

# Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand

## I. Population structures and tree growth rates in mature stands

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**Abstract** Twenty five plots of mature kauri *Agathis australis* (D. Don) Lindl., covering the range of the species in northern New Zealand, were sampled for density, basal area, and species composition using a modified point-centered quarter technique. Two increment cores were taken from at least ten trees at most sites, and used to estimate tree ages and growth rates. The density of kauri stems  $\geq 10$  cm d.b.h. ranged from 17 to 416 ha<sup>-1</sup>, and the basal area from 23 to 127 m<sup>2</sup> ha<sup>-1</sup> in the 25 stands. Diameter distributions ranged from highly skewed and unimodal to flat and multimodal, with all size classes represented in most plots. Combined frequency distributions suggest that two or three kauri generations (cohorts) may be present on many sites.

There is only a weak relationship between age and diameter; individuals in the same 10 cm diameter class may vary in age by 300 years, and the largest individual on the site is often not the oldest. Mean annual diameter increments range from 0.15 to 0.46 cm yr<sup>-1</sup> on different sites with an overall average of 0.23 cm yr<sup>-1</sup>, equivalent to 8.7 annual rings per cm of core, about half the commonly quoted figure for growth rate. Periodic mean annual increment and mean annual increment curves are presented. It is concluded that the “normally attainable age” is >600 years. Individuals >2 m d.b.h. probably often exceed 1000 years, but there is no reliable evidence for trees >2000 years in age.

**Keywords** *Agathis australis*; age; basal area; cohort; density; growth rate; kauri; size frequency distributions

## INTRODUCTION

Despite the great importance of kauri to the early economy of New Zealand (New Zealand Forest Service 1983, Fleet 1984) and the considerable public interest in the species (e.g., Reed 1954; Sale 1978), there are few published accounts of communities and forest types containing kauri (Ecroyd 1982). Quantitative studies are mainly restricted to stands of young trees generally known as “rickers” (e.g., Mirams 1957; Ogden 1983).

McKelvey & Nicholls (1959) recognised numerous forest types containing kauri and Nicholls (1976) defined 22 mappable types. The sample plot records given by Ecroyd (1982) reflect this rather detailed classification based on species composition. Cokayne (1928), on the other hand, suggested that kauri forest should be regarded as one association divisible into various sub-associations. Recent ordinations and numerical classifications of density and basal area data (Ahmed 1984; Ahmed & Ogden 1985) have emphasised that kauri-dominated communities are often remarkably homogeneous on a scale of a few hectares, and stands of similar species composition may be widely separated geographically.

Extensive kauri logging and forest clearance occurred in the nineteenth and early twentieth centuries. Kauri forest of various ages was logged and/or burned, only “over-mature” stands of very large trees or those in inaccessible locations being spared. As a result there is now a clear distinction between the original “mature” or “old-growth” forest and the young “second crop” stands which were mostly induced by fire. This distinction has been employed by all those who have worked in kauri forests, and is the basis of the management prescriptions of the New Zealand Forest Service (1983). These prescriptions recognise a total kauri forest resource of 67 144 ha, of which about 12% (7455 ha) can be regarded as mature, although some of this has suffered some partial logging. This area represents about 5% of the pre-European kauri forest and is now highly fragmented. In order to extend understanding of the regeneration processes in the primeval forest we have concentrated on the

remnant mature stands, sampling them throughout their geographical range.

In this paper we describe aspects of the structure of these mature populations, dealing only with trees  $\geq 10$  cm diameter at breast height (d.b.h., at 1.4 m). This arbitrary division of the population is justified by the aforementioned distinction between young and old stands, and by the customary use of this diameter to define "trees", in recent literature. Smaller size classes will be discussed in a later paper.

## DEFINITION OF STUDY AREAS

Criteria for the choice of study areas were that they should be situated in mature kauri forest covering an area of at least two hectares and containing kauri trees  $\geq 60$  cm d.b.h. Most areas in which plots were placed were considerably larger than this minimum and most contained several trees  $> 1$  m d.b.h. Additional, more subjective, criteria were that the sample areas should show no signs of disturbance such as evidence of past logging or fires, and should be relatively homogeneous in structure and composition. In a few cases, signs of disturbance were encountered as the sampling progressed. For example, evidence of past fire was noted at Mount William (Stand 24), Mount Moehau (Stand 18), and on Little Barrier Island (Stands 16, 17), and some selective logging may have occurred within the areas sampled at Manaia Sanctuary (Stand 19) and Katikati (Stand 25) (New Zealand Forest Service 1949; Barton 1982).

Using these criteria, 25 plots were chosen for study (Fig. 1, Table 1). These plots cover the geographical and altitudinal range of mature kauri forest.

## METHODS

Plots were sampled for density, basal area, and species composition using a modified version of the point-centered-quarter method (p.c.q., Cottam & Curtis 1956). Usually twenty points were sampled on a  $25 \times 20$  m grid, but this was sometimes modified to take account of the shape of the remnant mature forest area or the topography. At each point the species, diameter, and distance to the nearest tree ( $\geq 10$  cm d.b.h.) in each of four quadrants was recorded. In addition the species of the second nearest tree was recorded, and its diameter measured if it was a kauri. Thus, the overall density estimate was usually derived from 80 point-tree distance measures, absolute basal area from  $> 80$  diameter measurements, and relative composition from 160 separate identifications (cf. Ogden

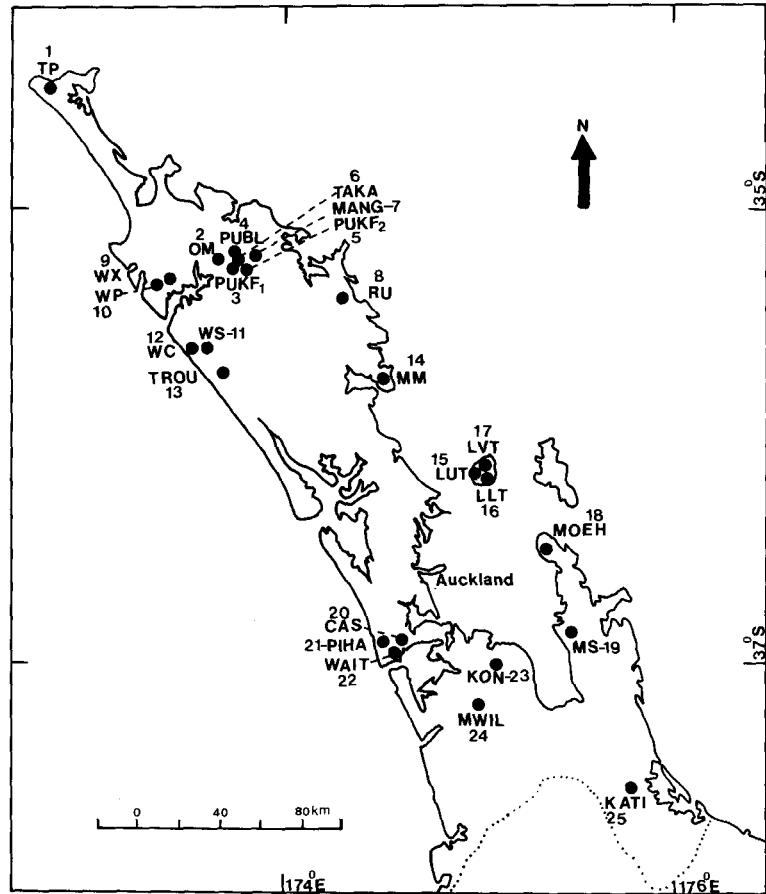
& Powell 1979). The diameters of additional kauris, occasionally encountered between sample points, were also measured, thus increasing the diameter frequency distribution data. The quantitative species composition of the plots was analysed using multivariate techniques (classification - TWINSPAN, ordination - DECORANA) and will not be considered further here (see Ahmed 1984).

Field trials showed that the mean point-tree distance had stabilised after *c.* 30 distance measurements (cf. Cottam et al. 1953). The sampling method has been shown to often over-estimate basal area (Mark & Esler 1970) but estimates independently derived from total enumerations of 0.25 ha plots in two of the study areas (Trounson, Puketi) gave similar basal area values to those presented here (Wardle 1984).

Two increment cores were taken from at least ten trees in the majority of sites. A 50 cm hand-operated corer was used on most trees, and an 80 cm corer on a few large trees. The d.b.h., the diameter at core height, and height of the core, were measured on each tree. Bark thickness was recorded on four aspects using a Swedish bark gauge. Coring was undertaken primarily with the aim of developing a chronology (Ahmed & Ogden 1985) but was concentrated in defined size classes, so that growth-rate comparisons could be made between sites. These classes were 10–20 cm d.b.h. (cored entirely for comparative growth rate studies), 50–60, 90–100, and 130–140 cm d.b.h. In total, more than 800 cores from approximately 400 trees were obtained from twenty one stands. The age and growth rate data presented, however, are derived from the 182 trees falling in the specified classes and in which the age estimate was  $\geq 60\%$  reliable. Reliability, in this sense, was defined by the length of increment core counted divided by the estimated under-bark tree radius, expressed as a percentage. Counting accuracy was enhanced by careful preparation of the core surfaces; the cores were mounted in wooden holders, sanded to a fine polish using an orbital sander, and counted under a stereo-microscope with variable magnification (usually  $\times 10$ ). Most of the cores used were cross-dated with others from the site, so that missing or false rings do not present a serious problem in the selected core set.

One or two seedlings, usually 2–3 m in height, were sampled in most stands, or an adjacent area. These were sectioned at various heights and used to provide an estimate of the number of years required for the tree to grow to the height at which the increment core was taken. This value was added to the ring count from the core, and to an estimate for any "missing radius" when the core did not bisect the pith, to provide the total tree age. The average growth rate of the innermost twenty rings

**Fig. 1** Locations of study sites. The dotted line indicates the approximate southern limit of kauri (*Agathis australis*). For key to name codes refer to Table 1. For further details of site locations see Ahmed (1984).



of the core was used to provide a rate for the missing portion of radius.

At Manaia Sanctuary (Stand 19) most kauri trees were measured for diameter and tagged by the New Zealand Forest Service in 1970 (Johnston 1970). These trees were relocated and remeasured, and 21 were cored, to provide data from a sample of large (old) trees on one site, and to allow comparison between growth rates estimated directly from diameter increments, and those derived from cores (cf. Palmer & Ogden 1983).

## RESULTS

### Density and basal area (stems $\geq 10$ cm d.b.h. $\text{ha}^{-1}$ ; $\text{m}^2\text{ha}^{-1}$ )

Density and basal area for all stems  $\geq 10$  cm d.b.h. are presented in Table 2. Stem densities generally ranged from 216 to 874  $\text{ha}^{-1}$  with a mean of  $579 \pm 49$ . One exceptional value (1299; Stand 14,

Mount Manaia) is accounted for mainly by the abundance of mature *Leptospermum ericoides* and *Coprosoma arborea*, indicative of past disturbance. This site was steep, with frequent light gaps and a high species diversity.

The density of kauri stems varied greatly between sites, ranging from 22 to 227 stems  $\text{ha}^{-1}$  with a mean of 129, and one exceptional value of 416. This latter stand (24, Mount William) represents a late stage of ricker development with a few larger survivors from the previous kauri generation (Fig. 2(a)). High kauri density was associated with low species diversity in this stand. Total basal area values ranged from 34 to 177  $\text{m}^2\text{ha}^{-1}$  with a mean of  $84 \pm 7$   $\text{m}^2\text{ha}^{-1}$ . These high values were generally accounted for by high kauri basal areas, usually the result of a few exceptionally large trees in the samples. Kauri basal area ranged from 23 to 127 with a mean of  $57 \pm 6$   $\text{m}^2\text{ha}^{-1}$ .

Some stands with similar basal area values had quite different densities (e.g., Stands 9, 23, and 24).

**Table 1** Site characteristics

Stand No.	Locations	Code	Latitude S	Longitude E	Altitude (m)	Slope (°)	Aspect
1	Te Paki Coastal Park	TP	34° 28'	172° 46'	220	24	W
2	Omahuta Sanctuary	OM	35° 15'	173° 37'	150	v	v
PUKETI STATE FOREST							
3	Te Harua Stream	PUKF <sub>1</sub>	35° 16'	173° 44'	305	35	N
4	Onekura Bluff	PUBL	35° 11'	173° 45'	305	30	N
5	Loop Track	PUKF <sub>2</sub>	35° 15'	173° 44'	274	31	NE
6	Takapau Track	TAKA	35° 13'	173° 45'	252	19	v
7	Manginangina Scenic Reserve	MANG	35° 12'	173° 48'	274	24	E
8	Russell State Forest	RU	35° 23'	174° 15'	221	26	SW
WARAWARA STATE FOREST							
9	Ridge site	WX	35° 22'	173° 17'	468	32	N
10	Plateau site	WP	35° 23'	173° 17'	358	28	N
WAIPOUA FOREST							
11	Waipoua Sanctuary	WS	35° 29'	173° 34'	145	19	SW
12	Waipoua Coastal	WC	35° 37'	173° 29'	244	21	SW
13	Trounson Kauri Park	TROU	35° 43'	173° 38'	175	19	N
14	Mount Manaia	MM	35° 49'	174° 31'	320	31	E
LITTLE BARRIER ISLAND							
15	Upper Thumb Track	LUT	36° 12'	175° 04'	335	32	S
16	Lower Thumb Track	LLT	36° 13'	175° 04'	213	26	NE
17	Valley Track	LVT	36° 13'	175° 04'	243	34	S
18	Te Moehau	MOEH	36° 31'	175° 24'	450	29	NW
19	Manaia Sanctuary	MS	36° 52'	175° 32'	350	30	NW
WAITAKERE RANGES							
20	Cascade Kauri Park	CAS	36° 53'	174° 31'	240	35	EW
21	Piha	PIHA	36° 58'	174° 30'	274	29	NW
22	Huia	WAIT	36° 58'	174° 34'	274	31	NW
HUNUA RANGE							
23	Konini Forks	KON	37° 04'	175° 08'	335	30	NE
24	Mount William	MWIL	37° 13'	175° 02'	350	26	N
25	Katikati State Forest	KATI	37° 36'	175° 52'	350	30	NW

v = variable

In mature stands, a given basal area may be achieved by low densities of large stems, high densities of small stems, or any combination.

### Size frequency distributions

Kauri diameter distributions, grouped by density, are presented in Fig. 2. It must be borne in mind that they are incomplete in so far as only stems  $\geq 10$  cm d.b.h. are included. Fig. 2(a) shows the distributions for stands with kauri densities ranging from 180 to 416 stems  $ha^{-1}$ . These high density stands all have highly skewed size frequency distributions with modes in the smallest (10–20 cm) diameter class. Some of them (stands 8 and 24) show second modes in classes  $>1$  m d.b.h. Low density stands (28–134 stems  $ha^{-1}$ ) on the other hand show much flatter frequency distributions, often with several modes and usually some indi-

viduals  $>2$  m d.b.h. (Fig. 2(b)). Intermediate size frequency distributions are found in stands of moderate density, rather arbitrarily grouped in Fig. 2(c). Some stands of similar densities have quite different size frequency distributions with peaks and troughs occurring in different classes.

In an attempt to synthesise the data in Fig. 2 the number of times each class showed a frequency mode or a "gap" was tabulated (Fig. 3). Modes and gaps were defined as classes with respectively more or less individuals present than those on either side. Due to the progressively poorer representation of larger classes these results must be interpreted with care, but some salient points can be emphasised. All size classes show both peaks and gaps somewhere amongst the 25 stands studied. Frequency peaks are commonest in d.b.h. classes 10–20 cm, 50–100 cm and 130–150 cm "alternating" with

**Table 2** Density and basal area values.

Stand	N(1)	Density stems $\geq 10$ cm d.b.h. ha <sup>-1</sup>		Basal area m <sup>2</sup> stems $\geq 10$ cm d.b.h ha <sup>-1</sup>	
		SD(2)	KD(3)	SB(4)	KB(5)
1	15	464	180	34.5	23.1
2	19	216	28	36.7	22.6
3	17	355	114	54.4	39.5
4	18	345	90	79.3	65.6
5	21	407	102	125.4	76.3
6	8	408	103	88.1	65.5
7	22	308	51	75.3	48.0
8	18	586	213	80.8	65.1
9	20	696	185	65.6	42.3
10	21	673	84	85.2	34.1
11	24	494	71	69.5	47.8
12	21	776	68	97.0	65.7
13	21	671	134	149.5	118.4
14	27	1299	227	122.3	66.7
15	19	824	108	70.8	44.0
16	14	673	177	73.4	46.0
17	12	764	201	78.5	40.0
18	15	758	40	75.0	34.6
19	20	621	47	177.1	127.3
20	17	464	188	126.4	113.2
21	21	239	63	90.7	74.8
22	25	240	48	48.1	33.7
23	18	589	144	66.8	30.0
24	11	874	416	66.2	51.8
25	19	724	149	59.6	38.0
Mean $\pm$ standard error	19 $\pm$ 1	579 $\pm$ 49	129 $\pm$ 84	83.8 $\pm$ 6.7	56.6 $\pm$ 5.7

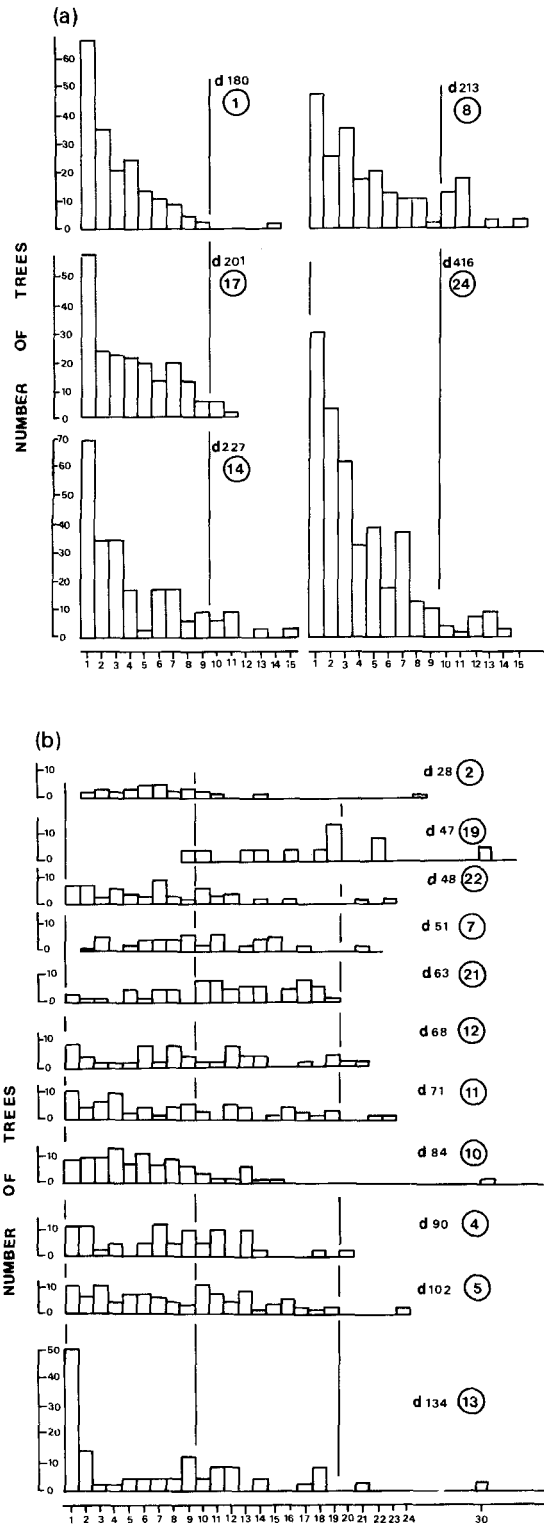
(1)N Number of species  $\geq 10$  cm d.b.h. recorded. (2) SD Stand density, all species. (3) KD Kauri density. (4) SB Stand basal area, all species. (5) KB Kauri basal area. Standard errors were calculated for the individual values based upon the variance of the point-tree distance measures in a stand in the case of density, and on the variance of the individual tree diameters (basal areas) in the case of the basal area figures. These calculations indicate that the individual density estimates have an average standard error of  $\pm 5.7\%$  of their value and the basal area estimates an average standard error of  $\pm 26.5\%$ .

“gaps” at (20)–40–50 cm, (100)–120–130 cm, and 150–180 cm. The latter “gap” may be an artefact of the low sample size in these classes.

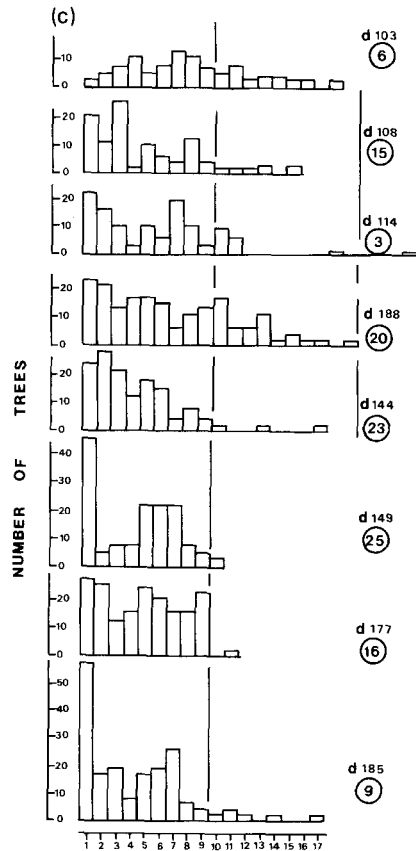
#### Age estimates

Table 3 summarises the mean ages obtained for individuals in comparable size classes in most of the stands. The estimated age of the largest and the oldest kauri is also given. The data indicate that individuals in the largest distinct size class mode in most forests (130–150 cm d.b.h.) are on average, *c.* 600 years old. Older individuals occur and trees  $> 2$  m diameter may normally exceed 1000 years (see discussion, Table 6). Trees in the smallest size class (10–20 cm d.b.h.) are commonly 120–140 years old, although the fastest growing individuals

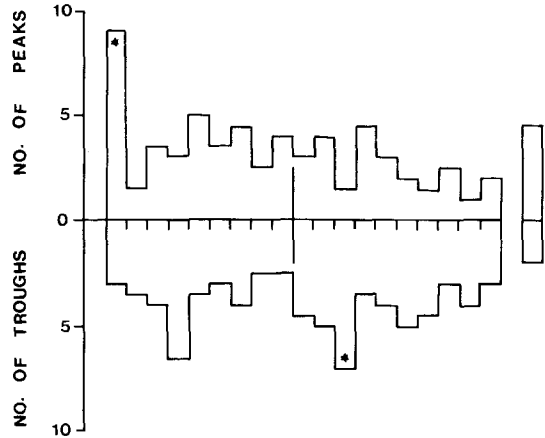
of this age may have reached 50–60 cm d.b.h. Thus, the relationship between age and diameter, though significant, is weak (e.g.,  $r=0.58$ ,  $n=18$ ,  $P<0.05$ ; and  $r=0.54$ ,  $n=11$ ,  $P<0.10$  for the largest and oldest individuals in Table 3, excluding the Mount Manaia (Stand 19) data for which ages are unreliable; see Table 4). The largest individual cored in a site was frequently not the oldest. For example, in Stand 4 the largest cored individual was 213 cm d.b.h. and aged 522 years, while a tree 115 cm d.b.h. was aged 709 years. This relationship is depicted, for the stand with the most data, in Fig. 4 which illustrates an age range of  $\geq 300$  years in 10 cm diameter classes  $> 30$  cm d.b.h., rendering the linear regression equation virtually useless as a means of predicting the age of an individual.



**Fig. 2** Diameter frequency distributions. Vertical axis gives the number of kauri measured in the stand. Horizontal axes are 10 cm diameter classes: 1 = 10 < 20 cm, 2 = 20 < 30 cm etc. Vertical lines mark 1 and 2 m class boundaries. d refers to stand density in stems  $\geq$  10 cm d.b.h. ha<sup>-1</sup>. The circled number is the number of the stand. (a) Size frequency distributions of high density stands with skewed unimodal structure. (b) Size frequency distributions of low density stands showing a flattened structure with some large trees. (c) Size frequencies intermediate between (a) and (b).



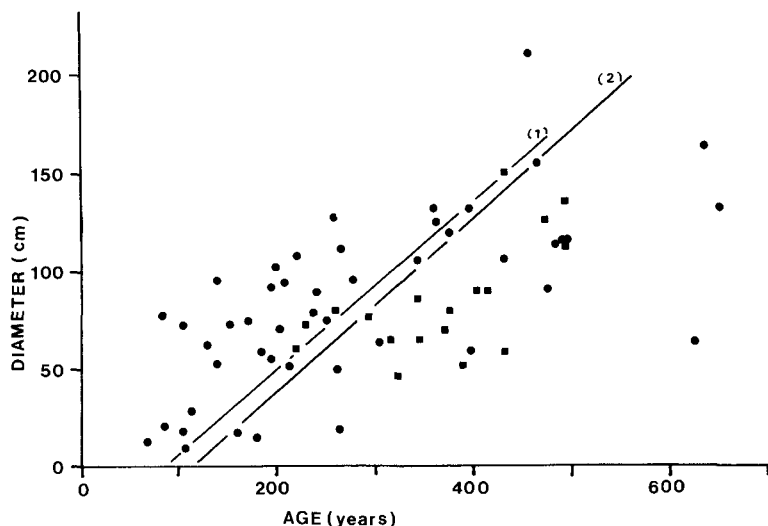
**Fig. 3** Distribution of all frequency modes (peaks) and gaps (troughs) in all stands (from Fig. 2). Frequency modes are indicated above the midline and gaps below it. The horizontal axis represents 10 cm diameter classes with a vertical line at 1.0 m. All peaks and troughs in size classes >2.0 m are summarised in the final separate bar. Asterisks indicate classes which deviate significantly ( $P < 0.05$ ) from an expected equal probability of peaks or troughs in any class (Chi squared test).



**Table 3** Estimated ages of kauri trees in various forests.

Stand(1)	Mean ages of d.b.h. class $\pm$ 95% C.L.(2)				Age of largest kauri cored(3)		Diameter of oldest kauri cored(4)	
	10–20 cm	50–60 cm	90–100 cm	130–140 cm	Age	Diameter (cm)	Diameter (cm)	Age
1	156 $\pm$ 13	185 $\pm$ 13	294	–	267	154	97	370
3	–	–	220 $\pm$ 38	–	292	112	–	–
4	–	185	437	590	522	213	115	709
5	83	124	–	451	377	115	132	519
6	194	237 $\pm$ 104	–	–	371	59	–	–
8	171 $\pm$ 25	256 $\pm$ 120	280	401	289	148	113	438
9	168	297 $\pm$ 120	435	675	419	152	134	712
10	106 $\pm$ 53	218 $\pm$ 31	–	–	535	174	–	–
11	104 $\pm$ 54	365	215	461	390	116	138	639
12	86 $\pm$ 22	253	415	703	515	152	137	703
13	82 $\pm$ 17	–	321	469	898	188	–	–
14E	127 $\pm$ 7	189	–	–	466	153	110	504
14W	132 $\pm$ 15	201	343	524	615	173	–	–
15	–	–	246	335	285	150	136	335
16	162 $\pm$ 27	223	322	–	335	96	–	–
19	–	–	652	1098	n.c.	299	175	1527
22	145	187	245	–	517	163	102	556
24	117 $\pm$ 6	–	396	377	512	150	–	–
25	103 $\pm$ 47	186 $\pm$ 50	173	–	249	117	80	320
Mean Age $\pm$ 95% C.L.	127 $\pm$ 9	231 $\pm$ 20	319 $\pm$ 44	579 $\pm$ 131	–	–	–	–
Total No. aged in each class	81	48	32	21	–	–	–	–

(1) Stands 2, 7, 17, 18, 20, 21, and 23 excluded due to too few cores or uncertainties in ageing. Cores were taken from two aspects on Mount Manaia, here distinguished as east (E) and west (W). (2) 95% confidence limits calculated only for samples  $\geq$  3 trees. (3) Larger trees occurred on most sites but were not cored. No estimate was made for the largest cored tree at Manaia Sanctuary (19) due to the inadequate core length. (4) Rows left blank where the largest and oldest trees cored were the same.



**Fig. 4** Relationship between diameter and estimated ages derived from two or three cores per tree (●) and from cross-sections (■) from Puketi State Forest. (From sites 3, 4, 5, and 6, and "hurricane ridge" plot A689, N.Z.F.S., Kaikohe, respectively.) The figure suggests that cores tend to underestimate the true age derived from cross-sections, but as the samples were obtained from different sites this conclusion may not be warranted. The linear regressions for predicting age from diameter from the cored trees (1) and both samples (2) are shown. The equations are:  
 (1) Age =  $86.635 + 2.337$  d.b.h. ( $r = 0.659$ ,  $n = 47$ ,  $P < 0.001$ )  
 (2) Age =  $115.387 + 2.271$  d.b.h. ( $r = 0.632$ ,  $n = 65$ ,  $P < 0.001$ )

Table 4 gives the results from remeasurement and coring of 29 large trees at Manaia Sanctuary (in and adjacent to Stand 19). In the twelve-year period between measurements, most trees showed a positive increment. In those cases where declines were recorded they were generally small and are likely to be accounted for either by measurement error, or bark loss, or both. The average increments recorded by remeasurement and by coring were not significantly different and the two sets of data are highly correlated (paired  $t = 1.295$ ,  $n = 21$ ,  $P < 0.10$ ;  $r = 0.72$ ,  $n = 21$ ,  $P < 0.001$ ). The trees are mostly very slow growing, and this, coupled with the low percentage of the total radius sampled (reliability sometimes  $< 20\%$ ), probably means that the ages given are overestimates.

#### Growth rates

Radial growth rates (R.G.R.) in years  $\text{cm}^{-1}$  are given in Table 5. These values must be divided into 2 to obtain the mean annual increment (M.A.I.) in  $\text{cm yr}^{-1}$ . Table 5 suggests that growth rates tend to increase as the trees grow from 20 to 100 cm d.b.h. but decline thereafter. However, the largest size class contains both fast and slow growing individuals, so that this class has a relatively high variance. The Puketi Forest data also show a general tendency for larger trees to have higher growth rates (Fig. 5).

Variability in growth rates between similar sized individuals at any one site has already been noted

(Fig. 4). The data in Table 5 also imply marked differences within d.b.h. classes between sites, ranging from small trees with  $7.5 \pm 2.9$  years  $\text{cm}^{-1}$  at Stand 12 (low altitude Waipoua stand) to  $21.3 \pm 12.5$  years  $\text{cm}^{-1}$  at Stand 6 (Takapau track, Puketi State Forest). These values correspond to mean annual diameter increments of 0.27 cm and 0.09 cm respectively, a three-fold difference.

The overall radial growth rates in Table 5 are based on all cores, not simply those in designated size classes. Again, three-fold differences between sites are implied. An overall average of  $8.7 \pm 1.8$  years  $\text{cm}^{-1}$  was obtained, with 11 stands showing mean values within the 95% confidence limits for the overall mean. Differences in growth rate between sites may indicate sampling bias rather than intrinsic differences in site quality or environment. For example, small trees were under-represented in stands showing fast growth rates and vice versa.

The data in Table 5 (and Table 4) were used to calculate periodic annual increments for contiguous diameter ranges (Table 6). These are plotted with mean annual increment in Fig. 6. The horizontal axis of this graph is expressed in terms of diameter, but approximate ages from the cumulative averages in Table 6 are also given. Fig. 6 summarises the growth rate data graphically in two forms. The first curve (circles) which reaches a maximum rapidly in the size range 50–80 cm d.b.h. (age *c.* 200–300 years) is the periodic mean annual increment calculated over varying periods. This curve represents growth of individuals of any particular size class while they are in that size class. It clearly indicates the rising growth rate of the sur-

\* M.A.I. =  $2/R.G.R.$



**Table 4** Growth rate and age estimates of labelled trees in Manaia Sanctuary 1970–82. Trees ranked from smallest to largest diameter.

Identification number (1)	d.b.h. (cm)		Radial increment (mm)		Maximum reliability of core (%)	Estimated age (years) (4)
	1970	1982	tree (2)	1970–82 core (3)		
131	54.2	54.3	0.05	nc	–	–
115	77.7	86.6	44.5	25.0	53	441
150	96.3	98.1	9.0	14.0	51	541
148	97.1	98.5	7.0	9.8	47	767
149	98.7	100.9	11.0	6.2	100	562
117	104.4	106.6	11.0	nc	–	–
161	123.8	122.0	–9.0	nc	–	–
130	129.4	135.6	31.0	nc	–	–
111	133.5	134.4	4.5	3.0	34	1382
151	137.5	137.0	–2.5	4.0	24	1355
107	144.8	146.3	7.5	5.2	25	920
113	155.3	158.8	17.5	13.0	43	988
135	157.7	157.0	–3.5	nc	–	–
152	157.7	157.5	–1.0	11.0	32	888
136	159.4	159.8	2.0	9.2	35	716
103	165.8	169.3	17.5	8.0	26	1032
155	179.6	179.4	–1.0	5.5	32	1527
110	180.4	180.6	1.0	10.0	66	1247
166	186.9	194.5	38.0	nc	–	–
108	187.7	190.7	15.0	19.5	18	955
96	189.3	189.0	–1.5	6.0	32	1025
129	189.3	189.5	1.0	nc	–	–
158	196.6	195.8	–4.0	4.3	54	1307
109	206.3	206.3	0.0	16.0	18	1725
105	225.7	226.2	2.5	4.5	21	2217
97	231.4	234.5	15.5	15.0	26	1233
167	241.1	243.7	13.0	nc	–	–
156	294.4	294.6	1.0	5.0	19	1638
112	296.1	298.6	12.5	10.5	14	2499
Mean ± standard error mm 12yr <sup>-1</sup>			7.5 ± 2.4	9.7 ± 1.2		
Mean ± standard error yr cm <sup>-1</sup>			15.9 ± 5.0	12.3 ± 1.6		

(1) Identification numbers in the New Zealand Forest Service file held at the Thames office; all preceded by the letters "BO". (2) Twelve-year radial increment based on direct remeasurement of tree diameters. (3) Twelve-year radial increment based on increment cores. (4) Probably mainly over-estimates, see text.

viving ricker trees as self-thinning progresses and a mature canopy develops. Maximum growth rates (c. 0.4 cm diam yr<sup>-1</sup>) are most likely to occur in the 50–90 cm range. Growth rate falls rapidly in trees > 1 m d.b.h., and is maintained at a low level (c. 0.15 cm diam yr<sup>-1</sup>) from then on. There is some indication, supported by some other general observations on cores from large trees, that the very largest individuals show an increase in growth rate. This may be a genuine increase in rate, arising perhaps from the reduced competition between individuals in populations composed of a few very large trees, or it may be an artefact due to the large-tree sample being biased by the greater survivorship of faster growing individuals, or both effects may occur.

The second curve (squares) on Fig. 6 represents the average growth rate of stems in any diameter class over the whole of their life (M.A.I.). This curve peaks later than the first, probably between 80 and 100 cm d.b.h. (age c. 300 years).

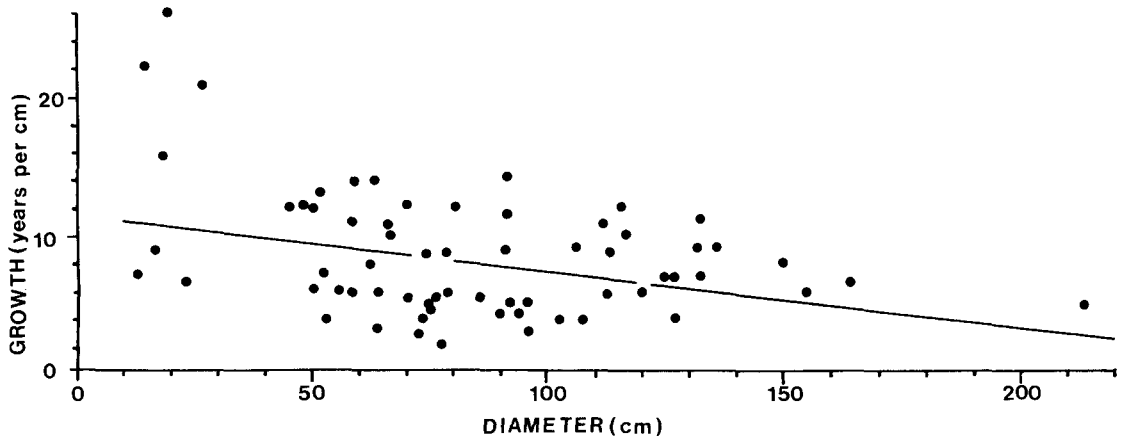
## DISCUSSION

The basal area values in Table 2 all lie within the range recorded for a variety of forest types, using plotless (p.c.q.) and plot methods, throughout New Zealand. For example, values in beech forest (*Nothofagus* spp.) commonly range between 30 and 80 m<sup>2</sup>ha<sup>-1</sup> (Franklin 1967; Westerskov & Mark

**Table 5** Radial growth rate of kauri in various forests. Figures are means over whole radius for trees in selected d.b.h. classes.

Stand (1)	Radial growth rate in years cm <sup>-1</sup> with 95% c.l. by d.b.h. class (2)				Overall mean radial growth rate years cm <sup>-1</sup> with 95% c.l. for each stand	
	10-20 cm	50-60 cm	90-100 cm	130-140 cm	Mean growth rate	Number of trees (3)
1	18.0	4.7±0.9	5.5	-	8.2±2.1	28
3	-	-	4.4±1.0	-	4.3±0.6	12
4	-	6.0	9.0	9.0	6.5±1.4	14
5	8.2	4.0	-	9.0	8.0±1.6	12
6	21.3±12.5	8.4±4.7	-	-	13.6±5.3	9
8	18.4±2.8	9.1±7.3	6.0	6.0	11.1±2.8	21
9	14.0	10.7±4.7	10.0	11.5	10.6±1.8	10
10	11.4±6.9	8.6±1.7	-	-	8.7±1.8	25
11	11.7±6.7	20.0	4.0	6.6	8.8±3.0	17
12	7.5±2.9	5.0	11.0	10.0	8.8±1.3	17
13	9.0±2.5	-	5.7	7.0	6.9±0.8	25
14E	12.0±4.4	6.0	-	-	8.9±1.6	16
14W	10.7±2.8	5.0	8.0	10.0	8.6±1.8	23
15	-	-	4.7	5.0	4.9±0.7	12
16	17.5±8.2	7.0	6.0	-	10.5±3.8	12
19	-	-	12.5	16.0	13.5±1.7	22
22	13.5	6.8	5.5	-	9.6±2.8	18
24	13.4±1.9	-	8.0	5.7	9.2±1.3	35
25	9.6±3.3	6.2±2.1	4.0	-	5.9±1.2	24
Overall mean with 95% C.L.	12.9±1.2	8.0±1.0	6.7±1.1	9.1±2.1	8.7±1.8	
Sample size (trees)	81	48	32	21	352	

(1) Some stands excluded, see notes to Table 3. (2) Mean annual diameter increment (M.A.I.) obtained by dividing each value into 2 cm. 95% c.l. calculated only for samples  $\geq 3$ . (3) Numbers in this column indicate the number of trees on which the mean growth rate was based; this may differ from the sum of numbers in the particular size classes given.



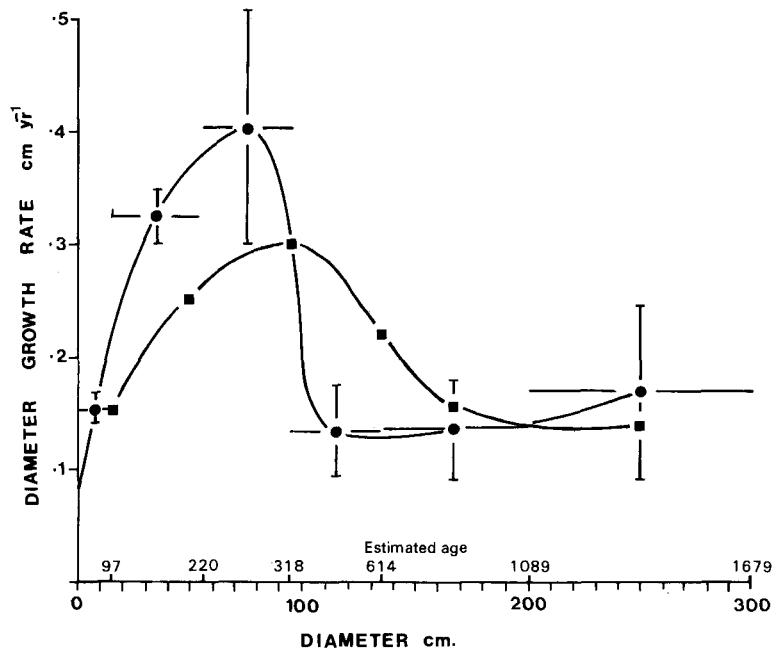
**Fig. 5** Relationship between radial growth rate (yrs cm<sup>-1</sup>; averaged over length of core) and diameter (cm d.b.h.) from trees at Puketū State Forest.  $y=11.53-0.04x$ . ( $r=0.663$ ;  $n=65$ ;  $P<0.001$ ).

**Table 6** Estimated growth rate of kauri at different diameters, and derived average ages.

Diameter range cm (1)	Mid-point cm	Years cm <sup>-1</sup> (3)	Cm year <sup>-1</sup> (3)	Years in class (4)	Cumulative age (5)
0-15	7.5	6.5 ± 0.6	0.15 ± 0.01	97	97
15-55	35	3.1 ± 0.2	0.32 ± 0.02	123	220
55-95	75	2.5 ± 0.6	0.41 ± 0.10	98	318
95-135	115	7.4 ± 2.2	0.14 ± 0.04	296	614
135-200(2)	167	7.3 ± 2.3	0.14 ± 0.04	475	1089
200-300(2)	250	5.9 ± 2.7	0.17 ± 0.08	590	1679

(1) Based on mid-points of class intervals in Table 4 and (2) data from Manaia Sanctuary (Table 5). (3) Periodic mean annual diameter increment while in diameter range ± 95% confidence limits. Figures rounded. (4) Mean years cm<sup>-1</sup> multiplied by number of years in diameter range. (5) Cumulative age at end of diameter range specified.

**Fig. 6** Diameter growth rate (cm yr<sup>-1</sup>) at different diameters. Overall average values derived from Table 4, 5. Circles: periodic mean annual increment covering the period indicated by the horizontal lines around the points; the vertical lines are 95% confidence limits. Squares: mean annual increment. The curve is eye-fitted and confidence intervals are omitted for clarity.



1968; Wardle 1970; June & Ogden 1978; Wardle 1984) although values in excess of 100 m<sup>2</sup>ha<sup>-1</sup> may be encountered in silver beech (*N. menziesii*) forest types (e.g., Mark & Sanderson 1962; Mark 1963; Scott et al. 1963; Mark et al. 1964). The figures for kauri forest are at the upper end of the range for New Zealand forests: published values exceeding 177 m<sup>2</sup>ha<sup>-1</sup>, the highest kauri forest value (stand 19, Manaia Sanctuary), are exceeded only by *N. menziesii* in Fiordland (195 m<sup>2</sup>ha<sup>-1</sup>, Mark & Sanderson 1962; 208 m<sup>2</sup>ha<sup>-1</sup>, Mark et al. 1964). Moreover, the average value in kauri forest is higher than that recorded for tropical rain forests of similar structure, which rarely exceed 60 m<sup>2</sup>ha<sup>-1</sup> (Enright 1982; Brunig 1983).

Individually, the size frequency distributions (Fig. 2) must be interpreted with caution, bearing

in mind the poor correlation between diameter and age. However, together with the age data they strongly suggest that some regeneration must occur in mature stands; it would be difficult to argue that the varied modes in the histograms of Fig. 2(b) represent individuals of the same age class. This conclusion has a bearing on the controversy as to whether kauri should be regarded as a true "climax" species, or as a seral species likely to be replaced by *Beilschmiedia* or *Weinmannia* spp. as its population matures (reviewed by Ecroyd 1982). The data presented are not inconsistent with a model in which dense regeneration following major disturbance ("ricker" development) is followed by a wave of regeneration as the first cohort senesces, which in turn is followed by later waves (Ogden 1985). The size structures and ages presented sug-

gest episodic regeneration occurring at intervals of between 100 and 300 years. If the initiating disturbances are not synchronous over large areas, cohort size structures are unlikely to agree from site to site.

The growth rates presented in Table 5, 6 are about half those commonly quoted for kauri. For example, Cheeseman (1914) found an average of 4 rings per cm of radius in trees approximately or >1 m diameter, and Lloyd (1960) gives the same value for emergent pole kauri. These values are close to the upper confidence limits given in Fig. 6 but are certainly encompassed by the great individual differences in rates. Slow diameter growth is a feature of small "rickier" stems, which are often suppressed and also tend to grow in height rather than diameter, and of some large trees, where the same amount of net productivity must be "spread" around a greater circumference.

The age attained by large kauri trees has been the subject of some controversy (Kirk 1889; Cheeseman 1914). We agree with Cheeseman in suggesting that the "normally attainable age" (Harper & White 1974) is probably 600–700 years, although some individuals, not necessarily the largest, may live much longer. Jansen (1962) obtained ring counts and a radiocarbon date from a 2.2 m diameter kauri, which indicated that it was c. 1000 years old. Our estimates for some trees conform with this, and even greater ages may apply to trees from Manaia Sanctuary (Table 5).

In an attempt to make some generalisations about normally attainable and possible maximum ages we have estimated growth rate for average trees while in different diameter ranges (Table 6). If the average growth rate in a diameter class is known, then the average span of years spent in that class can be calculated, and by cumulative addition the average age of large individuals can be obtained. This leads to the conclusion that 2 m diameter trees average c. 1100 years in age and 3 m diameter trees c. 1700 years. These results are not inconsistent with those in Table 4 bearing in mind the low reliability of the latter. In so far as most mature stands have some individuals >135 cm d.b.h. they suggest that the normally attainable age is >600 years. On the other hand, few individuals exceed 2 m d.b.h. (c. 1100 years) and trees >3 m d.b.h. (c. 1700 years) are now very rare. The previous conclusion that growth rates are highly variable must be kept in mind, and for simplicity, only average ages are given in Table 6 (95% confidence limits can be calculated from the growth rate data).

The general forms of the curves in Fig. 6 are similar to those presented for kauri from Waipoua Forest by the New Zealand Forest Service (1983; fig. 3). However, the Waipoua trees appear to be faster growing and achieve maximum periodic

diameter increments earlier (c. 100–200 years) than indicated for "average" trees in this study. It should be noted that trees from Waipoua (Stand 12, Table 5) were amongst the fastest growing in this study also, and that the wide confidence limits given (Fig. 6) or implied (New Zealand Forest Service 1983; fig. 2) suggest no discrepancy between the two data sets.

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