks in soil range between 166 and 2867 seeds/m² (Ogden, 1985b). Seeds of both species remain viable up to six weeks after shedding (Burrows, 1973) but some retain viability more than two years (Enright and Cameron, 1988).

Pohutukawa and kanuka, and manuka and bracken, sometimes grow together as mosaics of contrasting stands rather than as mixtures of both species. These can be distinguished as pohutukawa::kanuka or manuka::bracken stands with no suggestion that the paired species are linked in a successional sense.

Boyce (1954) noted that salt particles driven into leaves by wind have major effects on shoot architecture distinct from the effects of wave splash on halophytic plants near the shoreline. Flax, like pohutukawa, is very resistant to salt and characteristic of coastal cliffs and the shoreline fringe. It can dominate exposed slopes away from the shore following fires, as during the 1960s on Korapuki Island and southern Ohinau Island (I. Atkinson, *unpub. data*). Manuka is more resistant to salt than kanuka (*pers. obs.*; Esler and Astridge, 1974), but less resistant than pohutukawa. Bracken is the least resistant of these species (*pers. obs.*)

Bird-dispersed secondary immigrants

Five bird-dispersed species commonly establish within vegetation dominated by the primary immigrants. Widespread species in this group are mapou (*Myrsine australis*), mahoe (*Melicactus ramiflorus*), kohekohe (*Dysoxylum spectabile*), karaka (*Corynocarpus laevigatus*) and puriri (*Vitex lucens*). Mapou produces abundant seed that germinates readily, some remaining viable after two years (Enright and Cameron, 1988). It also produces adventitious shoots from the roots. Mahoe produces abundant viable seed and adventitious shoots from the base of the trunk. Kohekohe produces seed with high viability and no evidence of dormancy (Court and Mitchell, 1988). Karaka has limited seed viability (Enright and Cameron (1988). Seedlings of all these species are shade-tolerant except puriri, which requires relatively high light for establishment. Less widespread secondary immigrants are fivefinger (*Pseudopanax arboreus*), rangiora (*Brachylottis repanda*) and pigeonwood (*Hedycarya arborea*).

Later plant immigrants and coastal fringe species

Although many tree species can enter successions as later immigrants, only three are widespread: taraire (*Beilschmiedia tarairi*), tawa (*B. tawa*) and, under higher light, kauri (*Agathis australis*). Taraire and tawa have large bird-dispersed seeds and are relatively long-lived, although probably not as long as pohutukawa. Kauri is the longest-lived species in the study and was formerly more widespread on larger islands. It is wind-dispersed and can establish earlier than taraire or tawa.

In addition to pohutukawa and flax, six woody

species characterise the fringing zone between shoreline and forest, before and after fires. They are taupata (*Coprosma repens*), coastal karamu (*C. macrocarpa*), karo (*Pittosporum crassifolium*), kawakawa (*Macropiper excelsum*), coastal mahoe (*Melicytus novae-zelandiae*) and ngaio (*Myoporum laetum*). Succession in this zone is not discussed.

Pohutukawa::kanuka successions

The most widespread succession on the northern islands is initiated by the establishment of pohutukawa and kanuka on bare ground after fires. These two species form a mosaic, with the proportions of each in the early stages of successions determined by wind-carried salt, soil moisture and fertility (Figs. 2–4). Factors that control the sequence of species that follow are not necessarily those that control rates of successional change. The light environment beneath the canopy is clearly important in determining the sequence but so too are seed availability and soil moisture. Experiments are needed to unravel the various controlling factors.

Pohutukawa is found on all islands in the study, but has sometimes established on rockfalls unaffected by fire. In Figure 2, kanuka can be substituted for pohutukawa except near the coast where topography or pohutukawa may shelter the kanuka from salt (Table 2). On small islands with limited shelter, pohutukawa dominates and kanuka is uncommon, e.g. Korapuki I. (one small stand and one isolated tree; Atkinson, *unpub. data*), Stanley I. (one tree: Taylor and Lovegrove, 1997) and Cuvier I. (three trees in 1960, all now dead; Atkinson, *unpub. data*). Esler's (1978a) study shows kanuka absent from islands < 18 ha unless sheltered by the mainland.

Pohutukawa and/or kanuka can form scrub or shrubland with bracken, manuka and flax which are gradually shaded out by the taller species (Table 2). Manuka is less dependent on fire for establishment, frequently entering grasslands after reduction of grazing, as seen on Tiritiri (Esler, 1978b) and Motukawanui (Court, 1981) islands. Manuka shrublands are often invaded by kanuka.

An important attribute of pohutukawa is its limited ability to regenerate in shade. Pohutukawa can sometimes be found within taller vegetation, however close examination usually shows that, rather than invading taller vegetation, the pohutukawa have established first and then been over-topped by faster-growing trees. Examples are on the main ridge of Lady Alice I. and the lower slopes of Little Barrier I. If light is sufficient, pohutukawa seedlings can establish on tree or ponga (*Cyathea dealbata*) trunks, but these seldom survive.

Kanuka, like pohutukawa, forms apparently even-aged stands that mature without significant recruitment

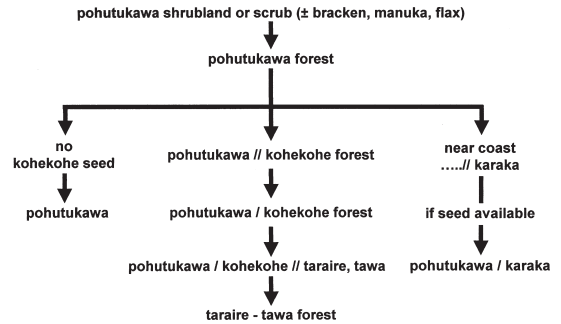


Figure 2. Forest successions initiated by pohutukawa (or kanuka) following fires on the northern offshore islands. Kanuka is usually absent from successions near the coast.

of kanuka and are replaced by other species, as for example, in northern basins of Hen Island. Unlike pohutukawa, small areas can be found where young kanuka has established beneath openings in a kanuka canopy, particularly on low-fertility soils such as on lower slopes of Little Barrier Island.

Entry of bird dispersed species

Once the pohutukawa and or kanuka have established, the succession is dominated by the entry of a suite of species that, with one exception, depend on birds, predominantly pigeons (*Hemiphaga novaeseelandiae*), for dispersal.

Kohekohe and karaka. Kohekohe can establish beneath a closed canopy of pohutukawa or kanuka (Table 2). Factors limiting this are uncertain, but kohekohe seeds are vulnerable to desiccation (Burrows, 1999) and canopy closure may be critical for germination. Court and Mitchell (1989) found that kohekohe is shade-tolerant, showing no etiolation when grown at 4% ambient sunlight. It is sometimes present on very small islands (Esler, 1978a), presumably in moist microsites. The development of dense understoreys of ponga or, in moister sites, mamaku (*Cyathea medullaris*) can reduce the rate at which tree species, such as kohekohe, establish within kanuka or pohutukawa stands.

Sizes of kohekohe on islands such as Cuvier and the Hen and Chickens suggest that on favourable sites, kohekohe can establish in pohutukawa or kanuka within 50 to 100 years of the initiating fire (Table 2). Establishment in kanuka forest may depend on prior entry of some understorey shrubs (e.g. Bellingham, 1984).

Like kohekohe, karaka depends on birds, particularly pigeons (*Hemiphaga novaeseelandiae*) for dispersal. Karaka establishes more readily than kohekohe near the coast. It is more resistant to wind-driven salt and its seeds are less vulnerable to desiccation

Table 2. Examples of successional patterns on the northern islands of New Zealand.

Successional pattern	Island locality	Nature of observation
Pohutukawa:kanuka patterns controlled by exposure to wind-carried salt	Western part of Lady Alice I., Chicken group Little Barrier I. Tawhiti Rahi, Poor Knights Is.	Vegetation description (Bellingham,1956) Vegetation survey ¹ , (Hamilton and Atkinson,1961)
Pohutukawa and/or kanuka establishing with bracken, manuka or flax	Western part of Cuvier I. Korapuki I., Mercury group Rakito (Arid I.)	Vegetation description (Beever <i>et al.</i> ,1969, also ¹) Vegetation map (Hicks <i>et al.</i> , 1975); vegetation map ¹ Vegetation description (Cameron and Wright, 1982)
Kohekohe entering pohutukawa	Lady Alice I., Chicken group Valleys on Cuvier I. South-western slopes of Stanley I., Mercury group	Vegetation map (Percy, 1956) and subsequent descriptions ¹ Permanent plots est.1960 ¹ Diameter/height class analyses ²
Karaka entering pohutukawa forest	Puka Bay, Hen I. East Double I., Mercury group Central basin, Korapuki I., Mercury group	Vegetation map (Atkinson and Campbell, 1966) Diameter/height class analysis of forest and permanent plot ¹ Population census repeated over 15 years ¹
Taraire or tawa entering pohutukawa or kanuka forests	South-western slopes of Stanley Island, Mercury group. Tirikakawa valley, Little Barrier Island Southern slopes of Hen I.	Diam./height-class analysis of taraire in pohutukawa forest ² Counts of taraire and tawa in kanuka forests ¹ Counts of taraire and tawa in old pohutukawa forest ¹

¹ I. Atkinson, unpublished data² I. Atkinson and J. Roxburgh, unpublished data

(Fig. 2, Table 2). Both kohekohe and karaka can regenerate under their own canopy.

Puriri. Puriri seedlings require higher light than those of kohekohe or karaka, but they establish readily in kanuka forest, sometimes before kohekohe, and in canopy gaps in pohutukawa forest. The headland immediately east of Dragon's Mouth Cove, Hen I., is covered by pohutukawa-kanuka forest, some of it wind-thrown. Kanuka is concentrated in the centre of the headland, partly protected from salt by surrounding pohutukawa. A relative density count made here of regenerating trees (5 to 30 cm d.b.h) in October 2001 gave 44% puriri, 16% mapou, 9% mahoe and 9% kohekohe ($n = 81$). Canopy-gap establishment of puriri can result in kohekohe-puriri stands or pohutukawa-puriri/kohekohe stands as on Lady Alice I.(Percy, 1956) and Whatupuke I. (Ritchie and Ritchie, 1970). Puriri can enter and maintain itself in taraire-tawa forest with periodic canopy disturbance. A recent sampling in mature taraire-tawa forest between 60 and 120 m a.s.l. on Hen I. showed three puriri in the canopy in a count of 51 canopy trees. Puriri is rare on extensively burnt islands, e.g. Red Mercury, Stanley and Double islands, a consequence of reduced seed source.

Taraire and tawa. The next stage in a pohutukawa:kanuka succession is entry of taraire and/or tawa. Their seeds dry out readily (Knowles and Beveridge, 1982). Larvae of the tortricid moth *Cryptaspasma querula* are major destroyers of fallen tawa seed in the central North Island (Beveridge, 1964) and this moth attacks both tawa and taraire seed on the northern islands. Both species depend on pigeons for dispersal and commonly establish within pohutukawa/kohekohe forest (Table 2). But if seed is available, either species may establish before kohekohe, particularly on sites protected from salt. Examples occur below 200 m a.s.l. on Hen and Little Barrier islands where some pohutukawa and kanuka forests have been replaced by taraire-tawa and tawa-taraire forests, or single-dominant stands of either species. It is not clear if these forests are self-maintaining.

Tawa is absent from islands smaller than 50 ha. Taraire appears more tolerant of droughts, but is generally absent from islands <30 ha. Kohekohe and karaka can replace themselves and also establish within taraire or tawa forests (*cf.* Court, 1978). Whether either could replace a canopy dominated by taraire or tawa seems doubtful, but Smale and Kimberley (1983)

describe a limited reciprocal replacement between tawa and kohekohe in forest on the Kaharoa Plateau. On Hen I. some taraire and tawa forest developed on cultivation areas abandoned without burning. Primary colonisers are likely to have been bracken, mapou and other shrubs, tree ferns, cabbage tree (*Cordyline australis*) and flax.

Kauri. Although wind-dispersed kauri frequently replaces kanuka on the mainland (Esler and Astridge, 1974), few cases are present on islands. Examples are present on the lower slopes of Little Barrier I. between 100 and 400 m a.s.l. (Hamilton and Atkinson, 1961). Three kauri found on Hen I. by Cranwell and Moore (1935), apparently established in kanuka. Kauri is uncommon in pohutukawa forest, but on Tawhiti Rahi, Poor Knights group, a kauri stand is developing through pohutukawa in the northern part of the island. A count here in April 1991 found three kauri emergent above the pohutukawa and 74 younger kauri beneath. On Arid I., Cameron and Wright (1982) record eight kauri trees, three with cones, growing on the outer coastal slopes of the island.

Effects of wind-driven salt and burrowing petrels on pohutukawa successions

The development of pohutukawa successions is influenced by the effects of wind-driven salt, and by the increased soil fertility generated by burrow-nesting petrels. The effect of salt damage is illustrated in Figure 3, which shows successional trends involving mahoe and mapou. These species establish soon after pohutukawa and kanuka and subsequently form a two-layered canopy. Following severe storm damage from wind-driven salt (a frequent event) mahoe re-sprouts more quickly than mapou. Pohutukawa/mahoe and pohutukawa/mahoe forests often become dominant on seaward-facing northern and western slopes. For example, mahoe is emerging through mapou and flax in some places on Stanley Island. The island's central north-south ridge includes more sheltered sites characterised by pohutukawa/mapou forest or dense stands of mapou (Taylor and Lovegrove, 1997; *pers. obs.*). These trends are the result of salt damage rather than animal browsing. Although rabbits and kiore were present on the island, there is no evidence that mapou or mahoe are suppressed by either rabbits (Esler 1978a) or kiore (Campbell and Atkinson 1999; 2000).

Another factor favouring mahoe over mapou is increased soil fertility associated with burrow-nesting petrels. On Coppermine Island there are concentrations of mahoe (within mahoe-puriri forest) associated with a colony of flesh-footed shearwaters (*Puffinus carneipes*) (Atkinson, 1968). Pohutukawa/mahoe forest on the lower north-west slopes of Korapuki Island is

associated with a colony of fluttering shearwaters (*Puffinus gavia*) and other petrels (Hicks *et al.*, 1975; *pers. obs.*). On slopes of rat-free Middle and Green islands in the Mercury group that have many petrel burrows, mahoe and wharangi (*Melicope ternata*) are major species (Atkinson, 1964). Pohutukawa/mahoe forest was dominant on petrel-burrowed slopes of Middle Chain Island in the Aldermen group (Court *et al.*, 1973), which then had kiore.

On more sheltered sites with fewer burrows, mapou is often prominent in developing stands of pohutukawa, subsequently forming a pohutukawa/mapou forest. This can be invaded by kohekohe and examples are present on Red Mercury I. (*pers. obs.*). Large parts of this island regenerated to mapou following a major fire in 1934 (Lynch *et al.*, 1972). The authors suggested that mapou in the understorey of the earlier forest "provided a seed source which enabled rapid colonisation of the burnt over areas...". However, most seed would be destroyed by fire. Instead, adventitious shoots from protected roots may account for the present abundance of mapou.

Similar trends favouring mahoe or mapou are identifiable within kanuka forest, especially if salt exposure has increased since the kanuka established. Esler (1978a) describes scrub on Motuoruhi (Goat) I., western Coromandel, as "mainly tall kanuka with mapou and mahoe gradually replacing it". Kohekohe can establish in mapou forest (as well as in pohutukawa forest) but as mapou has a much shorter lifespan than kohekohe the outcome will usually be kohekohe forest. Near the coast, karaka is more likely to replace mapou than kohekohe (Fig. 3).

Manuka::bracken successions

Another important succession following fires on northern islands is the development of manuka scrub and bracken fernland. Both species are widespread

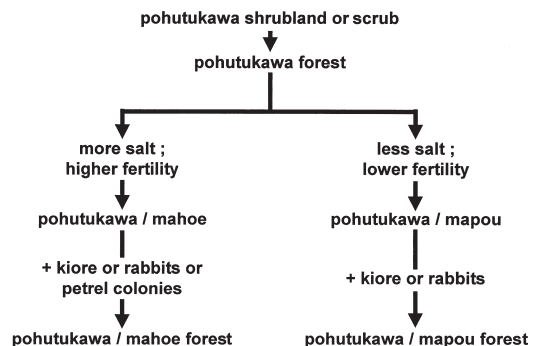


Figure 3. Effects of wind-driven salt and elevated soil fertility on pohutukawa (or kanuka) successions.

following fires, sometimes establishing together as a mosaic of stands. Manuka also establishes with kanuka (e.g. Bellingham, 1956) and is later overtopped. Figure 4 illustrates a manuka-bracken shrubland succession where bracken is overtopped by manuka while mapou establishes. Manuka is later suppressed by mapou. The expanding crowns of any scattered pohutukawa that established with manuka can result in a pohutukawa/mapou forest (Fig. 4). Mapou has a relatively short lifespan so the outcome will usually be kohekohe or karaka forest with scattered pohutukawa.

Persistence of manuka on inferior soils

On Little Barrier I., a Pliocene–Pleistocene volcano, triangular remnants of the original cone surface (planezes) remain at low altitudes between valleys (Kear, 1961). “Shag Track” crosses the planeze immediately west of the Tirikakawa stream where soils were mapped by Wright (1961) as brown granular clays (re-classified as Granular Soils by Hewitt, 1992). These are very compact, strongly acid clays with very low available phosphorus and less than 1 milliequivalent of total exchangeable bases (Wright, 1961).

Kanuka forest and scrub covers most of Shag Track. In May 1954, I drew a profile through a small

patch of manuka scrub along the north-eastern side of the track (Atkinson 1954; NZMG 260 S08 and T08 961512). Although the original markers had disappeared, the site was relocated in May 2001 and the profile redrawn within a metre of its original position (Fig. 5). Woody plants were counted in two 25 × 1 m transects placed at right-angles to each other and centred on the profile transect (Table 3).

This site has remained under manuka throughout the 47-year period between samplings, even though it is surrounded by kanuka forest. Remains of collapsed manuka were strewn over the ground throughout the site in 2001. Some manuka drawn in Figure 5 are survivors from 1954, particularly the larger diameter trees in the central and right-hand sections of the 2001 profile. The left-hand end of this profile passes through a patch of young manuka and the area containing akepiro (*Olearia furfuracea*), towards the right of the profile, contains an older group of regenerating manuka.

Leaving aside areas of younger manuka, there has been little change in canopy height between 1954 and 2001. The counts (Table 3) indicate little change in the canopy apart from localised increased density of manuka. Marked decreases in *Coprosma arborea* and *C. rhamnoides* were noted in the understory, whereas mingimingi (*Leucopogon fasciculatus*), mapou and akepiro show no substantial changes.

This example does not represent the most extreme “gumland” communities present on the island. Some of the western planezes are dominated by low-growing manuka (<1 m tall), the rushes *Schoenus tendo* and *Lepidosperma laterale*, and patches of *Lycopodium deuterodensum*.

Table 3. Number of trees in the canopy (individuals in a 25×1-m-transect) and number of shrubs in the understory (individuals >60 cm tall in two bisecting perpendicular 25×1-m-transects) counted in manuka scrub, Shag Track, Little Barrier Island, in 1954 and 2001 (see text and Fig.5).

Species	Year	
	1954	2001
Canopy trees		
<i>Coprosma arborea</i>	1	1
<i>Kunzea ericoides</i>	1	–
<i>Leptospermum scoparium</i>	14	22
<i>Myrsine australis</i>	–	2
<i>Olearia furfuracea</i>	2	2
<i>Pittosporum umbellatum</i>	–	1
Understorey shrubs		
<i>Carmichaelia australis</i>	1	–
<i>Coprosma arborea</i>	8	1
<i>C. rhamnoides</i>	14	1
<i>Cyathodes juniperina</i>	1	3
<i>Kunzea ericoides</i>	–	1
<i>Leptospermum scoparium</i>	–	5
<i>Leucopogon fasciculatus</i>	3	3
<i>Myrsine australis</i>	6	8
<i>Olearia furfuracea</i>	10	10
<i>Pittosporum tenuifolium</i>	1	–
<i>P. umbellatum</i>	1	1
<i>Pseudopanax arboreus</i>	4	–

Rates of pohutukawa and kanuka successions

Pohutukawa

From observations on several islands it appears that a pohutukawa stand can maintain a continuous canopy for at least 100 years, and that individual trees can live for 300 years or more. When they establish at low densities, pohutukawa trees can develop multiple stems at an early stage. Each of these contributes a foliage segment to the tree crown, and as a tree matures some of these stems die. The mortality rate of stems contributing to crown foliage was measured over 9–12 years on two permanent plots within 80 to 100-year-old stands of pohutukawa on Korapuki Island in the Mercury group. Although the number of pohutukawa stems in each plot decreased at rates of 14.6 and 7.6 stems/ha/decade, the foliage on remaining parts of the crown continued to grow and the total canopy cover showed little change (*unpub. data*). Thus, at this stage of the life-span, foliage area contributed to the canopy by a tree is not necessarily reduced by stem loss. However with increasing age, crown foliage area does

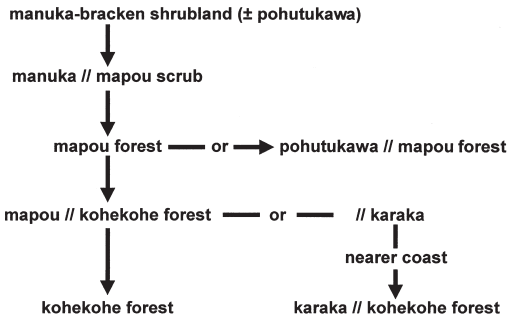


Figure 4. Forest successions initiated by manuka and bracken following fires on the northern offshore islands.

decrease as more stems die. Isolated trees may persist long after the surrounding pohutukawa has been replaced by species such as taraire, tawa and puriri. This can be seen on the southern slopes of Hen Island.

The tallest (although not necessarily the oldest) forest on Cuvier I. is the pohutukawa/kohekohe forest in the valleys. Cheeseman (1896) described one of these valleys as having the largest trees seen on the

island. The valley was “particularly noteworthy for magnificent specimens of *Dysoxylum* (kohekohe) - the largest I have seen - which must be quite 70 ft. in height. The largest specimens of pohutukawa seen in the island also are found there.” Given that the kohekohe here is likely to have established well after the pohutukawa, the latter is likely to have been at least 150 years old in 1896. Large pohutukawa are still dominant in this valley, and so presumably are now at least 250 years old. A 1-ha permanent plot was established in a catchment adjacent to the valley described by Cheeseman. The plot was established by C.R. Veitch for bird counts, and has rolling topography with rounded ridges and basin-like valleys. The plot is traversed by a set of parallel wires which I used as repeatable routes for point analyses of the canopy in 1970 and 1996. Over 26 years, pohutukawa canopy cover decreased from 96 to 56% and from 86 to 64% on ridges and valley sides, respectively. In contrast canopy cover of kohekohe increased nearly three-fold, from 4 to 12% on the ridges, and 10 to 26% on the valley sides. Although these differences were significant (at the 95% confidence level using the binomial distribution of probability values) for pohutukawa on the ridges and kohekohe on the valley

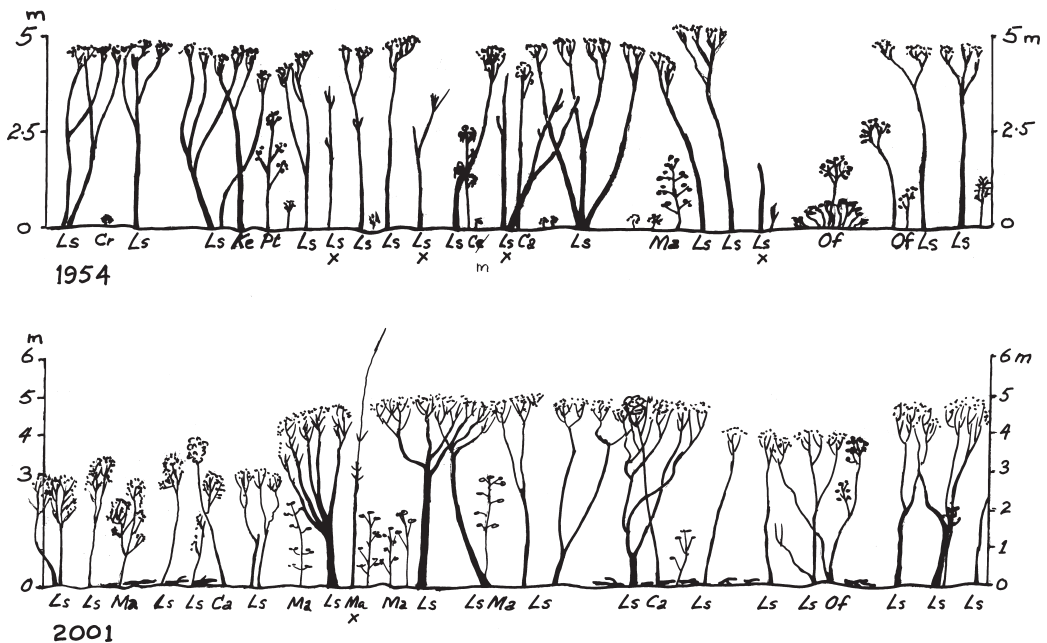


Figure 5. Profile diagrams made in manuka scrub at the same site on the Shag Track, Little Barrier I., in May 1954 and May 2001. Key to symbols: Ca = *Coprosma arborea*; Cm = *Carmichaelia australis*; Cr = *Coprosma rhamnoides*; Ke = *Kunzea ericoides*; Ls = *Leptospermum scoparium*; Ma = *Myrsine australis*; Of = *Olearia furfuracea*; Pt = *Pittosporum tenuifolium*; X = plant dead.

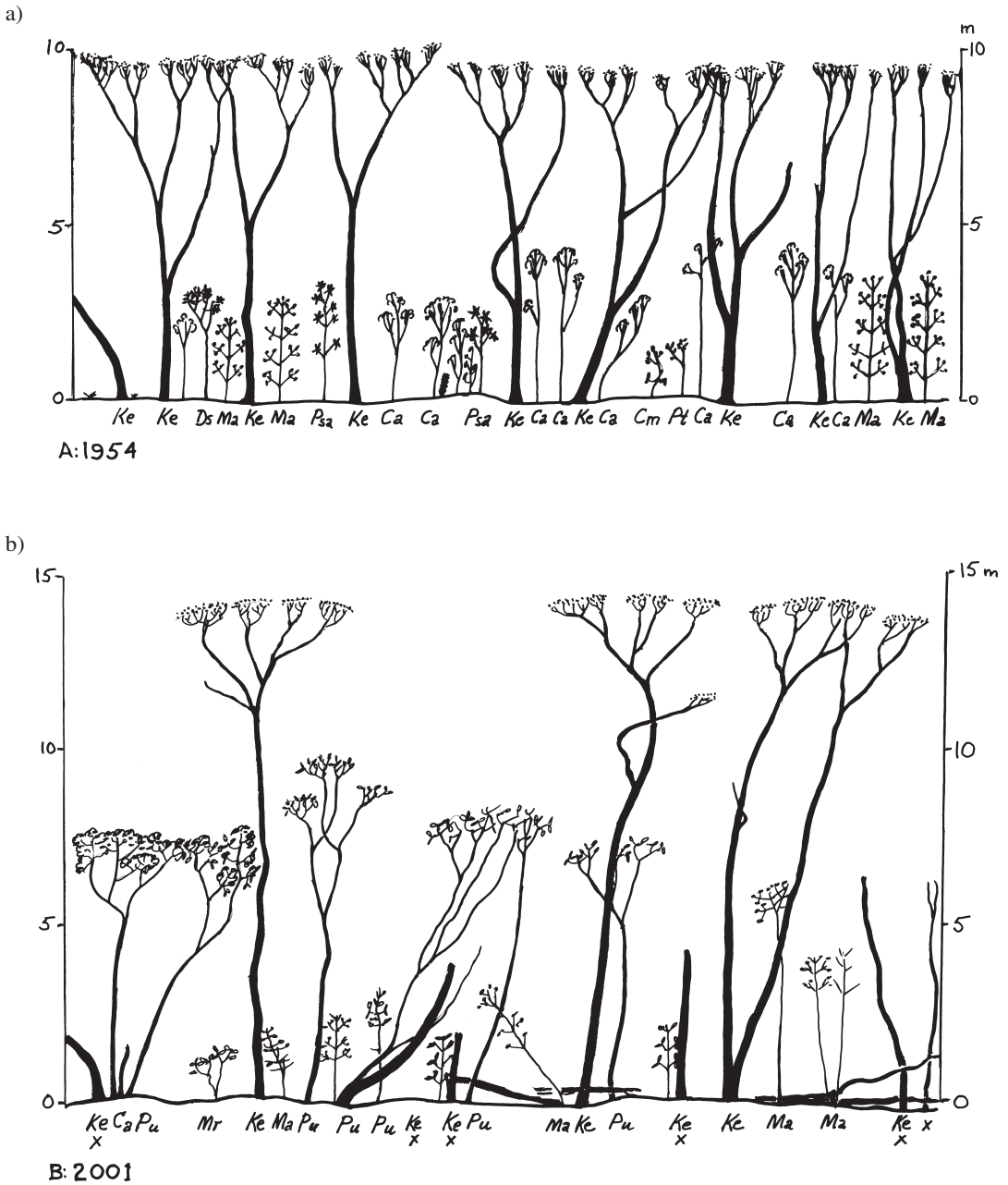


Figure 6. Profile diagrams made in kanuka forest on Quadrat 1 of Bellingham and Percy (1954) near the Thumb Track, Little Barrier Island in 1954 (A) and redrawn in 2001 (B). The 2001 profile was located as close as possible to the 1954 profile. Key to symbols: Ca = *Coprosma arborea*; Cb = *Coprosma robusta*; Ds = *Dysoxylum spectabile*; Ke = *Kunzea ericoides*; Ma = *Myrsine australis*; Mr = *Melicetyus ramiflorus*; Psa = *Pseudopanax arboreus*; Pt = *Pittosporum tenuifolium*; Pu = *Pittosporum umbellatum*; X = plant dead.

sides only, they are consistent with successional trends in pohutukawa forest identified on many islands.

On favourable sites on Hen Island if either taraire or tawa (or both) establish within a pohutukawa forest shortly after it has formed a closed canopy, they can become dominant within 200 years of the initiating fire.

Kanuka

Kanuka has a shorter lifespan than pohutukawa on the northern islands, probably in the range of 100 to 150 years. Data on rates of change of kanuka successions area available from kanuka forests growing on Little Barrier Island. Much of the extensive kanuka forest on the lower ridge and valley slopes of south-eastern parts of the island originated in the latter part of the 19th century (Hamilton, 1937; Hamilton and Atkinson, 1961) and is therefore between 100 and 125 years in age. Kanuka in this forest is now thinning rapidly and many trees have died since 1960. Smale (1993) re-surveyed two permanent plots established in 1960, and found that the density of kanuka measured in one of the plots (Quadrat 1, 60 m a.s.l.) in 1990 was half that measured in 1963 by English and Brock (1964). The effect of this loss is illustrated by Figure 6 which shows vegetation profile diagrams I drew along contours through the stand in 1954 (Fig. 6A) and 2001 (Fig. 6B). Changes in the kanuka stand were so great that the line of the original profile was not accurately located and so these diagrams are only representational of the changes. The increase in height of the kanuka and decrease in density are clear. The original understorey was dominated by mapou at a time when few haekaro (*Pittosporum umbellatum*) were present (Bellingham and Percy, 1954). Mapou has been replaced by a much taller understorey of haekaro, sometimes forming a new canopy beneath the open kanuka (Fig. 6). Observations in 2001 over a much larger area of the island showed that Quadrat 1 is typical of many, but not all, of the low-altitude changes in kanuka on the island. A discontinuous canopy of haekaro is widespread on some slopes and ridges. Juvenile kohekohe and puriri are often present, but not frequently enough to produce the kanuka/kohekohe forest shown in Figure 1. On low-fertility soils, remaining kanuka will probably be replaced by kauri, at present uncommon at low altitude. Where taraire or tawa have established in kanuka, particularly valley sites, either or both will dominate within 150 years of the initiating fire; the replacement rate for kanuka is greater than for pohutukawa.

Discussion

Court (1978) described successions on Hen Island and identified two major trends that are similar to those reported here. The first was from kanuka-pohutukawa to a mixed forest (with pohutukawa) changing to tawa-taraire. A subsidiary trend culminated in karaka (or pukaniui [*Meryta sinclairii*]-karaka) forest. The second major trend (inland) was through kanuka to a mixed forest (without pohutukawa) also changing to tawa-taraire.

These trends can readily be related to those of the present study, except that kohekohe was not included. Court (1978, p. 114) noted that kohekohe was "well represented by smaller size classes [and] will be a component of tawa-taraire forest". He also identified an above shore trend originating from mixed forest (with pohutukawa) and culminating in "karaka, parapara, tawapou, milk tree, ?nestegis". In view of what we now know about kiore effects, excepting karaka, this trend is unlikely while kiore remain on the island (see below).

Kiore and successional trends

Most islands discussed either have kiore, or had them until they were eradicated in the 1990s. Campbell and Atkinson (1999, 2002) showed that kiore significantly reduce recruitment of some species, raising the question of how much they have influenced successional trends. There is no evidence that kiore affect any of the primary post-fire species discussed here. Some secondary immigrants discussed have fleshy fruit with seeds (or seedlings) eaten by kiore. Campbell and Atkinson (2002) investigated the effect of kiore on the recruitment of tree species and found no recruitment depression for mapou or mahoe. However they found that karaka recruitment was slightly depressed on some sites, and that kohekohe seeds are eaten, but the species is frequently common in the presence of kiore. Kiore also eat puriri seeds, but not all trials showed more seedlings of puriri in the absence of rats. Thus, the extent to which kiore can retard the rate of kohekohe or puriri establishment is unclear. No kiore effect was found on taraire or tawa recruitment.

Nikau (*Rhopalostylis sapida*) is absent from most islands discussed. Where moisture is adequate it is important in the understorey, and sometimes canopy, as on Little Barrier, Hen, and parts of Cuvier islands. Kiore eat nikau seeds and seedlings, sufficient to depress recruitment (Campbell and Atkinson, 2002), but their effect on successional pathways is unclear.

Recruitment of coastal maire (*Nestegis apetala*), milk tree (*Streblus banksii*), tawapou (*Pouteria costata*) and parapara (*Pisonia brunoniana*) is reduced by kiore (Campbell and Atkinson, 1999, 2002). These species are generally rare or absent on islands where kiore are,

or have been, present. Any one or all of these species may once have been of major importance. For example, I visited rat-free Motukokako (Piercy) Island, Cape Brett, with I.M. McFadden in October 1984. This 7-ha island is very steep with shallow rocky soils, mostly free of petrel burrows. In a count of 100 canopy trees made across the main ridges and slopes, the most important species were tawapou (33%), puriri (20%) and milk tree (14%). We recorded 8% coastal maire, and parapara, though not in the canopy, was abundant. Thus some 75% of the forest canopy is composed of kiore-vulnerable species. Cameron and Taylor (1991) suggest the island's vegetation may have originated in the 1850–1900 period; small trunk diameters suggested a young forest. This may be an effect of restricted moisture related to the very shallow soils. Whatever the explanation for trunk size, canopy composition on this island is very different from that of a kiore-inhabited forest.

Pohutukawa and restoration programmes

Pohutukawa colonises a wide range of sites after fires. Compared with kanuka, its large size, long lifespan and copious production of slowly decomposing litter have a strong influence on other plants and animals. Thus development of a diverse canopy is retarded relative to development in kanuka. This should be considered in planning restoration programmes. When pohutukawa is used as the major initial cover, e.g. on Tiritiri I., plant and animal diversity will increase relatively slowly. This may not matter provided other habitats are established and maintained. Much depends on the way in which restoration goals for individual species are integrated with overall goals for plant-animal communities on the island.

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Appendix 1. Checklist of islands included in this study (see also Figure 1)

Island/group	Location	Area (ha)	Island/group	Location	Area (ha)
Aldermen Islands	36° 57' S, 176° 5' E		Mokohinau Islands	35° 55' S, 175° 6' E	
Hongiora		16	Atihau		16
Middle Chain		23	Burgess		56
Ruamahuaity		25	Fanal		75
Ruamahuanui		32	Noises Islands	36° 12' S, 174° 13' E	
Cavalli Islands	35° S, 173° 57' E		Otata		15
Motukawaiti		47	Ohinau Islands	36° 44' S, 175° 52' E	
Motukawanui		380	Ohinau		43
Panaki		16	Poor Knights Islands	35° 27' S, 174° 43' E	
Chicken (Marotere) Islands	35° 54' S, 174° 43' E		Aorangi		110
Lady Alice		155	Tawhiti Rahi		163
Coppermine		80	Arid (Rakitu) Island	36° 8' S, 175° 30' E	328
Whatupuke		102	Rimariki Island	35° 25' S, 174° 26' E	22
Mauitaha		26	Tiritiri Matangi Island	36° 36' S, 174° 53' E	196
Cuvier (Repanga) Island	36° 28' S, 175° 46' E	195	West Coromandel islands		
Goat Island, Leigh	35° 16' S, 174° 47' E	15	Motukahaua		22
Hen (Taranga) Island	35° 48' S, 174° 42' E	500	Motuoruhi (Goat)		57
Little Barrier (Hauturu) Island	36° 11' S, 175° 5' E	3083	Moturua (Rabbit)		24
Mercury Islands	36° 35' S, 175° 53' E		Motutapere		45
Great Mercury (Ahuahu)		1860	Motuwi		22
Double		34	Rangipukea		34
Korapuki		20	Waimate		70
Red Mercury		203	Whanganui		282
Stanley		86			

