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A review of New Zealand kauri (*Agathis australis* (D.Don) Lindl.): its ecology, history, growth and potential for management for timber.

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Abstract

Kauri (*Agathis australis* (D.Don) Lindl.) is endemic to New Zealand, where it is the only indigenous member of the Araucariaceae. It has the most southerly distribution of any species in the genus and is currently confined to the warm temperate areas of the North Island. At the time of European settlement, forests containing kauri covered 1 000 000 ha or more in New Zealand. Following uncontrolled logging, land clearance for alternative land use and destruction by fire, only 7500 ha of virgin or primary forest remain, mainly in conservation reserves. An additional 60 000 ha of scrub/shrubland and secondary forest contain varying amounts of regenerating kauri.

Kauri is reputed to produce greater volumes of wood from single stems than any other timber tree in the world. Its timber is regarded as one of the finest due to qualities of decay resistance and dimensional stability under moist conditions. A wide range of products was developed by Maori and European settlers. Kauri timber and gum made a substantial contribution to the physical and economic development of New Zealand between 1830 and 1900.

Agathis australis shares a number of biological characteristics with lowland *Agathis* species found in the tropics and subtropics. These include a juvenile form with narrow tapering crown; mature emergent trees with massive, spreading, dome-shaped crowns and upwardly-arched branches; self-pruning in sapling and pole-stage trees; flaking bark; wind-dispersed, small-winged seeds formed in cones that disintegrate at time of seed maturity while still on the tree; and only a few months of seed viability after shedding. Juvenile trees with taproots and mature trees with wide-spreading lateral roots and descending peg roots are windfirm, assisting longevity. Although surviving trees of massive dimensions (3–5 m diameter) are usually hollow, their life span may be 1500 years or more. Large kauri have a podsolising effect on some acidic soils, making them less fertile. Efficiency in the use of water and nutrients has enabled the species to become dominant on infertile and drought-prone ridge tops. Observations of growth in natural stands indicate mean annual increment of 2.5–6.0 mm in diameter and 0.3 m in height.

Interplanting of kauri in scrub and shrubland developed on former kauri forest sites has produced poor results. Mean annual increments of 6.9 mm in diameter and 0.44 m in height have been recorded in young untended plantations. Greater success has been achieved through attention to site selection, improved establishment techniques and silvicultural tending. The most suitable sites for planting are those with fertile, well-drained, light-textured soils, a warm, humid climate, and a history of previous occupation by broadleaved (angiosperm) plant species. Current research suggests that rotation length can be reduced by best-practice management, and that planted stands could be a continuing source of kauri timber in the future.

Keywords: *Agathis australis*; history; ecology; distribution; growth; management.

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Introduction

Kauri (*Agathis australis* (D.Don) Lindl.)[1] is one of New Zealand's most renowned and researched native coniferous tree species. In its earliest days the effect on New Zealand's landscape of logging of kauri and the export of timber[2] and gum was only rivalled by the harvesting and use of harakeke (flax – *Phormium tenax* J.R.Forst. & G.Forst.) (Hochstetter, 1867; Poole & Boyce, 1949). This review of current knowledge about New Zealand kauri and the forests in which it grows focuses on the discovery and description of the species, its uses, and its growth in natural and planted stands.

Numerous scattered pieces of information already exist; together they have potential for guiding management to the point where kauri could once more contribute to New Zealand's economic well-being. Detailed information on the biology of kauri gathered by Ecroyd (1982) followed concise general accounts given by Hooker (1867), Kirk (1889), Cheeseman (1906), Laing and Blackwell (1907), Hutchins (1919) and Hinds and Reid (1957). A list of more than 600 references held in the National Forestry Herbarium has provided valuable material for the present review. We also consulted a large number of publicly available, but unpublished, reports held in the New Zealand National Forestry Library which describe experiments with kauri and observations of kauri forest and forest management dating back to the early 1900s.[3]

Large kauri trees have cultural significance for the indigenous Maori people. Kauri as a species and the forests in which it grows are now widely appreciated by all New Zealanders and increasingly by visiting scientists, foresters and tourists. In 1983, 87% of the 7500 ha of mature kauri forest and 23.5% of the second-growth kauri forest was under the control of the New Zealand Forest Service (Halkett, 1983a). Most of the remainder was in private ownership. Prior to Forest Service disestablishment in 1987, policy included the acquisition of second-growth stands in order to protect and tend regenerating kauri. State-owned forests containing kauri are now included in conservation reserves where logging is prohibited. Since 1987, management by the Department of Conservation has included protection from the effects of fire, browsing animals and invasive weeds.

History of discovery

Hooker (1853), Cheeseman (1906) and Cockayne (1921) provided early summaries of botanical exploration and research in New Zealand. These include information about the first collections of Sir Joseph Banks and Dr D.C. Solander in 1769, descriptions by G. and J.R. Forster in 1776 and 1786, and collections by other eminent botanists in the mid 1800s. The first European explorers (Abel Tasman in 1642, James Cook and Jean-Francois-Marie de Surville in 1769) did not identify the presence of kauri, even though Cook anchored within the natural range of kauri at Mercury Bay on the Coromandel Peninsula (Halkett & Sale, 1986). Loudon (1838) suggested that Cook may have discovered kauri in 1769 because "an enormous tree was cut down" in the Thames River area. However, it seems that this statement referred to kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub.), a species that was used (unsuccessfully) for spars. While Banks and Solander made no reference to kauri trees in 1769, they did observe kauri gum, wrongly describing it as a resin from mangrove (*Avicennia marina* (Forssk.) Vierh.) (Cheeseman, 1906).

The first drawing of kauri (Lambert, 1824) was made from material collected by Captain Downie of the ship *Dromedary*. Downie appears to have been responsible for the first collection and removal of live kauri seedlings from New Zealand. These were presented to the Horticultural Society in England in or about 1821 (Loudon, 1838). Another early botanical collection including kauri was made by Allan Cunningham in the Bay of Islands during an expedition to New Zealand in 1826 (Cunningham, 1838).

Nomenclature and related species

The correct nomenclature for kauri is *Agathis australis* (D.Don) Lindl. in Loudon, as presented by Franco (1949). Earlier references attributing the binomial *Agathis australis* to Salisbury (1807) are incorrect. Salisbury described the genus *Agathis*, but he did not describe *A. australis.*

Synonyms are:

Dammara australis D. Don in Lamb. Lambert, Descr. Pinus 2: 14t. 6 (1824);

[1] *In this paper, names of plants follow the New Zealand Plant Names and the New Zealand Fungi Databases maintained by Landcare Research.*

[2] *Where timber volume has been presented in this paper, it has often been converted from imperial to metric units. The conversion factors used were 12 super ft = 1 ft^3; 35.3 ft^3 = 1 m^3.*

[3] *Some of these unpublished reports are detailed in subsequent footnotes*

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Podocarpus zamiaefolius A.Rich. In Lesson & Richard, Voy. Astrolabe Bot. [Ess. Fl. Nouv. Zél]1: 360 (1832); and

Agathis australis (D.Don.) Loudon, Encycl. Pl.: 802 (1829) (Farjon, 2001).

Kauri is New Zealand's only representative of the Araucariaceae (Henkel & W. Hochst.). This ancient family of coniferous trees consists of three genera: *Araucaria*, *Wollemia* and *Agathis* (Setoguchi et al., 1998). The Araucariaceae achieved maximum diversity in the Jurassic and Cretaceous periods, when the distribution of its members was almost worldwide. The family became extinct in the northern hemisphere at the end of the Cretaceous period (Singh, 2006). The 19 species in the genus *Araucaria* are found in Australia, Norfolk Island, Papua New Guinea, New Caledonia and South America (Setoguchi et al., 1998). *Wollemia* is represented by one species, *Wollemia nobilis* W.G. Jones, K.D. Hill & J.M. Allen, discovered recently in New South Wales, Australia (Jones et al., 1995). The genus *Agathis* (Salisb.) consists of 21 species (Farjon, 2001). Its range extends west to Sumatra; north to the Philippines; east to Fiji; and south to New Zealand (Hooker, 1867; Kirk, 1889; Whitmore, 1977). The greatest representation of the genus (five species) occurs in New Caledonia (Whitmore, 1977). While each species has a local name, all are known by the New Zealand Maori name "kauri" or "kauri-pine". They are highly prized for their fine-grained, uniform timber (Whitmore, 1977, 1980).

Of *Agathis* species currently grown for timber, *A. dammara* (Lamb.) Rich. & A.Rich. in Indonesia and *A. moorei* (Lindl.) Mast. and *A. lanceolata* (Pancher) Warb. in New Caledonia have been the most productive. In Queensland, Australia, *A. robusta* (C. Moore) F.M.Bailey was grown in plantations until damage by the kauri coccid (*Conifericoccus agathidis* Brimblecombe) resulted in cessation of planting in the 1960s (Nikles, 2009).

Botanical features of New Zealand kauri

Foliage

Leaves are usually dull olive-green but occasionally have a bluish, glaucous appearance. The adult form is lanceolate–oblong, 2.0–3.5 cm long, (Figure 1). Juvenile leaves are lanceolate, 5–10 cm x 5–12 mm (Hooker, 1867; Ecroyd, 1982). The leathery adult leaves are functional for 3–6 years (Ogden & Ahmed, 1989), some remaining on the tree for up to 15 years (Silvester & Orchard, 1999). Budburst occurs in September–October when average daily maximum temperature starts to exceed 17 °C (Bieleski, 1959). Growth and stand productivity have been linked to leaf/shoot architecture, efficiency of light capture being shown to decrease with increasing tree age and size (Niinemets et al., 2005).

Branching

In natural stands, the lower branches abscise cleanly from the stem from the sapling stage onwards (Hutchins, 1919; Licitis-Lindbergs, 1956). There is no lasting damage to the bark and no knots form in the stemwood. This mode of abscission is a valuable characteristic because the timber has few of the defects usually associated with branch development (Kirk, 1889; Hutchins, 1919; Bergin & Steward, 2004). Wilson et al. (1998) showed that it was possible to induce branch abscission in 6–8 year-old trees in a tightly-stocked natural stand (10 000 stems/ha). When a 40–50 mm branch stub was left after pruning, almost all of the stubs were shed within six weeks. Unpruned branches remained attached over the same period. Advantages of pruning kauri when grown in low-density plantations (625 stems/ha) where branch abscission was not occurring naturally, have been identified by G. A. Steward, (unpublished data). Branch stub abscission was initiated in 70% of pruned branches if pruning was carried out before branches reached 4 cm in diameter, leaving a stub 4–5 cm in length.

Roots

The root system of mature trees is extensive, with lateral roots often reaching beyond the crown. Deeply penetrating "peg" roots descend from the laterals, giving firm anchorage. Kauri trees are generally windfirm until senescence sets in or rot develops. Young kauri have a well-developed taproot, and it is possible that penetration and exploitation of free-draining soils is important for optimum growth (Morrison & Lloyd, 1972). Observations of windthrown mature kauri indicated no evidence of a taproot, which was presumed to disappear with tree maturity. Fine feeding roots are superficially distributed in layers of raw humus and litter. They bear nodule-like beaded rootlets which contain vesicular arbuscular mycorrhizal endophytes. The relationship between the roots and these microorganisms has been reviewed by Ecroyd (1982). Potted or bare-rooted kauri seedlings do not form balanced fibrous root systems (Morrison & Lloyd, 1972; Bergin & Steward, 2004). Slow development of roots may account for the slow establishment of naturally established and planted seedlings.

The anatomy of kauri root wood has been described by Donaldson (1983). Root grafting, presumed to occur in this species (Beddie, 1941), has been confirmed by observation (Hillary, 1944).

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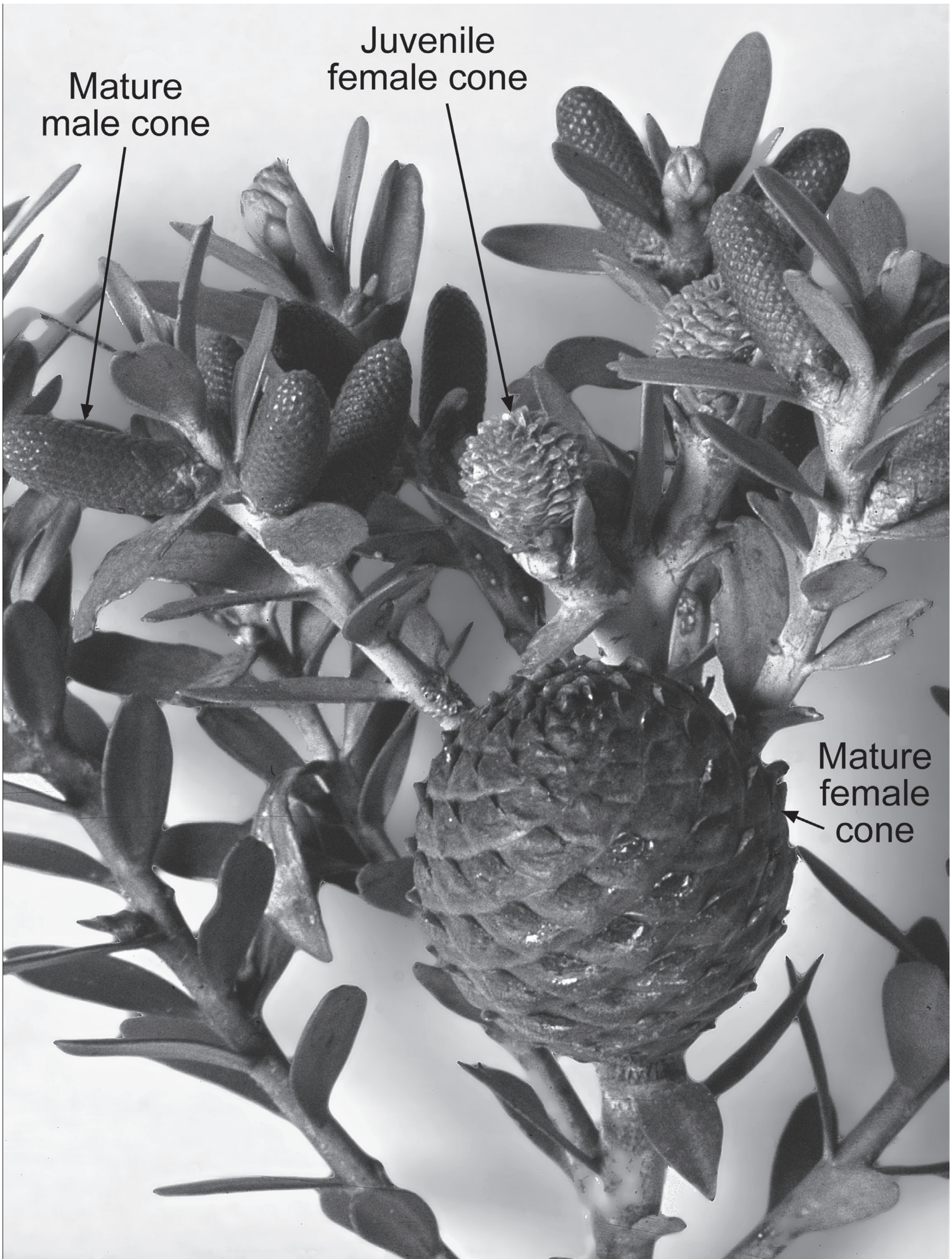

FIGURE 1: Kauri is monoecious; male and female cones develop in close proximity on the same branch. Note mature and immature female cones.

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Tree dimensions

Mature kauri trees have straight, untapered, cylindrical stems averaging 12–25 m in length. The stems have flaking bark and are typically free from branches or epiphytes (Figure 2). Crowns of emergent trees are massive with upward-arching branches producing flat or slightly rounded tops (Anon., 1868). Darwin (1839) commented that "the largest trees, from the parallelism of their sides, stood up like gigantic columns of wood". Total height generally reaches 30–50 m, and occasionally 60 m (Hooker, 1867; Allan, 1961). Stem diameter of trees aged 400–800 yr is commonly 1–2 m, but in living giants may be 3–5 m. Massive stems with diameters exceeding 6–7 m were recorded during logging and burning for land clearing carried out by early settlers. A stem with diameter of 6.4 m and clear bole length of 30.5 m was observed on the Tutamoe plateau in Northland (Hutchins, 1919; Burstall & Sale, 1984; Halkett & Sale, 1986). A large kauri tree at Mercury Bay on the Coromandel Peninsula, measured 7.0 m in diameter and 24.4 m to the first branch (Cheeseman, 1913). The greatest diameter (8.5 m) was reported from the Tararu Creek area of the Coromandel Peninsula (Sale, 1978).

Wood

The wood of kauri has been shown to become mature at approximately 70 years of age. Average tracheid length is then 4.9 mm (Loose, 1997). Differences in kauri wood characteristics, from prehistoric to modern kauri, have resulted from environmental rather than evolutionary effects (Loose, 1997).

The heartwood of mature kauri has the reputation of being one of the finest softwoods in the world (Hochstetter, 1867; Cheeseman, 1914; Clifton, 1990). It was described as the most valuable product of the North Island (Darwin, 1839) because it "could be finished to perfection" (Hinds & Reid, 1957). The timber has a light honey to rich reddish-brown colour, with a distinctive silvery speckled lustre (Clifton, 1990). Average values for density (560 kg/m^3), strength (modulus of rupture 88 MPa, modulus of elasticity 13.0 GPa), and shrinkage (tangential 4.1%, radial 2.3 %) are given by Hansson (1924) and Hinds and Reid (1957). Kirk (1874) and Campbell (1891) recorded early observations on the durability of heartwood and indicated a service life for building, construction and maritime use of more than fifty years. A computer model designed to estimate the amount of heartwood present in planted and second-growth natural kauri stands has been developed by Steward and Kimberley (2002). Stem diameter was identified as the principal factor for predicting heartwood presence and quantity. Age was found to be a secondary factor, the older, smaller stems in natural stands having more heartwood than the amount predicted from stem diameter.

Sapwood is less durable than heartwood, and is attacked by the wood boring beetle (*Anobium punctatum* De Geer) (Clifton, 1990). It decays rapidly when in contact with the ground (Kirk, 1874). Timber from second-growth kauri has a high proportion of sapwood, and until recently its properties were assumed to be inferior to those of heartwood from old-growth trees. When the quality of sapwood from 68-year-old plantation-grown kauri was tested, it was found to be similar to that of old-growth kauri in terms of density, modulus of elasticity, and shrinkage (Steward & McKinley, 2005). These findings agreed with the less technical observations of Hutchins (1919), who believed that kauri sapwood was as good as heartwood provided it was used indoors and kept free from borer.

Reproductive biology

Kauri is monoecious. Male strobili are axillary, 2.5 x 8–12 mm, and distal to female cones when borne on the same branch (Figure 1) (Morrison, 1950). Viable pollen, produced from as young as six years of age in open-grown planted trees, is shed during September–October. Detailed descriptions of the pollen are given by Cranwell (1940) and Pocknall (1981). Cranwell noted that pollen is not viable for long and is sometimes attacked by fungi.

Female cones are 5–7.5 cm in diameter (Figure 1) when they ripen in late summer. They produce seed with a membranous wing which is about 10 mm wide. Sometimes a secondary rudimentary wing is also formed. Trees usually begin to produce viable seed when they are 25–40 years of age (Halkett, 1983a). Ecroyd (1982) reported formation of seed on 15-year-old trees. Female cones and viable seed have been observed on planted trees as young as 6 years old (Maurice Sutton, personal communication, 2009). Seed crops are annual and vary in terms of quantity and viability. Seed-bearing cones disintegrate on the tree in late summer and early autumn, approximately 18 months after initiation (Hutchins, 1919; Lloyd, 1960; Ecroyd, 1982). Under moist, warm conditions, germination occurs soon after shedding. Although viability is lost after only a few months on the forest floor (McKinnon, 1937a; Whitmore, 1977), it can be increased by storage at 4 °C (Morrison, 1955). Preest (1979) found that seed stored for 5–6 years in airtight containers under conditions of low moisture and temperature was still viable.

[4] Hansson, A. (1924). *A preliminary forest inventory of the Dominion of New Zealand.* New Zealand National Forestry Library heritage collection (unpublished).

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FIGURE 2: Stages in kauri tree development. A: Young trees (rickers) with monopodial growth habit; B: Mature tree with upward arching branches and columnar stem, C: Ancient tree, 5.2 m in diameter, possibly 1500–1700 years old.

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The average weight of winged seed is very low (approximately 34 mg: A. J. Dakin personal communication, reported in Ecroyd, 1982). The winged seeds usually fall within 150 m of the parent tree, but dispersal distances up to 1.5 km have been recorded (Mirams, 1957; R. C. Lloyd in Ecroyd, 1982). Dispersal distances are probably greater when seedfall coincides with storms, and where seed separates from the cone scales during cone disintegration. On Rangitoto Island in the Hauraki Gulf, young kauri have been found 3.5 km from the nearest mature tree (Auckland Botanical Society, 2007).

Age

During the juvenile or "ricker" stage, kauri trees have narrow, tall, tapering crowns with a strong monopodial habit (Figure 2A). In natural forests this form may persist for 150–200 years, when stems reach 50 cm diameter and the crowns start to spread. From data collected in several forests, Ahmed and Ogden (1987) estimated a mean age of 127 years for trees 10–20 cm in diameter and 231 years for those in the 50–60 cm diameter class. Individuals with a full spread of healthy emergent crown (e.g. Figure 2B) were likely to be 250–350 years old. These estimates agree with those of Steward and Kimberley (2002) who calculated a mean stand age of 120–218 years for 27–40 cm diameter trees in natural second-growth stands.

Cheeseman (1914) reviewed early attempts to define the longevity of kauri. Estimates of 1300–2000 years made by Laslett (1875) in the early 1840s were more accurate than later suggestions of 3600–4000 years based on diameter measurements (Kirk, 1889). Kirk believed that "the immense pressure exerted by the outer cylinders [of wood] consolidates [compresses] the inner portion of the trunk, so that the number of rings to an inch is greatly increased." He also assumed that the balance of evidence was in favour of kauri producing more than one growth ring per year, and that growth rings were, therefore, of little value in determining age. Stewart (1905) showed that growth rings in planted kauri were annual, and could be used to assess growth rates and tree age. Growth rings are usually clear and can be counted with little trouble (Hutchins, 1916; Steward & Kimberley, 2002). Using increment core analysis, an age of 2144 years was estimated for a 5.2 m diameter tree in Waipoua Forest (Reed, 1953). Dendrometer band studies have shown statistically significant correlation between radial increment measured by bands and data derived from diameter increment cores (Palmer & Ogden, 1983). Enright and Ogden (1995) suggested typical longevity of 600 years for trees in old-growth stands, and a maximum estimated longevity of 1679 years. Ahmed and Ogden (1987) examined cores from trees of different diameter classes in 25 stands covering the geographical range of kauri. They derived the age of large trees by adding ages of the average-sized tree in each diameter class, and concluded that trees 2 m in diameter average 1100 years, while 3 m diameter trees are approximately 1700 years old. Using growth measurements from sections removed from a number of large kauri logs, Cheeseman (1914) estimated that stems approximately 2.5 m in diameter were 465 years old, while those with diameters up to 6.5 m were "not in excess of 1280 years". Figure 2C shows an ancient tree 5.2 m in diameter.

Estimates of maximum age of kauri show considerable divergence. It is often assumed that larger stem diameter indicates greater age. Highest estimates have rarely been based on a complete count of growth rings in cut stumps or logs. Most of the few surviving trees with stem diameter 3–5 m are known or assumed to be hollow, and this prevents accurate determination of age (Beveridge et al., 2009). Many large-diameter stems have been found to be hollow during felling (Sale, 1978) or when windthrown (Bergin & Steward, 2004). No relationship between diameter and age has been found in natural stands (G. A. Steward, unpublished data) and the assumption that maximum age is associated with large diameter may be unfounded. The wide range of diameter found in natural stands (see Section on Growth) suggests that large dimensions may simply be the result of above-average growth rate sustained over long periods of time. Wood decay fungi are found in natural forests under the climatic conditions in which kauri grows (McKenzie et al., 2002). Individual trees growing for more than 1000 years would almost inevitably have experienced some damage to the crown or stem from storms, falling trees, insects and/or fungi. When variable growth rate is taken into account, it can be assumed that the maximum age for kauri is not likely to be more than 1500–1700 years.

Modern and subfossil (swamp kauri) stems have been used to construct tree-ring chronologies dating from 1724BC to 1998AD (Fowler et al., 2004). These have potential for use as high–quality indicators of palaeoclimate, especially during investigation of the southern oscillation phenomenon (Boswijk et al., 2006). They have also been applied to the investigation of extreme environmental events, dendroecology, archaeology and radiocarbon calibration.

Natural distribution

Distribution in prehistoric times

Barton (1983) and Halkett and Sale (1986) have summarised the prehistoric distribution of kauri. Eagle (2009) has recently updated Ecroyd's (1982) account of fossil records of *Agathis* in New Zealand. Distribution of the southern conifers, including kauri, derived mainly from pollen records of the Quaternary period, has been discussed by Kershaw and McGlone (1995). Araucarian ancestors of kauri appeared in the

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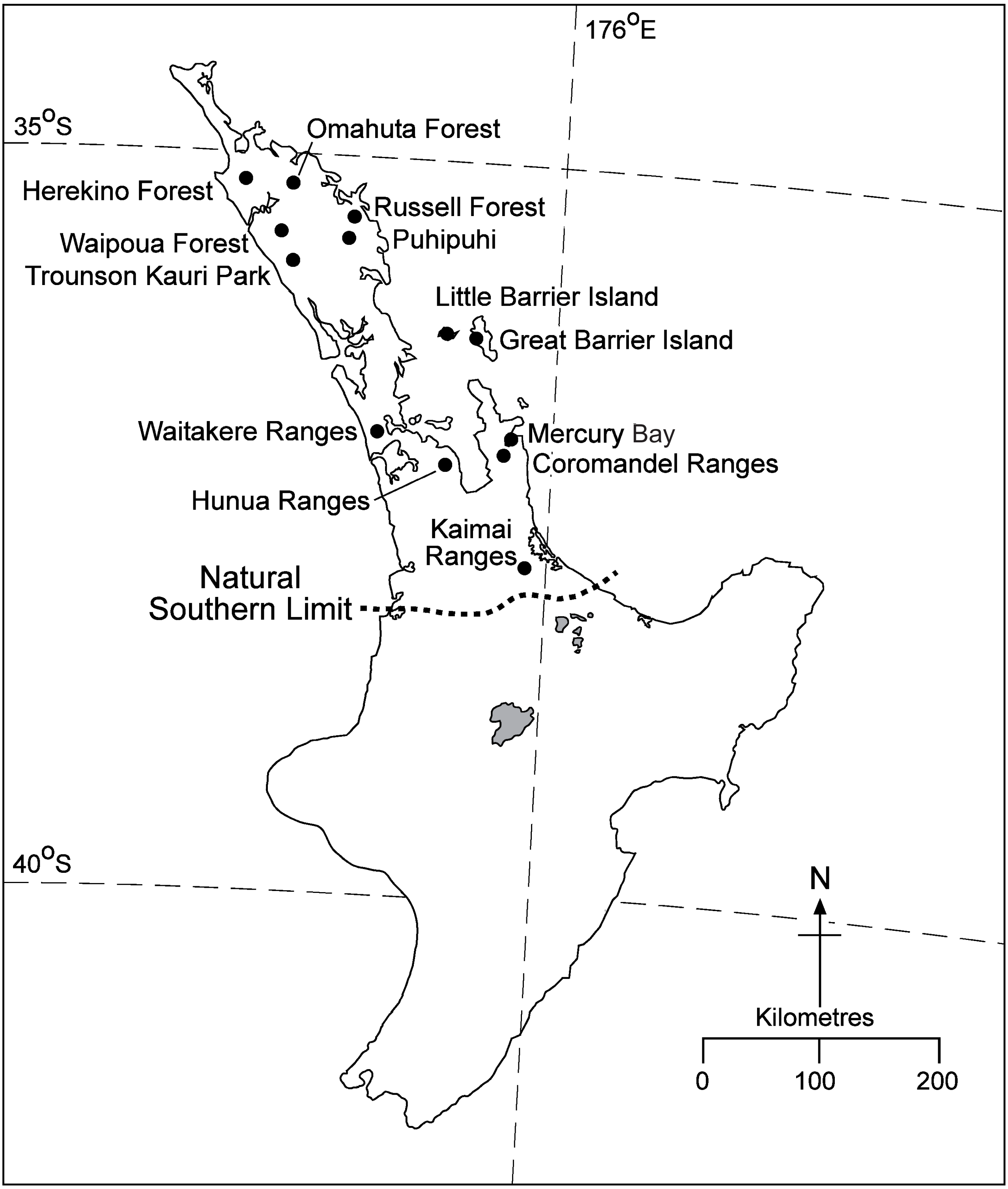

FIGURE 3: Location of current populations of kauri referred to in the text. The natural southern limit of kauri is also indicated.

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Jurassic period (Halkett & Sale, 1986). The genus *Agathis* first appeared in New Zealand during the Cretaceous period. Its members were very similar to modern kauri (Barton, 1983). *Agathis australis* appeared during the Oligocene epoch (Fleming, 1979). Molecular sequence data suggests that kauri survived the Oligocene drowning of New Zealand, and indicates that it is the oldest living species of the genus (Stöckler et al., 2002). Kauri was widespread in New Zealand until the Pleistocene epoch (400 000–14 000 years BP), when glaciation caused retreat to the northern half of the North Island. Resin of *Agathis australis* has been identified in fossilised material found in Tertiary lignite deposits in the Roxburgh and Mataura areas of the South Island (Evans, 1937). Numerous well-preserved logs, stumps and roots of large kauri trees located in recently drained lakes, swamps and bogs close to the present northern and southern limits of kauri have been carbon-dated and are considered to be up to 37 000 years old (Ogden et al., 1993). Kauri was uncommon within its present geographical range during the mild, moist conditions of early post-glacial periods. It became more prominent from 7000 BP (3000 BP in the southernmost parts of its present range).

Present distribution

Hochstetter (1867), Sando (1936a), and Hinds and Reid (1957) all considered that the current natural range of kauri is confined to the northern part of the North Island of New Zealand, latitude 34–38 °S (Figure 3). The species is most common on the Northland and Coromandel peninsulas. It is found from sea level to altitudes of approximately 360 m (Cockayne, 1928) although a few stunted trees exist at 800 m on Mt. Moehau on the Coromandel Peninsula (Anon., 1868; Hutchins, 1919; Cranwell & Moore, 1936). Kauri also occurred on the small islands east of the mainland. On Great Barrier Island and Little Barrier Island some old-growth forest remains and second–growth forest has established on sites following the initial logging (Bergin & Steward, 2004).

Failure of kauri to recolonise land further south in recent geologic times has been discussed by a number of authors (e.g. Mitchell, 1991; Ogden et al., 1992; 1993) to be mainly due to climatic factors. Barton (1983) noted the slow spread by seed dispersal, and suggested that mice (*Mus musculus* Linnaeus.) destroyed large quantities of kauri seed after their introduction in the late 18th century. The Pacific rat (kiore, *Rattus exulans* Peale), now thought to be extinct in the North Island, may have had a similar impact after its introduction by Polynesians approximately 750 years ago (Campbell & Atkinson, 1999). Other factors limiting expansion of kauri from existing stands include low seed germination rate and low rate of subsequent establishment of shade-tolerant but slow-growing seedlings under natural forest conditions (Barton, 1983).

Eco-physiology

Climatic tolerance

The effects of climate on kauri growth have been reviewed by Ogden and Ahmed (1989). Lowlands within the geographical range generally have warm summers, mild winters, evenly-distributed rainfall and mean annual temperatures of 13–16 °C. Typical kauri habitats have a mean annual rainfall of 1000–2500 mm, a mean maximum temperature in the hottest month of 28 °C and mean minimum temperature in the coldest month of 3 °C. Frosts are few and light in Northland and in coastal localities but more frequent and severe inland and near the southern limit. Sakai and Wardle (1978) found that kauri twigs were not affected until temperatures dropped to -7 °C. Barton (1982; 1985) reported frost damage in cotyledonary seedlings exposed to temperatures below -1 °C. For 18-month-old seedlings, damage occurred below -2 °C, although severely damaged, seedlings were able to survive temperatures of -6 °C. There are no records of frost damage in planted kauri or young trees in sheltered localities, even those located near Dunedin at latitude 46 °S (Bergin & Steward, 2004).

Soils and nutrient cycling

Prior to European colonisation in the 1840s, kauri grew on a wide range of terrain and soils (Anon., 1868; Hansson, 1924[4]; Hinds & Reid, 1957). Gibbs et al. (1968) listed these soil types as strongly leached and podsolised northern yellow–brown earths, podsols, strongly leached brown granular clays, and brown loams of very low fertility. Kauri is often found on soils of low fertility, and renders them even less fertile (Beveridge, 1975). Enright (1999) noted the very slow decomposition rate of kauri leaves. The accumulation of litter is associated with a decrease in soil pH (Jongkind et al., 2007). Mor humus layers up to 3 m deep have been observed beneath large kauri trees. The influence of individual trees can be seen in the "egg-cup" conformation of soil horizons, particularly evident in the strongly-weathered soils of North Auckland (Gibbs et al., 1968). Jongkind et al. (2007) suggested that the effect of kauri on soil was due to its longevity and the quantities of litter and leachates deposited, rather than to litter quality. Enright (1999) studied litterfall in a mature remnant of mixed kauri–broadleaved forest. Reproductive structures, particularly those of kauri, contributed a considerable proportion (13–21%) of the five year mean annual increment of 7.76 t/ha of litterfall.

Kauri makes efficient use of nitrogen and phosphorus. Biomass and nutrition studies of kauri in a 130-year-old pole stand in the Hunua Ranges (Madgwick et al., 1982) confirmed earlier work of Peterson (1962) and Silvester (1978) who suggested that levels of

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both nitrogen and phosphorous needed for maximum growth were low. The availability of nitrogen may be a limiting factor for growth of *Agathis*. Richards and Bevege (1968) found there was little height growth of *Agathis robusta* on lateritic podzolic soils in southern Queensland when nitrogen was not available. When nitrogen was added, *A. robusta* height growth increased, and the species was also able to utilise more phosphorus. Enright (2001) found that the conifer component of litterfall in kauri-dominated forest in the Waitakere Ranges contained lower concentrations of many plant nutrients than the angiosperm fraction. Detailed analysis of biomass and litterfall at four sites indicated greater accumulation of litter on flat terrain, especially around large kauri stems (Silvester & Orchard, 1999). At one of these sites (Trounson Kauri Park) 2214 t/ha of litter containing 956 t/ha of carbon had accumulated to a depth of approximately 2 m. The total nitrogen content of biomass in the kauri stand at Trounson Kauri Park was 15 t/ha, half of which was located in the organic layers in a form unavailable to plants. Verkaik et al. (2006) concluded that tannins present in kauri leaves inhibit nitrogen mineralisation and could account for the accumulation of nitrogen. Nitrogen sequestration during a 600–700 year lifespan was estimated to be 0.09–0.5 kg/m^2 (i.e. 0.9–5 t/ha). This amount is comparable to that estimated by Silvester (2000) to be present in the organic layer. The ability of kauri to occupy sites for long periods of time over one or more generations is also thought to account for the exceptionally large amounts of nitrogen accumulated (Verkaik et al., 2006).

Water relations

Bieleski (1959) found that waterlogging decreased both root length and stem branching of kauri at the seedling stage. Conversely, drought increased root development at the expense of stems (Bieleski, 1959). Stephens et al. (1999) measured isotope carbon ratios in trees growing on ridge crests and valley sites and concluded that kauri may make more efficient use of water than many other species do. This would contribute to its relatively high productivity on dry, infertile ridge crests. Verkaik et al. (2007) reported that young kauri seedlings growing beneath a kauri canopy compete successfully with other plant species under conditions of low soil moisture and fertility. Observations in a natural stand at Huapai showed that diameter growth of trees 31 cm or less in diameter was limited by soil moisture over the summer period, while peak growth was observed in trees with diameter greater than 31 cm (Ferguson, 1997). Of the three seasonal variables investigated (mean temperature; maximum temperature; soil moisture deficit), mean temperature was shown to have the closest relationship with diameter growth in medium-sized (31–41 cm diameter) and large kauri. Growth of smaller trees was not affected.

Stand dynamics

Associated tree species

Cockayne (1908) recognised six types of forest containing kauri in Waipoua Forest. Hansson (1924)[4] classified kauri forest over its entire range into two types; kauri-dominated and kauri-taraire (*Beilschmiedia tarairi* (A.Cunn.) Benth. & Hook.f.). Nicholls (1976) divided kauri forest into three classes and 22 types. Class A comprised five types in the limited areas in the north of the North Island where kauri was abundant. It included remnant dense old-growth and the more numerous areas of abundant pole and ricker stands. Class B comprised twelve types in kauri-softwood-hardwood mixtures in forests of the Waikato, Bay of Plenty and Coromandel. Class C comprised five types where hard beech (*Nothofagus truncata* (Colenso) Cockayne) and silver beech (*Nothofagus menziesii* (Hook.f.) Oerst.) were found with kauri-softwood-hardwood mixtures. The relationship between kauri and hard beech has been investigated in forests of the Waikato Region (Collins & Burns, 2001). Age structure of the stands indicated that both species establish in disturbed forest areas, rather than by reciprocal replacement where either species acts as a nurse crop.

Cathersides (1972) described vegetation in two kauri forests, recording the presence of individual tree canopies in specified height tiers. At Waipoua, kauri was the only species present in the upper two canopy layers. It was present in the B layer (12–24 m) but absent from the C layer (2–10 m). In the B layer it was often associated with other native conifers, particularly tanekaha (*Phyllocladus trichomanoides* D.Don), totara (*Podocarpus totara* G.Benn. ex D.Don), Hall's totara (*P. hallii* Kirk) and rimu (*Dacrydium cupressinum* Lamb.). At Mangatangi, in the Hunua Ranges, kauri/hard beech and kauri/tanekaha types were found. Here kauri and up to four other softwood and hardwood species were present in the upper canopy layers (15–30 m). At both sites, kauri was well-represented in the small-seedling category.

Regeneration

Conditions favouring kauri seed germination and seedling establishment have been summarised by Barton (2000). Germination occurs at temperatures above 11 °C, but rates are higher between 19 and 27 °C. Regeneration is most prolific in secondary forest, scrub or grassland invaded by small-leaved species such as manuka (*Leptospermum scoparium* J.R.Forst. & G.Forst.) or the taller–growing kanuka (*Kunzea ericoides* (A.Rich.) Joy Thomps.). It has been observed on disturbed sites near the present southern limit of the species (Beveridge et al., 2009). Mirams (1957) and Bieleski (1959) showed that in terms of light, temperature and thin litter

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layer, secondary forest was more favourable for the establishment of kauri seedlings than old-growth forest. Enright et al. (1993) observed that seedlings grew very slowly when the degree of canopy closure was more than 90%. According to Bieleski (1959) and Barton (1982), small seedlings are shade-tolerant, while saplings and young trees require full overhead light for vigorous growth. McKinnon (1937b) counted individual seedlings, saplings and rickers in 12 plots on spur and ridge sites (location unknown). Kauri in size classes from seedlings to large trees totalled up to 77 000 stems/ha. McKinnon (1945) also investigated the regeneration potential of kauri at Waipoua Forest. Where competing vegetation had been removed from 0.2 ha plots beneath a kauri-dominated canopy, seedling counts of 44 500–61 800/ha were recorded. Substantial mortality results from root competition and the desiccation of humus layers during prolonged dry periods unless seedling root systems have penetrated to the A1 soil horizon (McKinnon, 1945).

Although female cones and viable seed have been produced by kauri trees planted as nursery-raised seedlings in many locations south of the natural range, regeneration is rare. Two examples of persistent natural regeneration have been recorded south of latitude 38 °; one in New Plymouth and the other in Wellington (Steward et al., 2003). Regeneration has also been observed in Hawkes Bay on two sites.

Forest pattern and development

Aspects of the ecology of kauri have been discussed by Enright and Hill (1995). Ogden and Stewart (1995) examined existing hypotheses about the ecological status of kauri described in terms of forest pattern and process. Burns and Leathwick (1992) surveyed and mapped vegetation in Waipoua Forest and drew attention to the mosaic pattern of distribution. Ogden et al. (1987) suggested that two processes were involved. In the first, catastrophic disturbance (e.g. fire, volcanic activity, windthrow) was followed by the development of secondary vegetation in which the kauri component reached maturity in relatively even-aged patches. In the second process, cohorts of trees aged and died. Gaps of various sizes formed and were colonised by broadleaved species or kauri. Kauri eventually predominated on ridges and droughty or infertile sites. The presence of established kauri seedlings and saplings in or near gaps made by the death of old kauri trees provides good evidence for the gap-phase process (Ahmed & Ogden, 1987). Enright et al. (1999) referred to the theory of mosaic development as the “temporal stand replacement model”. Cathersides (1972) reviewed Bokyo’s geoecological law of distribution (Bokyo, 1947) with reference to the occurrence of rimu, tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. & Hook.f. ex Kirk) and kauri in Waipoua and Mangatangi Forests. He recorded considerable numbers of regenerating kauri trees in areas where kauri was the dominant canopy species. Cathersides maintained that climatic fluctuation and cultural interference (e.g. logging) were the two most important factors determining vegetation distribution. Burns and Leathwick (1996) investigated the relationship between environment and vegetation in Waipoua forest. Topographic variation in soil fertility and soil moisture, combined with altitudinal effects on temperature and precipitation influenced vegetation patterns. Conifers, including kauri, tended to occur on the infertile soils on ridges, while broadleaved species dominated the fertile lower slopes and gullies.

Growth

Early estimates

Under natural conditions, kauri growth rates vary widely at all stages of development. Many early assessments of diameter growth were made from individual cut stumps and logs. Data were not presented in the context of forest composition, the place of individual trees within a forest structure, or stage of development (i.e. ricker or mature form), however.

Matthews (1905) considered that the rate of kauri growth was too slow for timber culture. This view was supported by Laing and Blackwell (1907) who stated that “kauri is of such slow growth that no man thinks it worth his while to plant trees which take a thousand years to mature”. Conversely, the species was considered to be eligible for “industrial culture” and naturalisation in New South Wales and Victoria, Australia (Mueller, 1881; 1888). It was also named among 20 New Zealand tree species considered to be of economic importance (Zon & Sparhawk, 1923; Forbes, 1932).

Hutchins (1919) estimated that the timber volume of mature kauri in Puhipuhi Forest averaged 700 m^3/ha. Hansson (1924)[4] developed a stand table representing a typical acre (0.404 ha) of mature kauri forest of the kauri/taraire type from Waipoua Forest. Diameters and stem counts for kauri from 20–279 cm in diameter indicated a stand density of 116 stems/ha (423 stems/ha for all species), and a volume of 400 m^3/ha.

Diameter growth

Cheeseman (1914) agreed with Laslett’s (1875) early assessments of mean diameter growth (2.5 mm/y) after counting growth rings in sections taken from felled trees 1 m or more in diameter (Silvester & Orchard, 1999). Kirk (1889) recorded growth of 1.9–3.6 mm/y in free-growing trees. A study of kauri from 25 sites over the range of the species led Ahmed and Ogden (1987) to conclude that stems 10–140 cm in diameter grew at a mean rate of 2.3 mm/y. Mature trees were found to grow for long periods

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at a rate of 5 mm/y. Slocombe (1921)[5] assessed more than 250 cut stumps at sites located throughout the natural range and estimated diameter growth rates of 3.6–6.1 mm/y in trees 250–500 years of age. From measurement of increment cores taken from poles and saplings in a range of diameter classes at Omahuta Forest, McKinnon (1940) reported a maximum rate of 6.3 mm/y in 76 cm diameter trees, although the average for 37 stems approached 4 mm/y. Burns and Smale (1990) found that the maximum rate in a 100–200-year-old second-growth stand (4.3 mm/y) on the Coromandel Peninsula occurred in sub-mature trees 25 cm or more in diameter. Most of these were still at the ricker stage, but the crowns of larger diameter trees were beginning to spread. Although there were large numbers of tanekaha trees in the stand, most of the basal area increment (0.6 m^2/ha/y) was attributable to kauri. Large kauri trees suppressed all other vegetation, including smaller kauri. Steward and Kimberley (2002) reported diameter increment values of 1.3–3.4 mm/y in four 120–218 year-old natural second-growth stands that had been monitored over periods of up to 35 years.

Hutchins (1919) suggested that natural stand density reaches 150–200 stems/ha, while Halkett (1983a) reported an average of 85 stems/ha in old-growth forest. At a mean diameter of 90 cm and stand density of 80–100 stems/ha, basal area would be 50.9–63.6 m^2/ha. Basal area increment of kauri in two thinning × fertiliser trials in natural second-growth stands was measured annually between 1967 and 1972. Basal area increased by approximately 0.3 m^2/y in control plots, 0.1–0.4 m^2/y in thinned plots, and 0.3–0.8 m^2/y where trees were thinned and fertiliser was applied. Some of the increment was attributable to recruitment as well as to growth of selected trees (Anon., 1974). Barton and Madgwick (1987) found that application of fertiliser increased mean annual diameter increment to 5.1 mm from an unstated average for control trees. Data derived from stems removed from thinned plots indicated that an increase in diameter growth brought about by earlier thinning in or about 1900–1912 had been sustained for at least 30 years. In a later thinning × fertiliser trial in a second–growth kauri stand estimated to be 130 years old, reduction of the number of stems/ha by 75% (and basal area by 55%) had a negligible effect on basal area increment after five years (Barton & Madgwick, 1987). Addition of nitrogen fertiliser doubled basal area growth after five years to 1.0 m^2/ha/y.

Ferguson (1997) found that stand density was the best predictor of basal area increment in a natural kauri stand at Huapai. Chikumbo and Steward (2007) developed a basal area model for kauri, using data obtained from 13 plantations in the North Island. Predicted basal area values of 60 m^2/ha at age 40, and 95 m^2/ha at age 80 were considerably lower than the 116 m^2/ha predicted by Herbert et al. (1996) for stands of the same age. Some of the data used in both models were derived from stands located outside the natural range of the species, however.

Height growth

Hutchins (1919) drew attention to the scarcity of foresters able to measure height growth of kauri. Basing his observations on a few planted specimens around Auckland, he presumed that kauri was “decidedly faster in height growth than the European forest trees”. Kauri is shade tolerant only when seedlings are small. Annual height growth of seedlings under favourable light conditions is usually 10–25 cm. Shaded seedlings may stagnate or grow very slowly for 50 years or more. Suppressed saplings in a stand that was probably in existence since pre-European times had a mean age of 40 years and a mean height of 1.4 m (Burns & Smale, 1990). As saplings emerge into full overhead light, height growth increases and rates of 30-40 cm/y are common in rickers in uncrowded stands (Beveridge et al., 2009). At Waipoua, height increments of 22–30 cm/y were recorded in kauri saplings measured over a period of 11 years (McKinnon, 1940). In second-growth stands located in Northland, Great Barrier Island, Hunua and Kaimai Ranges, height increments of 10–25 cm/y were observed (Steward & Kimberley, 2002).

Growth of planted kauri

Planted kauri is known to grow faster than natural second-growth kauri stands on moist, fertile soils (Beveridge et al., 2009). Cameron (1959) suggested that sites usually occupied by larger-leaved mesophytic species are the most suitable for kauri planting. In some plantations average annual diameter growth has exceeded 10 mm for periods of up to 40 years. Height increments of 1 m/y have been recorded for individual trees (Ecroyd et al., 1993). In a survey of planted indigenous trees, annual growth of kauri was found to average 7 mm in diameter and 36 cm in height (Pardy et al., 1992). Using data from a wide range of sites with different stocking rates and management history, Pardy et al. (1992) predicted a mean annual height increment for planted kauri of 44 cm at 20 years, reducing to 26 cm at 80 years. This rate was among the highest for the eight major indigenous conifers surveyed. Predicted annual diameter increment in kauri, measured at 1.4 m above ground level, was 6.9 mm for stands less than 100 years of age. Individual trees planted at Rotorua

[5] Slocombe, C. S. (1921). Report on the investigation on the rate of diameter growth of native trees. New Zealand National Forestry Library heritage collection (unpublished).

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were 40 cm in diameter and 20 m in height after 50 years. This growth rate is equivalent to that of trees planted further north. While growth of young planted kauri has been enhanced by careful site selection and management, this does not necessarily imply that early rates will be sustained or that growth rates of more mature planted trees will differ from those in natural stands.

Volume increment

McKinnon (1946a) compared several methods used to calculate wood volume in kauri stems in natural stands. Results from the "centre–girth" method (based on girth-over-bark at breast height, estimated log height, and estimated centre girth-over-bark) were compared with those derived from the actual diameter and length of 164 felled stems. The centre–girth method was found to underestimate standing volume by 7.1%. Actual log measurements were then used to construct a local log-volume table. Tables based on measurements from a number of stands have been produced for old-growth (Lloyd, 1978) and second-growth (Ellis, 1979) kauri. McKinnon (1946b) also calculated an individual tree merchantable-volume and increment table from measurements obtained from 50 trees from Omahuta and Waipoua forests. Periodic annual increment culminated between the 250th and 300th year (0.04–0.05 m^3), while mean annual increment culminated in the 350th year (0.03 m^3). Volume increment (mean annual increment) in mature kauri forest was found to be in the order of 1–3 m^3/ha/y. This estimate was based on limited data and did not take the influence of stand composition and structure into account (Halkett, 1983b). Estimates of total stem volume increment (periodic mean annual increment) in second-growth kauri stands were 2.8–8.8 m^3/ha/y (untended) and 4.1–9.9 m^3/ha/y (thinned), and were dependent on stand density (Halkett, 1983a, 1983b) (Table 1).

A preliminary growth and yield model, based on data from two 60-year-old unthinned kauri plantations at New Plymouth (96 km south of the natural range limit), predicted tree height of 25 m and diameter of 34 cm at age 80 years (Herbert et al., 1996). At this age, total wood volume in stands containing 1300 stems/ha was predicted to be 1103 m^3/ha. According to Steward and Kimberley (2002), only a small proportion of this volume would be heartwood.

Health and stability

Until recently, pathogens and pests were considered to be of low or local importance for kauri that had developed beyond the seedling stage.

Fungi

Species of fungi causing local damage to kauri were listed by Ecroyd (1982). McKenzie et al. (2002) presented a checklist of fungi found on kauri and this was amplified by Gadgil (2005) who indicated their relative importance. Fungi known to cause damage in living kauri trees are:

Armillaria limonea (G.Stev.) Boesew. and *A. novaezelandiae* (G.Stev.) Herink: root rot disease in young trees;

Fomes hemitephrus (Berk.) Cooke: white heart rot;

*Ganoderma applanatum (*Persoon) Patouillard: white heart rot extending to the sapwood when the heartwood is completely decayed;

Heterobasidion araucariae (P.K.Buchanan) Hood: sap rot;

Pestalotiopsis funerea (Desm.) Steyaert: a facultative parasite, invading damaged leaf tissue;

Phaeolus schweinitzii (Fr.) Pat.: destructive red-brown cubical rot in mature trees;

*Phytphthora cryptogea (*Pethybr. & Latt.)*, Pythium irregulare* Buisman.*, Pythium ultimum* Trow*, Rhizoctonia solani* J.G.Kühn: damping off and seedling root rots;

Phytophthora nicotianae Breda de Haan: Isolated from stem lesions on a 20-year-old tree;

TABLE 1: Total stem volume increment (periodic mean annual increment) in untended and thinned natural second-growth kauri stands (from Halkett, 1983a).

Stand density (stems/ha)	Volume increment (m^3/ha/y)	
	Untended stands	Thinned stands
<200	2.85	4.16
200–400	4.83	6.45
400–600	7.65	9.90
>600	8.85	9.80

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Phytophthora cinnamomi Rands: (possibly associated with mortality of trees); and

Phytophthora heveae A.W.Thomps.: isolated from basal cankers on dying trees on Great Barrier Island and shown to be pathogenic to *A. australis* seedlings (Gadgil, 1974). Recent molecular analysis has indicated that this fungus cannot be identified on morphological characters alone, and it is now known by the temporary name “*Phytophthora* taxon Agathis”. It has been isolated from dying trees in the Waitakere Ranges and from Northland. It may be one of the causes of death and ill-thrift in regenerating kauri stands on poorly drained sites (Beever et al., 2007).

Four pythiaceous fungi, *Phytophthora cryptogea*, *P. cinnamomi*, *Pythium irregulare* and *P. ultimum* were found to be the cause of rootlet rot in kauri seedlings grown on heavy, poorly drained soils by Newhook (1959) and Robertson (1973). *Phytophthora cinnamomi* and *P. nicotianae* have been associated with stem lesions on older kauri trees, causing minor damage (Newhook, 1959; Brien & Dingley, 1959). Johnston et al. (2003) considered that *P. cinnamomi* may have had a significant impact on regeneration of kauri, and could have a greater impact if weather patterns change. Podger and Newhook (1971) described death and dieback of kauri and other species in two small areas of 80–100-year-old kauri regrowth in the Waitakere Ranges. *Phytophthora cinnamomi* was isolated from roots of kauri and other plants, and the authors discussed a possible link between the presence of the fungus and damage to the vegetation occurring under conditions favourable to the fungus. Zentmyer (1985) showed that *P. cinnamomi* grows best in mild temperate or subtropical regions. It does not survive at soil temperatures below 6 °C or above 34 °C. Optimum temperatures are in the range 21–27 °C. It does not tolerate low soil moisture conditions.

Insects

Insect species causing local damage have been listed by Ecroyd (1982). Those found on living trees (Miller, 1984) are:

Acrocercops leucocyma Meyrick (Lepidoptera: Gracillariidae): leaf miner;

Planototrix excessana Walker (Lepidoptera: Totricidae): leaf roller;

Platypus apicalis White (Coleoptera: Curculionidae): pin hole borer; and

Xenocnema spinipes Wollaston (Coleoptera: Curculionidae): short nosed weevil, following attack by *P. apicalis.*

A number of wood borers not listed by Ecroyd (1982) have been found on kauri, but are not considered to be important (J. Bain, Scion, personal communication, 2009).

Ridley et al. (2000) listed a number of exotic pathogens and insect pests that can be regarded as possible external threats to New Zealand’s indigenous forests. Three rust fungi were identified as potential pathogens: *Aecidium fragiforme* Ces. which occurs on *Agathis* in Queensland, Malaysia, Indonesia, New Guinea and Fiji; *Aecidium balansae*, found on three species of *Agathis* in New Caledonia; and *Caeoma sanctae-crucis* Espinosa, which occurs on *Araucaria araucana* (Molina) K.Koch in Chile. Potential insect pests include twelve species of aphid in the genus *Neophyllaphis*, and the coccids *Conifericoccus agathidis*, *Eriococcus araucariae* Maskell and *Nipaecoccus aurilanatus* Maskell. The two last-mentioned insects have been recorded on introduced *Araucaria* species in New Zealand.

A large indigenous orthopterous insect, the common weta (*Hemideina thoracica* White), feeds on fallen seed (Mirams, 1957). An indigenous parrot, the kaka (*Nestor meridionalis* J.F.Gmelin), can break open ripening cones to obtain the seed. It also strips bark from trees, including young kauri, to feed on sap. Another parrot, the Australian eastern rosella (*Platycercus eximius* Shaw) eats kauri seed and is common in the Auckland and Northland regions (Beveridge et al., 2009). Kauri seeds are highly palatable to mice and rats (*Rattus rattus* Linnaeus) introduced from ships in the late 18th century. These rodents are now widespread in kauri forests.

Browsing animals

Northern forests in New Zealand have suffered less damage from introduced browsing animals than forests to the south. Small fragmented areas containing kauri have been exposed to grazing stock in the past, but only feral goats (*Capra hircus* Linnaeus) have damaged kauri seedlings and saplings since the introduction of animal control (Beveridge et al., 2009). Brush-tailed possums (*Trichosurus vulpecula* Kerr) have spread to the far north during the past 30–50 years. P. Cowan (1990) reported their presence in Waipoua Forest in 1963. Payton et al. (1997) found that an increase in the possum population there during the 1980s had a negative impact on some of the broadleaved species commonly associated with kauri. Possum damage to kauri seedlings planted at Cornwallis, west of Auckland City, was reported by Johnston et al. (2003).

Fire

In a review of the occurrence of natural fires in New Zealand, Ogden et al. (1998) noted that lightning has been the cause of forest destruction since prehistoric times. Burns (2000) reported the presence of charcoal in the soil profiles of five out of 13 stands of 150–250-

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year-old kauri in old-growth forest at Waipoua. This suggested that fire had destroyed previous vegetation. More recent disturbance of kauri habitat has been the result of small-scale burning during Polynesian settlement (from about 700 BP) and by the extensive burning, logging and land clearance associated with European settlement over the past 160 years.

Wind

There are few records of windthrow in natural kauri forest. Large trees damaged by fire and others in partially logged forest or areas located near stand margins have fallen during severe storms (Conway, 1959). In Puketi Forest, a dense kauri stand occupying an area of 0.5–1 ha was flattened when several large trees fell from a ridge top (Ian Barton, personal communication, 2009). The *New Zealand Herald* newspaper recorded that on 30 July 1933, 50 kauri trees were windthrown in a part of Trounson Kauri Park that had been previously damaged by fire.

Gum collection

Many old trees were damaged by gum collectors through notches cut in the stems for “bleeding” (Nestor, 1935). Damage was also caused by the spikes used by climbers when collecting gum (Reed, 1964). The association of rots with lesions on larger stems has been observed in several kauri forests. Kauri bled for gum in the Hunua Ranges showed defects in wood adjacent to the wound site, probably resulting from the activity of decay organisms (Cathersides, 1972). Recognition of the danger of gum bleeding to tree health led to official prohibition in 1905 (Ward, 1911).

Use and exploitation

Use by Maori

Kauri is highly prized by Maori. In Maori mythology, it is sometimes linked with the stories of creation (Orwin, 2004). Many large trees were identified by name (Kirk, 1889). The straight, branch-free stems of kauri growing beside harbours or near rivers were once used to make large sea-going canoes (Dieffenbach, 1843; Best, 1925). Some of these canoes, constructed from a single stem, were 30 m long and 4.5 m wide (Reed, 1953). The wood was also valued for carving (Anon., 1868; Clifton, 1990). Prior to European settlement, it is likely that only limited numbers of easily-accessible trees were used, since the stone-tool-and-fire method of felling required the expenditure of considerable amounts of effort and time (Maning, 1863; Best, 1941).

Resin or gum was more important to Maori than kauri timber; valuable enough to transport over long distances. Large pieces, presumably for use or trading, have been found beside an ancient walking track in the south of the North Island (Mair, 1905). Inland Maori traded quite small pieces of gum (Halkett, 1983a), which could be used for starting or fuelling cooking fires (J. Cowan, 1955) and in torches for night fishing (Laing & Blackwell, 1907; Reed, 1953), for as much as a European blanket. When soft, gum was also a “masticatory” (Anon., 1868; Best, 1924; Riley, 1994). Soot from burnt gum was used as the colouring agent in tattooing (Dieffenbach, 1843; Anon., 1868; Tua-O-Rangi, 1894; Best, 1941). Best (1941) referred to occasional use of gum to create a smouldering fire, the smoke from from which controlled caterpillar pests on kumara (*Ipomoea batatas* (L.) Lam.). After European settlement, Maori realised the commodity value of their kauri resource and began to trade both gum and timber (Davis, 1876; Cyclopedia Company Ltd., 1902).

Use by European settlers

Marion du Fresne was the first European to harvest kauri when his vessels *Mascarin* and *Marquis de Castries* sought shelter in the Bay of Islands in 1772, and repairs were needed (Cheeseman, 1914). By 1794, kauri on Great Barrier Island was being felled for ship spars (New Zealand Forest Service, 1975). Royal Navy interest in the kauri resource (1840–1841) and an account of the kauri spar and timber trade have been summarised by Roche (1983, 1990). Spars were exported to Sydney and London from the late 1820s, and in the 1830s sawmills and boat building yards utilising kauri timber were established around northern harbours. The first powered mill was brought to New Zealand in 1839 and was used to produce sawn kauri timber in Northland (Hansson, 1924)[4].

The initial extraction of kauri logs for spars was not straightforward. Trees for spars had to be sought further inland once suitable trees close to harbours had been harvested (Campbell, 1955). Away from harbours, kauri often existed on rugged and precipitous terrain, making the manual extraction of large, heavy logs difficult. An early discovery was that kauri logs would float (Polack, 1838). Trees were felled directly into or alongside waterways and logs rolled into the bed of the watercourse. Subsequent storm and flood events would carry logs down to harbours for collection and milling, however this was an unreliable method. From 1837, dams were constructed to control water flow, frequently in series into the upper catchments (Reed, 1953). Logs were driven on more substantive bodies of water to major river confluences or harbours. It was estimated that more than of 60% of all kauri timber was removed from the forest in this way. Considerable loss and destruction of logs occurred in boulder-strewn streams, and where logs passed over high waterfalls (Reed, 1953). The ability of kauri logs to float made it preferable for logging over all other timber species, even within mixed forest types (Campbell, 1955). This, in turn, drove the exploitation of the species.

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For nearly 100 years, until the early 20th century, large quantities of high-class timber were extracted from kauri forests. Matthews (1905) reported a 1900 prediction that "in only thirteen years the kauri forests would be exhausted at the present rate of conversion, not including losses caused by fire". Output reached a peak in 1907, when production of approximately 1.2 million m^3 of sawn kauri timber was reported (Roche, 1990). In 1909, an estimated 1.1 million m^3 of kauri remained from all sources (State Forest Service, 1909).

A considerable quantity of kauri timber was used to construct dams, sluices, chutes, "rolling roads" and tramways to facilitate the transport of logs (Sale, 1978; Kirk, 1889). Technically, winter was the preferred season for felling because the dormant growth period was supposed to impart superior timber qualities (Firth, 1874; Kirk, 1874). In fact, trees were usually felled during spring and summer when weather conditions were more favourable for log extraction. Rapid economic development of the Colony of New Zealand increased the demand for timber and resulted in the use of "summer-sawn" kauri without appropriate drying or workmanship. This led to timber failure and some questioning about the suitability of the species for construction work (Kirk, 1874). Application of appropriate drying and grading procedures increased recognition of the usefulness of kauri timber (Kirk, 1889; Reed, 1953). Resistance to decay and dimensional stability under moist conditions made it eminently suitable for ships spars and masts, boat building (both commercial and recreational), bridging, railway sleepers, mine props, roof shingles, churns and vats, railway carriages, fence palings and road pavers (e.g. Hochstetter, 1867; Kirk, 1874; Barlow, 1888; Cyclopedia Company Ltd., 1897; Cheeseman, 1914). It was also used for house construction, including panelling, doors, flooring and weather boards; also for furniture, mouldings, and decorative carving (e.g. Reed, 1953; 1964; Sale, 1978; Clifton, 1990). Timber was exported in great quantities, "thousands of homes in Australia being constructed of kauri-pine" (Perceval, 1896). Export of sawn kauri was approximately 77 300 m^3/y during the period 1904–1909 (State Forest Service, 1909). Fossil kauri wood was tested for suitability in paper-making (Phillips Turner, 1926) and buried logs from the Papakura District were used extensively as railway sleepers (Kirk, 1874). Together with gum dug from the ground or collected from standing trees, these products contributed greatly to the general economy of the country (Hochstetter, 1867).

Logging in Crown kauri forests ceased in 1981. Since then, sustainable timber production from old-growth or secondary forest has been carried on by private landowners operating under the Forest Amendment Act (1993). Currently, only a few hundred cubic metres are used each year for production of high-class furniture and musical instruments, turned items and craft work. Other sources of wood are ancient logs recovered from swamps (Clifton, 1990) and the old kauri heads and high stumps left behind after logging (Beveridge et al., 2009). Recycled kauri timber from old buildings is also used for cabinet-making.

In spite of its vegetable origin, kauri gum has been classified as a mineral (Cyclopedia Company Ltd., 1897). Recognition of its value in the production of high-grade oils and varnishes formed the basis of an export industry which started slowly in 1815. Amounts sent overseas increased from 800 tonnes in 1853 to 8100 tonnes in 1894. From 1857 to 1900 kauri gum exports were more profitable than those of timber, wool or gold (University of Auckland, 2008). Gum collectors gathered surface deposits at first, but later drained swamps and bogs to reach sub-fossil layers. Gum was also collected from forks in the largest trees and from notches cut in the stems for "bleeding" (Nestor, 1935). Gum diggers often lit fires to clear land, and large areas of standing forest were burnt for this purpose (Hochstetter, 1867; Anon., 1868; Lloyd, 1979). A fire lit by gum diggers in Puhipuhi Forest in the late 1800s (Hutchins, 1919) lasted several weeks and destroyed 700 000–1 500 000 m^3 of kauri (Harding, 1892; Halkett & Sale, 1986). Foster (1928)[6] reported results of gum-tapping experiments in Waipoua Forest carried out in the early 1920s and suggested that long-term supplies might be obtained by limiting the depth and number of notches in the stem, and the length of the collecting season. By the 1920s, kauri logging and gum collection had both declined.

Forest policy and management of kauri

Concern about the decline of the kauri resource was expressed in the 1830s, causing the Lords of the Admiralty to make recommendations to Governor Hobson for appointment of a conservator of kauri forests (Roche, 1990). The German naturalist Ernest Dieffenbach, who travelled in New Zealand between 1839 and 1841, called unsuccessfully for reservation of kauri stands prior to land clearance for settlement (Roche, 1990). Under the prevailing view that one blade of grass was worth more than two trees (Masters et al., 1955), decline of the resource continued. Hursthouse (1857) prescribed the felling and burning of all trees under one metre in diameter during conversion of forest to pasture. Fire was used to kill large trees and recovery of timber was not a priority. By 1873, the kauri resource had been reduced by 70% (Masters et al., 1955). It was not until 1877 that a Lands Act

[6] Foster, F. W. (1928). *Tapping of kauri for kauri-resin.* New Zealand State Forest Service. Rotorua, New Zealand: New Zealand National Forestry Library heritage collection (unpublished).

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prohibiting unlicensed harvesting of kauri passed into law (Jourdain, 1925).

Legislation and forest policy applied from earliest European settlement until the mid 1900s have been reviewed by Jourdain (1925) and the New Zealand Forest Service (1964). Following signing of the Treaty of Waitangi in 1840, destruction of native forest was aided by official reference to New Zealand's forested area as "waste lands". Emphasis was placed on development of pastoral farming through the clearance of forest and the draining of swamps. Prior to 1853, sale or disbursement of forested lands was controlled by the New Zealand Government Act (1846), the Crown Lands Ordinance (1849), and the Constitution Act (1852). The Waste Lands Act of 1854 was the first of a series that followed later. Between 1853 and 1876 much of the regulation became provincial and there was considerable divergence in its application (Jourdain, 1925). The first Forests Act (1874) established the position of Conservator of Forests and a second Forests Act in 1885 created a Forestry and Agriculture branch of the Department of Lands with a Chief Conservator. In 1893, the Minister of Lands was appointed as Commissioner of State Forests. This was the first ministerial appointment for forest administration. In 1918, the position of Commissioner of State Forests was separated from that of the Minister of Lands. The New Zealand Forest Service was established under the Forest Act of 1921–1922.

Opportunities for preservation of the kauri resource existing in the mid-1800s (Firth, 1874; Hutchins, 1919) were lost through destruction and wastefulness that continued into the 1920s. Hutchins was an early colonial forester who made proposals for the sustainable management of the kauri resource. The policy of restricting export of native timbers (particularly kauri) coincided with the first national forest inventory in 1921–23 which found that remaining kauri comprised only 0.6% of the available milling resource. At this time, New Zealand began to plant exotic timber species in order to preserve the remaining natural forest. A move that prompted Hutchins to comment that "for reasons which have never been satisfactorily explained, it has been thought to replace the valuable native forest of New Zealand by artificial plantations of exotics – a quite unusual proceeding in forestry". In a review of Government policy specific to the management of kauri forest, Barton (1975) observed that research evidence obtained between 1800 and the early 1970s was insufficient to support policy for kauri management. Various working plans for management of State-owned kauri forest were developed between 1935 and the mid-1900s. The 1946–1951 plan included provision for reservation and production through selective harvesting. Kauri exceeding 90 cm diameter could be harvested at an average rate of 2360 m^3/y, the equivalent of 250–300 trees. Attempts at long-term management commenced in 1936 when thinning trials were established in Herekino Forest (Sando, 1936b; 1936c). At this time, private landowner interest in sustainable management of kauri was also increasing. Rudolf Hohneck, for example, extracted timber and also planted seedlings in the southern Hunua Ranges from the early 1940s (Barton, 2007). Long-term management plans covering the whole of the resource were not developed until the final years of State Forest logging in the 1970s and 1980s. In the 1960s and 1970s a number of thinning trials had been undertaken in dense natural second-growth stands in Russell Forest, on the Hunua and Kaimai Ranges, and on Great Barrier Island (Lloyd, 1978). These stands contained up to 7000 stems/ha of kauri greater than 5 cm diameter. In the late 1970s, the New Zealand Forest Service was responsible for the thinning and milling of kauri in a 120-year-old ricker stand in Northland (Halkett, 1979, 1980; Gibson, 1985; Ecroyd et al., 1993). Fewer than 1% of the boards were classified as heartwood and recovery of clear timber was 37%, only half that expected from mature kauri logs.

Barton and Madgwick (1987) recorded a moderate diameter growth response to thinning and fertiliser application in ricker stands south of Auckland. In other projects, kauri regeneration on Great Barrier Island and also in the Russell and Herekino Forests was managed by felling or ring-barking overstorey vegetation (mainly kanuka) to release developing kauri saplings (Sando, 1936b; Lloyd, 1960; 1963; Halkett, 1983b). Small-scale, partial-logging operations in several kauri forests were permitted until 1979. Following the prohibition of logging in old-growth forests, helicopters were used to extract logs during the thinning of dense stands of sub-mature kauri. This caused little apparent damage to residual trees in Russell Forest (Halkett, 1983a) or in the Hunua Ranges (Barton & Madgwick, 1987).

During the 1940s, concern about the extent of forest devastation and loss of kauri centred on Waipoua State Forest, the largest remaining area of old-growth

[7] Sando, C. T. (1936b). Part 1. Kauri Management Plan, Herekino State Forest. New Zealand State Forest Service. New Zealand National Forestry Library heritage collection (unpublished).

[8] Sando, C. T. (1936c). Part 2. Kauri Management Plan, Herekino State Forest. New Zealand State Forest Service. New Zealand National Forestry Library heritage collection (unpublished).

[9] Gibson, L. J. (1985). Second-crop kauri: evaluation. *Auckland Conservancy Section Report No. 10.* New Zealand Forest Service (unpublished).

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forest containing this species. Although the creation of a reserve had been suggested at the turn of the century (Cockayne, 1908), it was not until 1952 that the Waipoua Forest Sanctuary (9000 ha) was established. Concise accounts of the history and vegetation of this area are given by Cockayne (1908), Hutchins (1918) and Burns and Leathwick (1992). Publication of the 1992 description coincided with the designation of a Kauri Research and Management Area adjacent to the Sanctuary, extending the total protected area to 13 000 ha.

The meaning of the expression "management of kauri" has changed since the era of timber exploitation. It now includes the protection of forest and indigenous wildlife and the fostering of diversity in native flora and fauna. Effective predator control and the protection of endangered species are important collateral aims. The Department of Conservation has established several "mainland islands" in which the presence of introduced mammals is reduced to the lowest possible levels. Trounson Kauri Park, the only mainland island containing kauri, provides a model for expansion of the practice to other kauri stands in Northland (Saunders, 2000).

A further aim of modern kauri management is forest restoration through the widespread planting of nursery-raised seedlings. The New Zealand Forest Service started experimental plantings of kauri in Waipoua Forest in the 1940s and carried out supplementary or enrichment planting in tall scrub and partially logged forest until the demise of the Service in 1987. By this time, hundreds of thousands of nursery-raised kauri had been planted over a total area of 1000 ha (Halkett, 1983a; Halkett & Sale, 1986), mainly on sites formerly occupied by kauri forest. Only cursory attention has been paid to evaluation of these results. Newly planted kauri seedlings are vulnerable to drought, and survival in exposed sites on open and compacted ground or in short scrub has generally been poor. Improved survival has been noted beneath an intact tall canopy but there has been little height growth for many years.

Morrison and Lloyd (1972) considered that soil texture and condition were two major factors affecting kauri seedling establishment. Growth rates were usually enhanced in soils with a loose, friable structure while nutritional characteristics had a smaller effect. Best growth of planted kauri has been observed in fertile, sheltered sites such as those chosen for plantations established by the New Zealand Forest Service in Northland and Great Barrier Island (Halkett, 1983a). Other vigorous plantations have been established in urban parks in Whangarei, Auckland and New Plymouth, and small stands have been planted by private landowners (Pardy et al., 1992). Some of these are now 82 years old. Many stands with high stocking rates (in excess of 1000 stems/ha) show a decrease in growth rate and some mortality as competition becomes more intense (e.g. Herbert et al., 1996). In general, the objectives of kauri plantation establishment or enrichment planting have not been clearly stated, and "kauri policy" has not been applied consistently. Strong arguments have been put forward for management of second-growth kauri and some planted stands for wood production (e.g. Barton & Horgan, 1980). Recognition of the effects of kauri exploitation in the past and continued veneration of the small remnants of old-growth forest have stimulated support for the planting of kauri and for promotion of natural regeneration of the species.

Summary and Conclusions

Kauri is the only species of *Agathis* native to New Zealand. Forests containing kauri have been greatly reduced in area, especially since European settlement over the past 200 years. Kauri timber was cut from as early as 1772. The harvesting of kauri was driven by the demands of supplying timber for the new colony, the clearance of land for pastoral use, and development of a local economy. By 1873, the kauri resource had already declined by 70%. The export of kauri gum was initially not as successful as that of timber but from 1857 until 1900 kauri gum was worth more to the New Zealand economy than gold, wool or timber. The export of native timbers was restricted by the Commissioner of State Forests in 1918. By 1920, kauri logging and collecting of gum had declined, and in 1981 logging on Crown land had ceased entirely. The management of New Zealand's native forests became the responsibility of the new Department of Conservation in 1987, at which time less than 1% of the original kauri forests remained. Management of kauri now focusses on ensuring the long-term survival of the species despite a severely altered population and in the presence of new diseases.

The disease causing kauri dieback (*Phytophthora* taxon Agathis) in the Northland and Auckland regions poses a threat to the long-term survival of kauri at the local and national level, and also to those proposing to plant kauri in plantations. While management options have been proposed to limit the spread of the disease, further investigation into this *Phytophthora* spp. and its relationship with kauri is required to ensure that kauri continues to exist in New Zealand's forests and landscapes.

Kauri grows slowly in its natural habitat but, under favourable conditions, it is one of the faster-growing indigenous conifers. Although seedling growth is slow in logged areas, there is considerable evidence that regeneration takes place in old-growth forests. Trees surviving for many years as suppressed saplings assume a faster growth rate when gaps form in the forest canopy.

Climatic changes during the Quaternary period are

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likely to have been responsible for restriction of the natural range of the species to areas north of latitude 38 °S. Vigorous growth is possible if trees are established artificially on fertile, free-draining soils in sheltered areas south of the current natural range. When young, kauri is easily suppressed by other plant species. Its efficient use of water and nutrients probably accounts for competitive advantage on relatively infertile sites.

Over the last 160 years, emphasis has shifted from destructive exploitation to conservation, and more recently to expansion of the national kauri resource. The current research focus on improvement of establishment techniques and enhancement of early growth rate offers good prospects for the widespread planting of kauri for amenity and cultural purposes, and for timber production on appropriate sites. Planting of kauri in New Zealand will continue, and the rate is likely to increase, especially within the natural range of the species.

Numerous historical and contemporary references indicate that kauri has a potential role in the development of New Zealand's economic well-being. Careful management is likely to allow the production of a very desirable timber over much shorter rotations than were previously thought to be possible. Those wishing to plant kauri for future timber production will require more information about best-practice regimes and potential yield. Continued development of techniques and growth models is likely to accelerate the expansion of a unique national resource.

Research to meet some of these needs is currently underway. Growth and yield models are being developed for kauri grown in plantations, and include comparisons with managed second-growth natural stands. These models for plantation grown kauri will include data from young, exceptionally performing stands, and older stands established in the 1930s. These models may be constrained by the relative scarcity of plantation grown kauri and the lack of silviculture applied to them. Selected silvicultural data may be extrapolated from the response to thinning treatments applied to second-growth natural stands from the 1950s. New plantings of kauri are also being established to identify the effects of initial stand density on growth and productivity, and the effect on branch development and abscission. As these plantings develop the data will be included into the models.

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