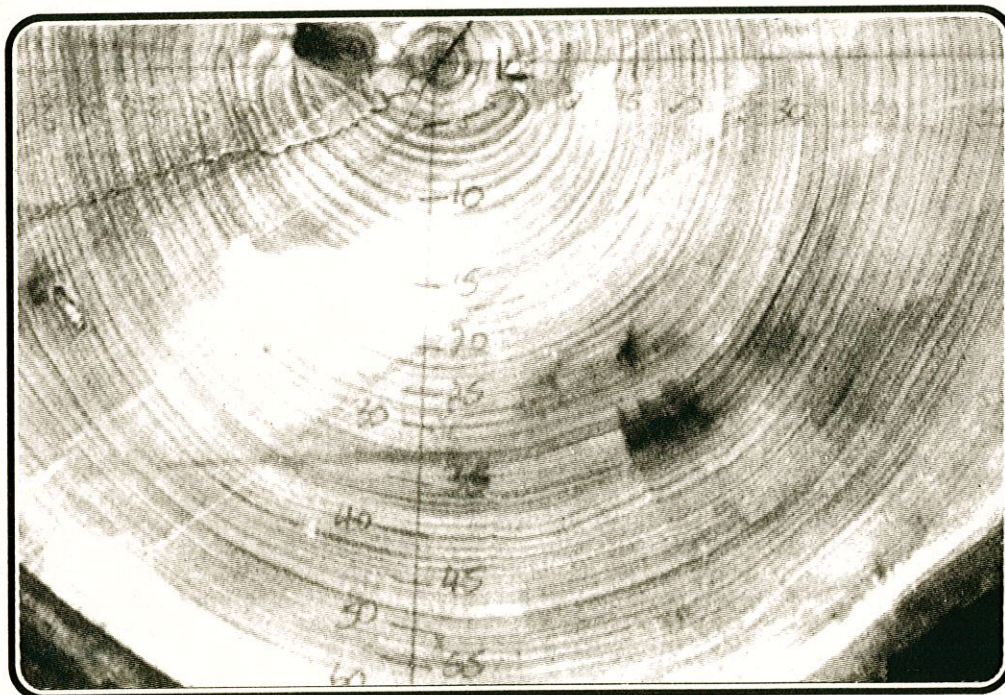


**Application of
Dendrochronology, Stem Analysis and Inventory Data
in the Estimation of
Tree and Stand Ages in Karri Forest**

M. E. Rayner



Technical Report No. 27

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Department of Conservation and Land Management

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Published by the
Department of Conservation and Land Management
Como Western Australia

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ISSN 0816-6757

Marianne Lewis Editor
CALM Corporate Relations Production and distribution

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Application of Dendrochronology, Stem Analysis and Inventory Data in the Estimation of Tree and Stand Ages in Karri Forest

Summary

This report reviews the application of dendrochronological, stem analysis and inventory techniques to the interpretation of stand age in karri (*Eucalyptus diversicolor* F. Muell.) forests. Data from a number of studies are collated and preliminary interpretations of stand age and structural relationships are summarized.

Karri trees are amenable to annual growth ring dating, allowing a chronology of past stem growth to be developed. The use of growth rings to determine tree age in forest-grown conditions is most accurate for dominant trees, while the number of rings on trees which have experienced density-dependent suppression may underestimate true age by up to 50 per cent in even-aged stands. The relationship between tree diameter at breast height and tree age (number of annual growth rings) for the dominant trees in unmanaged stands is strongly linear, providing an indirect method of estimating the age of stands. Application of this imprecise relationship to inventory data collected throughout the range of the virgin (unlogged) old-growth forest suggests that for the majority of the estate the largest trees are less than 350 years old, with many stands no older than 250 years.

The age composition of virgin old-growth stands may range from even-aged to multi-aged in patches varying in area from one-tenth to hundreds of hectares. The age of trees in multi-aged old-growth stands correlates strongly with regeneration events in which the role of fire is paramount and subsequent tree survival depends on gap size relationships.

Further studies of the age structure and fire frequency within old-growth stands are advocated and appropriate experimental techniques are described.

INTRODUCTION

Knowledge of the structure and function of the forest ecosystem is essential when developing practices to achieve management objectives for that forest. Interpretation of the age and structural relationships in stands within the karri (*Eucalyptus diversicolor* F. Muell.) forest in south-west Western Australia is fundamental to such tasks as the evaluation of reserve systems, the development of silvicultural systems, or the examination of forest protection practices. Quantitative data on tree and stand age are also necessary for the development of growth and yield simulation systems.

Over the years considerable data on tree and stand age have been collected within the karri forest. However, these data have often remained unpublished because the objectives of the studies generating such data were usually mensurational or inventory-based (see, for example, Armstrong 1984; Rayner 1991; Brennan *et al.* 1991). Nonetheless, the information generated from these applications of dendrochronological, stem analysis and inventory techniques can contribute to the interpretation of the forest.

This report aims to provide a background to the application of dendrochronological techniques to the determination of karri ages, and to collate existing data relating to tree and stand age as a basis for interpretation of the forest. Throughout this report the discussion refers to forest-grown trees (cf. open-grown individuals commonly used in dendrochronology for climate studies). Because data from a number of sources have been re-worked, Appendices have been included to provide the details used for collecting the original data, and any derivation. Unfortunately, the varied data sources, with their disparate measurement practices and timing of collection of the data, mean that any inferences concerning the distribution of tree or stand ages in old-growth forest are tentative. The information does, however, provide a framework for future dendrochronological studies in karri. Until recently, limited work has been undertaken on those other species which occur in association with karri and they have therefore been arbitrarily excluded from the scope of this report.

DETERMINATION OF TREE AND STAND AGE FOR KARRI

Application of dendrochronology to estimating tree age

The determination of tree age using dendrochronological or stem analysis techniques depends upon the species exhibiting a seasonal pattern in annual growth ring deposition. Karri trees display a seasonal trend in the growth of girth (White 1971), with most of the annual wood production occurring during the early winter months (Loneragan, cited by McArthur and Clifton 1975). Wood production is correlated with leaf production during the preceding spring, which depends in part on soil moisture conditions, but is modified by flowering which occurs irregularly within a four to six-year cycle (Loneragan 1979). Macroscopically distinct annual growth rings, comprised of definite earlywood (lighter coloured wood with a high frequency of vessels) and latewood (darker coloured, low vessel frequency) bands, are produced. The species is therefore comparatively easy to date by standard dendrochronological techniques (see Fritts 1976; Schweingruber 1988). However, even between seasons, karri tree growth and hence ring deposition can be episodic owing to the vagaries of stand and environmental influences. Many factors therefore influence the interpretation of tree age from direct counts of annual growth rings. These factors include the position of the tree in the stand relative to competing stems, tree age, and the cumulative impact of full or partial defoliation following fire, drought or insect attack.

Tree dominance or vigour class

Within forest stands, the growth rate of individual karri trees is highly correlated with their relative position (dominance) in the stand (White 1971). The influence of inter-tree competition on ring deposition must be accounted for when estimating the age of trees from forest stands.

1. Even-aged stands

Karri is characterized by fast growth rates and a capacity to rapidly occupy a site in the early years of stand development. This leads to intense density-dependent competition and hence self-thinning among individual trees in the stand. Segregation into crown (or tree vigour) classes rapidly occurs in these vigorous stands and suppressed and subdominant strata develop.

Table 1 presents annual growth ring counts for stems in each dominance class in two even-aged stands of known age. These data were collected as part of a wider investigation of the growth and productivity of regrowth stands (Appendix I) (Rayner 1991, 1992; Brennan *et al.* 1991). The data illustrate that the age of karri trees can be estimated from counts of annual growth rings, but that only the dominant trees (generally also the tallest and largest diameter at breast height over bark - d.b.h.o.b.) possess ring numbers corresponding to true stand age. The trend of decreasing

ring number with decreasing crown class is consistent with the d.b.h.o.b. increment recorded in permanent sample plots. Figures 1a to 1c show the relationship between annual d.b.h.o.b. increment and d.b.h.o.b. for individual trees over a five-year period in three stands. In each stand the majority of suppressed and subdominant trees averaged zero or negative increments over the period, and it is likely that readily discernible annual growth rings would not have been produced for many consecutive seasons.

Non-incrementing trees will be present in any fully-stocked stand and some may persist for many years before mortality occurs (Hopkins 1968; West 1981; Rayner 1992). Table 2, which shows the ring counts of trees in each dominance class from stands across the range of site index, demonstrates that the relationship occurs across the site and age range of regrowth karri. In general, the ring counts of the codominant trees may underestimate tree age by 10 per cent, irrespective of site quality and age, while suppressed trees may underestimate tree and hence stand age by 20 to 50 per cent.

2. Multi-aged or old-growth stands

Records of stand establishment dates do not exist for old-growth stands, but similar principles to those described above may be expected to apply when determining tree and stand age from ring counts. By inference, ring counts must be performed on stems in the dominant stratum in old-growth if an accurate age of a stand is to be determined. However, several additional factors complicate the interpretation of tree and stand age in old-growth stands.

Trees in stands which contain a mixture of regeneration periods (age classes) will also experience, in addition to density-dependent competition between similar aged trees, a competitive interaction with the older overstorey strata. Rotherham (1983) demonstrated that the suppressive influence of a single veteran on the growth of adjacent 50-year-old regrowth stems extends a distance equivalent to the crown diameter of the veteran. On this basis Bradshaw (1985) estimated that, depending on the size and vigour of veterans, a minimum distance of 60 m between the boles of veteran trees is required for one regrowth tree to develop within a gap relatively unimpeded by overstorey competition. The zone of influence of veterans would overlap at approximately 20 to 25 per cent crown cover, so that above this crown cover any regrowth will experience some degree of suppression from the overstorey trees. The extent to which suppression might affect annual growth ring deposition and hence bias the determination of tree age remains unquantified. However, as most virgin old-growth stands carry crown cover of 70 to 80 per cent (Aerial Photograph Interpretation maps) it is likely that most stems in the older multi-tiered stands are experiencing some degree of overstorey competition. If the hypothesis that ring counts of dominant trees provide an accurate indication of age for each age class is valid, then sample trees in old-growth stands must show no evidence of past crown damage or density suppression and must occupy a dominant position in gaps.

Table 1

Number of annual growth rings observed in trees of each dominance class in two even-aged, regrowth karri stands. Sample trees were in a 16 m radius of a fully stocked sample point.

Forest Block	Tree Number	Dominance Class ^a	Tree Height (m)	Number Of Rings ^b	Age of Stand (Years) ^c
Weld	1	D	27.9	21	21
	2	CD	24.4	21	
	3	CD	26.3	20	
	4	SD	21.8	21	
	5	SD	20.4	18	
	6	SU	18.3	18	
Warren	1	D	24.0	15	15
	2	CD	21.5	15	
	3	CD	22.6	13	
	4	SD	17.4	13	
	5	SD	14.9	12	
	6	SU	11.1	9	

^a D denotes Dominant, CD Codominant, SD Subdominant, SU Suppressed.

^b Annual growth rings were counted at stump height (0.3 m).

^c Both stands were regenerated from seed trees (Weld 1966, Warren 1972) and sampled in August 1987. The stands were pure karri and had been unburnt since establishment.

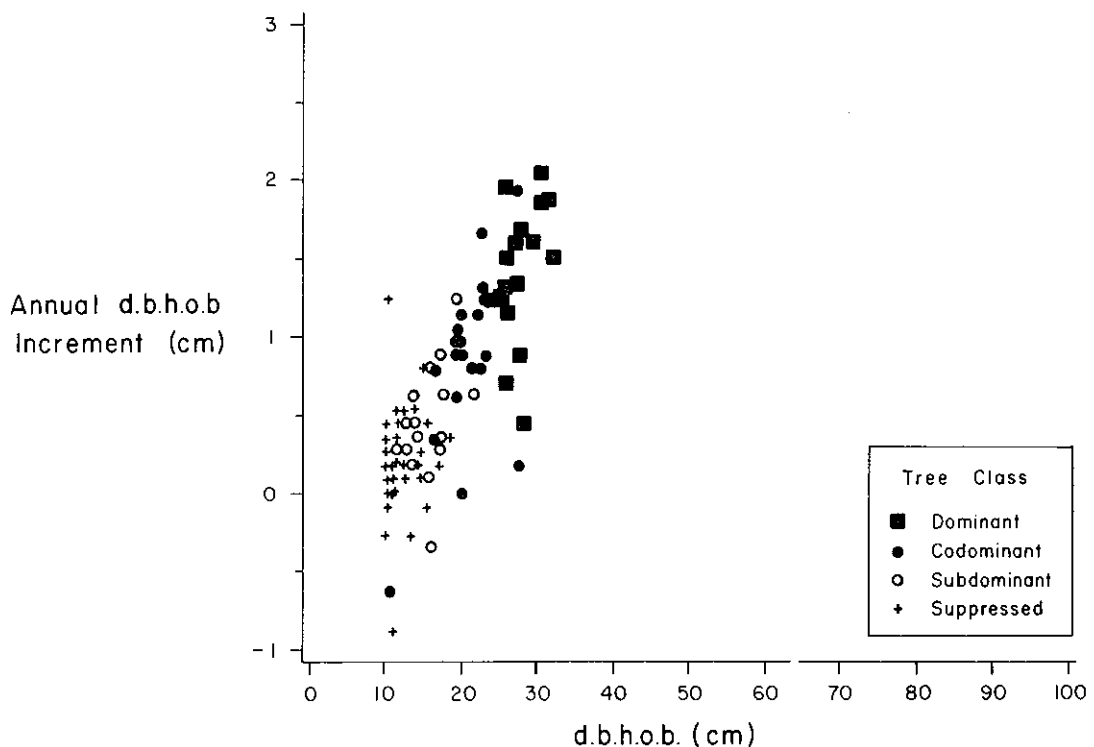


Figure 1a

Annual increment in tree diameter (d.b.h.o.b. increment) plotted against diameter (d.b.h.o.b.) at the commencement of the increment period for trees of each dominance class within an unmanaged, even-aged regrowth stand. Trees were 13 years old at the commencement of the increment period (PSP No. 306, 1985-1987).

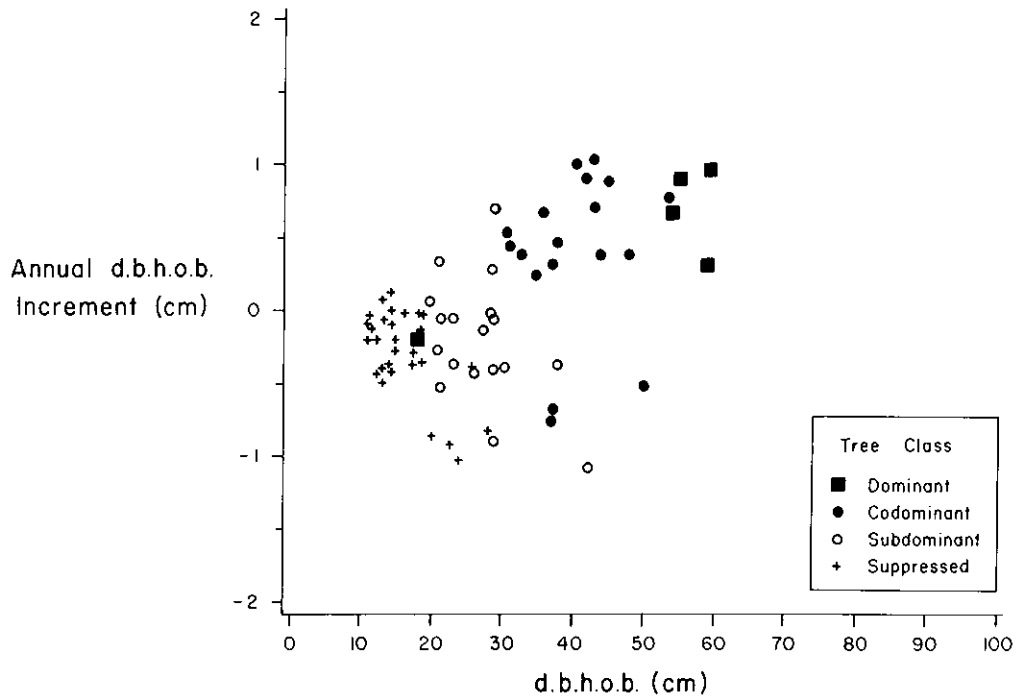


Figure 1b

Annual increment in tree diameter (d.b.h.o.b. increment) plotted against diameter (d.b.h.o.b.) at the commencement of the increment period for trees of each dominance class within an unmanaged, even-aged regrowth stand. Trees were 45 years old at the commencement of the increment period (PSP No. 905, 1982-1987).

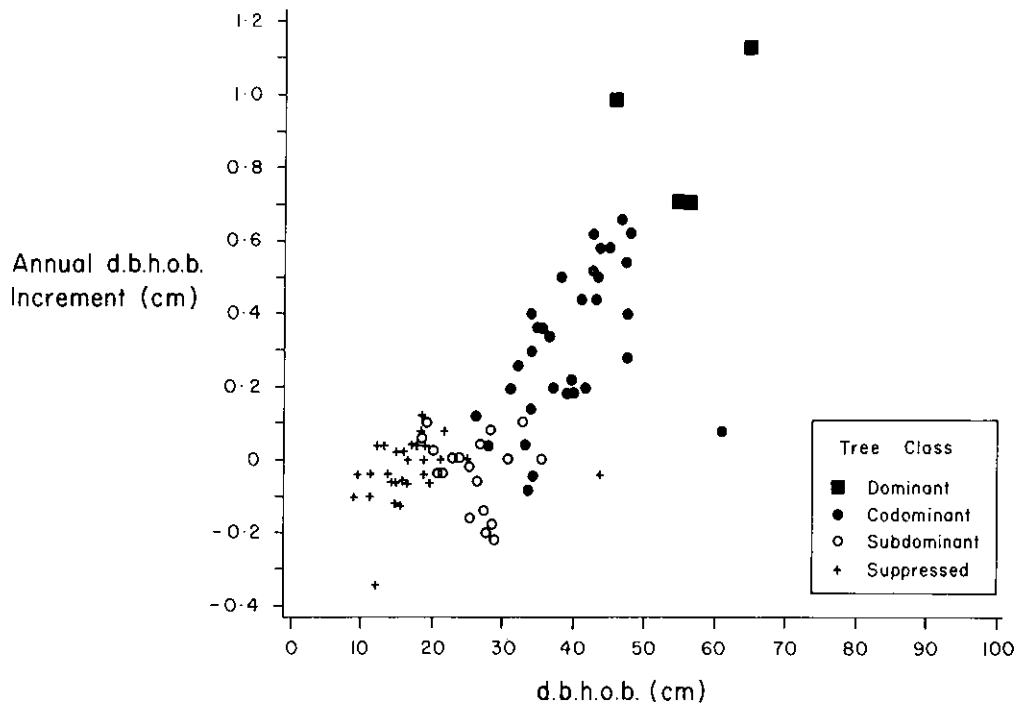


Figure 1c

Annual increment in tree diameter (d.b.h.o.b. increment) plotted against diameter (d.b.h.o.b.) at the commencement of the increment period for trees of each dominance class within an unmanaged, even-aged regrowth stand. Trees were 44 years old at the commencement of the increment period (PSP No.842, 1981-1986).

Table 2

Number of annual growth rings recorded at stump height (0.3 m) for trees in each dominance class in even-aged stands representing the range in site quality for regrowth karri. Sample trees on each site occurred within a 16 m radius in a fully stocked stand.

Forest Block	Inventory PSP ^a Number	Stand Site Index (m) ^b	Tree Number	Dominance Class ^c	Tree Height (m)	Number of Rings	Age of Stand (years) ^d
Court	995	50.8	1	D	49.4	53	53
			2	CD	43.6	49	
			3	CD	48.2	45	
			4	SD	45.5	52	
			5	SD	33.8	43	
			6	SU	31.4	43	
Channybearup	842	46.2	1	D	47.0	49	49
			2	CD	45.5	49	
			3	CD	41.3	47	
			4	SD	30.8	34	
			5	SD	38.5	36	
			6	SU	22.4	27	
Yanmah	842	44.4	1	D	44.4	50	51
			2	CD	44.5	51	
			3	SD	43.7	42	
			4	SD	35.2	43	
			5	SD	29.1	35	
			6	SU	24.9	39	
Channybearup	990	42.7	1	D	41.7	55	55
			2	CD	35.5	53	
			3	CD	38.7	53	
			4	SD	30.4	41	
			5	SD	28.6	44	
			6	SU	22.1	42	
Maringup	904	42.5	1	D	41.0	45	45
			2	CD	39.2	45	
			3	CD	38.4	42	
			4	SD	30.7	34	
			5	SD	27.6	34	
			6	SU	21.9	21	
Sutton	887	39.3	1	D	43.3	58	58
			2	CD	39.1	56	
			3	CD	37.8	53	
			4	SD	34.7	41	
			5	SD	34.2	50	
			6	SU	17.8	26	

Table 2 (continued)

Forest Block	Inventory PSP ^a Number	Stand Site Index (m) ^b	Tree Number	Dominance Class ^c	Tree Height (m)	Number of Rings	Age of Stand (years) ^d
Keystone	905	38.6	1	D	34.8	38	38
			2	CD	34.6	35	
			3	CD	33.3	33	
			4	SD	29.0	34	
			5	SD	27.5	34	
			6	SU	18.3	29	
Murtin	886	36.2	1	D	39.8	70	70
			2	CD	39.1	59	
			3	CD	36.5	70	
			4	SD	33.6	49	
			5	SD	32.1	51	
			6	SU	24.9	31	

^a Permanent sample plot. All stands were of even-aged structure and d.b.h.o.b. distribution, sampled adjacent to plots.

^b Stand dominant height at a base age of 50 years (Rayner 1991).

^c D denotes dominant, CD codominant, SD subdominant, SU suppressed

^d Stand age was determined from the number of rings of the dominant stems.

Tree age

Annual diameter increment, and hence annual growth ring width, decreases with increasing tree age. Figures 1a to 1c demonstrate the larger increments (associated with wider ring widths) of young dominant trees relative to older dominants. By old age rings may become very narrow and difficult to count because of poorly defined ring boundaries. Definition of successive rings may also be complexed by intra-annual latewood bands (false rings) or missing rings. In these instances cross-dating (i.e. comparing ring patterns between trees which overlap in time) is necessary for accurate age estimation.

Climatic patterns

Any climatic aberration which results in severe defoliation will influence annual growth ring width, and in some instances, ring number. The magnitude of this influence will vary according to the limiting factors of the site. Prolonged drought is probably the most common climatic cause of dramatic reduction in the effective leaf area of eucalypt trees (Pook 1985, 1986).

For karri an observed correlation between drought events (measured as the percentage deviation from average annual rainfall) and the occurrence of very narrow rings provides a useful sequence when cross-matching tree chronologies. In an approach similar to that described recently by Yamaguchi (1991), Rayner (1991) used the ring widths associated with major rainfall deficits (<75 per cent of average) in 1940, 1959, and 1969 as pointer years when estimating the age of regrowth stems for stem analysis purposes. Meteorological records were less helpful in identifying possible false or additional rings arising from unseasonal rainfall, and for many sites their capacity to assist ring pattern interpretation is limited by the absence of long-term records.

Insect attack

Morrow and LaMarche (1978) demonstrated a strong, long-term suppression by phytophagous insects on ring deposition in alpine eucalypt species. They suggested that natural fluctuations in insect populations may be responsible for much of the variability seen in ring width series of eucalypts, possibly exerting a greater influence than the direct limiting effects of climate.

Mazanec (1989) documented the retarded rate of cambial division, and resulting modifications to the appearance of annual growth rings, of jarrah (*E. marginata*) trees damaged by leafminer (*Perthida glyphopa*). Incomplete or partial rings may affect dating accuracy.

Abbott (1985) listed eight species of leaf eating insects on karri, including species from the *Heteronychus*, *Catasarcus*, *Polyphrades*, *Rhadinosomus*, *Chrysophtharta*, *Paropsis*, and *Uraba* genera. However, little is documented

of the frequency or intensity of defoliation which might result from outbreaks of such insects, and the relative effects (if any) on ring production.

Accuracy of estimating tree age

The effects of each of the above factors on annual growth ring deposition are cumulative, and each interacts with tree age. However, the required level of dating accuracy will depend upon the purpose of the study.

The use of stem analysis for mensurational purposes requires precise estimates of tree age to minimize bias in projection systems developed from the data. Experience has shown that properly conducted visual counts obtained with a x10 magnifying lens, combined with cross-dating, can provide accurate results for dominant trees aged less than approximately 150 years. Rayner (1991) used X-ray techniques to test the accuracy of visual ring counts and found no difference between the number of rings counted with a magnifying lens and the number determined from counted X-ray images. This test also included the comparison of ring counts on trees in stands of known age (Table 1). In veteran trees the relative accuracy of the ring counts is diminished if it is necessary to estimate a portion of the chronology due to the frequent occurrence of rot in the centre of the tree. White (1971) suggested that ring counts on veteran karri trees have an accuracy of ± 5 per cent, but this may be an underestimate on some drier, marginal sites.

In contrast, dendro-climatic or dendro-ecological studies examine the patterns of events, and although accurate annual growth ring chronologies are desirable, they may not be essential. In these instances it is often the relative frequency of events that is important rather than specific dates.

TREE SIZE/TREE AGE RELATIONSHIP FOR KARRI

Tree diameter/age for forest-grown dominants

Knowledge of the relationship between the size of individual, forest-grown dominant trees and their age enables the likely age of a stand to be estimated from diameter measurements of the largest trees in the stand. Tree d.b.h.o.b. is a convenient measure of size which is highly correlated with stem volume and precise for measurement. Records of the variation in tree d.b.h.o.b. across the forest are readily available from inventory databases. Data collected during the estimation of age of regrowth stands (Armstrong 1984), site index (Rayner 1991) and dendrochronology studies in virgin stands (see Appendix II) have been collated to examine this relationship.

Tree diameter exhibited a strong linear relationship with age for dominant seed trees sampled from logging coupes within seven virgin stands (Fig. 2). The seven stands from which the trees were sampled include the range from pure karri to mixtures of marri (*Eucalyptus calophylla*), karri, and jarrah. The linear form of the relationship is consistent with data reported by Banks (1990) for stands of *Eucalyptus fastigata* and *Eucalyptus sieberi* in Glenbog State Forest in NSW.

The considerable variance associated with the relationship for any one forest block in Figure 2 is probably the cumulative effect of inaccuracies in ring counting, the variation in site quality within each forest block, and the differences in age between stands within the one forest. The relationship is therefore imprecise for predicting stand age from the size of the largest trees in the stand without further qualification of the site quality and scale of sampling. It does, however, provide a broad indication of the possible range of stand ages within the virgin karri forest. Few trees in this sample exceeded 250 cm d.b.h.o.b., with the likely ages of the stands varying from approximately 150 to 350 years.

Range of stand ages in virgin old-growth forest

Applying the linear relationship in Figure 2 to the largest trees in the d.b.h.o.b.-class distributions observed in the virgin forest provides an indication of the range of stand ages within these old-growth forests. Table 3 presents the d.b.h.o.b. distributions obtained from Management Level Inventory within virgin old-growth forest (Rayner and Williamson 1984). The stands represented in Table 3 were subjectively selected to include the largest stem diameters observed within the inventory database (Appendix II). Few stands carried trees with d.b.h.o.b. exceeding 250 cm, inferring that the data in Figure 2 are representative of the range of large tree sizes within the forest. On this basis the majority of old-growth stands in Table 3 would be less than 350-400 years of age. These data corroborate an earlier assertion by White (1971) that the majority of the virgin karri stands are aged between 150 and 200 years, although this inference was based more on preliminary growth-rate data than on actual dendrochronological work.

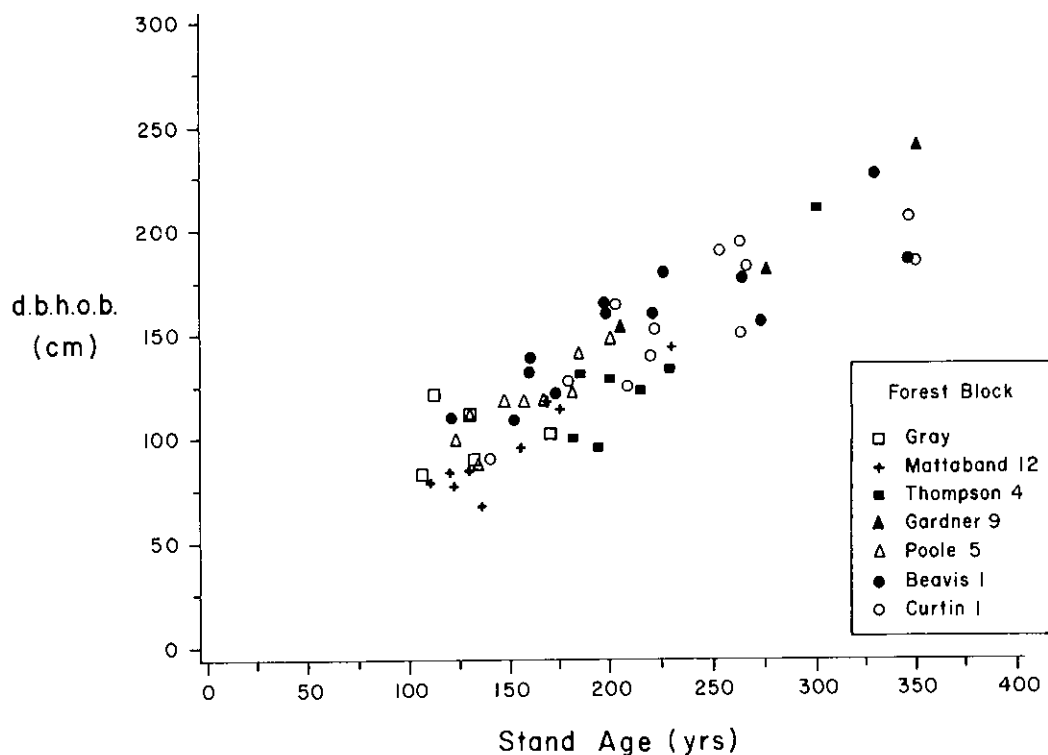


Figure 2

Tree diameter (d.b.h.o.b.) plotted against tree age (annual growth ring counts) for dominant trees (largest 10 per cent) in seven virgin old-growth stands. Karri trees only are shown, although marri occurred in some stands. Data for stands less than 100 years old are not shown.

Table 3

Number of trees per hectare within 10 cm d.b.h.o.b. classes on select transects through virgin old-growth karri stands.
Minimum plot size was 1 ha and only trees larger than 15 cm d.b.h.o.b. were recorded.

Forest Block/ API ^a Stratum	Species ^b	Diameter (d.b.h.o.b. cm) Class MidPoint																									Total Stems Per Hectare	
		25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	175	185	195	205	215	225	235	245	255	305		315
Beavis1 KMA M70	K		3	3	1	2	7	2	1	2		3	3	1	1	1	3	2				1						
	M		6	6	9	4	5	3	2	2	1			1	1	1												
	J							1	1	2	1																	5
Boorara4 KMA M70	K				1	1		1	3	1	1	2	1	1	2													14
	M		2	6	3	5	1	3	3		2																	25
Boorara9 KMA M70	K						1	1		1					1				1	1						1		7
	M				2	1	2	2	1	1			1															10
MKA M70	K		1					3		1		1	1			1		1							1			10
	M		1	2	2			1		2		1			1													10
Carey5 KMA M70	K		1	3	2	2	4	3	7	3	7	4	2	2		1	2	1			1							45
	M		2	2	2	1	2	2	2	2	1		1	1	1	1												15
Carey3 KMA M70	K		1	1	2	2	2	5	3	1	1	2		1				1										22
	M		1		4	1	1		1	2	3	4		1	3	3	1		1		1							26
	J		1		1																							2
Curtin1 KMA M70	K			3	6	7	7	4	6	5	4	2	6	4	1			1										57
	M		8	8	10	6	3	1	2		2	1		1														42
	J			1			1																					2
Curtin3 KA M70	K		3	1	2	3	3	4	1	2	2	3	1	1	2		2		2					1				33
	M		4	7	1	2		1																				15
MKA M70	J				1																							1
	K				4	1	3	1	1			2	1				1	1	1									16
	M		6	5	7	8	1		1			1																29
Deep1 KB M70	K				1	1	1				1	2	1	1	1	1	4	1		1								16
	M				1				1																			2
KMA M70	K				1	5	3	4	3	5	5	4	1	5	1	5	1											43
	M		2	3	4	4	6	5		1	1																	26
Dombakup13 MKA M70	K		2					1						1						1					1			6
	M				2	3	1	2	3	1	1		1											1		1		15
Dombakup16 MKA M70	K		6	9	1	1	1		2	1	5		4	2	4	3	4	2	3	2		1	1					52

Table 3 (continued).

Forest Block/ API ^a Stratum	Species ^b	Diameter (d.b.h.o.b. cm) Class MidPoint																									Total Stems Per Hectare	
		25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	175	185	195	205	215	225	235	245	255	305		315
Dombakup2 MKA M60	K		2	4			2	3	2	1	1	1	1		1		1	1			1							
	M		2		2	3	2	3	3		1	1	1		1							1						
Dombakup5 KMA M70	K		2					1	3	1	2	2	1		1	1	1			2			1					
	M		9	5	2	7	2	5	7	1	4	4	1		3													
Dombakup7 KMA M70	K		3	1		3	2	1	1	2	1				1	2									1	1		1
	M		2	1	1	2		2	1																			
Gardner2 KMB M70	K	1	9	4	1	2					2	1	1	1	1	3	3	1				1		2				
	M			1					1		2		1															
Giblett2 KMA M70	K		2	8	12	13	5	4	3	3	7	5	7	2	4	5	5	4	2									
	M					1			1			1																
Mattaband10 KMB M70	K				2	2	2	1		2	1	2	1		1	1	2	1				1						
	M				2	5	1	1	2	1	1																	
Mattaband11 KA M60	K		2			2	4	3	1	3	4	5	3	3	3	2	4	2										
	M					1	1					1	2															
	BBt		1			1	1																					
Mattaband12 KA M70	K	1		1	2	4	2	1	4	2		1	1	3	1	2	1	2										
	M	1				2																						
Mattaband9 KMA M70	K					3	1	2		2	1		2	3	1	1	2			2	1	1						
	M			1	5	5	2		3	1			1															
Murtin9 MKA M60	K		1	4	2	5	3			1						1												
	M	1	4	2	5	1	2	1	2		1		1			1												
	J		1	2		1																						
MKA M70	K			7	3	3	1		1	2	2	2	3	1			2			2								
	M		4	7	3	3	1		2	1	1	1	1															
Sutton12 KMA M70	K				3	2	1	2	3	2	2	2																
	M		2	7	2	1	5	1	2																			
MKA M70	K	1	3	7		6	2	6	3		2	2			2	4			2									
	M	7	26	16	12	3	8	4	3	3	1		1															

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Table 3 (continued).

Forest Block/ API ^a Stratum	Species ^b	Diameter (d.b.h.o.b. cm) Class MidPoint																												Total Stems Per Hectare
		25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	175	185	195	205	215	225	235	245	255	305	315	355		
Sutton6																														
KMA M70	K			5	6	3	5	2	3	2		4	2	3	1	2	1	1	3											
	M		5	4		7		2	1			1																		
Westcliffe10																														
KA M70	K		2	3	1		1	1	2	4	3	2		1	3	1	3		2	2	1	2		1						
KMA M70	K		2	5		2	3	5	3		2	2	2	5	5	4														
	M			4	1		1		2		1					1														
	J					1																								
Wye2																														
KA M60	K		1	3	6	3	4	3	4	7	6	2	4	1	3	1	3		1											
	M		1	1		2	1	1			2	2																		
KMB M60	K						2	3	1		1	1	2			1														
	M				1	2	1				1																			
KMB M70	K	1	1	1	1	1		1	1	2	2			1	1					1										
	M		1		1																									
Wye6																														
KMA M70	K			1	1	2	3	2	5	3	5	4	5	4	1	2	1	2	1											
	M				8	7	9	5	2		1					1														
	J								1																					
KMB M70	K		2	1	2	3	3	2	1	4	5	2	2	3	2	3														
	M		1		1	3	5	2	1																					
MKB M70	K						2	3	1	1		3	1	1		1		1		1										
	M				3	6	5	8	5	4	2	1																		
	J				2					1																				
II																														
		25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	175	185	195	205	215	225	235	245	255	305	315	355		

^a Air Photo interpretation stratum. Refer Rayner and Williamson (1984).

^b K denotes karri, M marri, Bbt blackbutt, and J jarrah.

Individual trees may attain diameters beyond the range included in the present data. The d.b.h.o.b.'s of the largest trees on record are 362, 355, 318, and 291 cm, but these are unique individuals of exceptional size (large tree register, CALM Inventory, Manjimup). White (1971) suggested that physical maturity of karri trees was probably reached by 250 years and that degrade would be rapid by 400 years.

RANGE IN TREE AGES WITHIN A STAND

Preliminary Studies in two coupes - Beavis 1 and Curtin 1

A pilot study was conducted in 1979 to investigate the range of tree ages within virgin old-growth stands. Three locations within each of two coupes (Beavis 1 and Curtin 1) near Manjimup were selected following logging operations in these mixed karri-marri forests. At each of six locations stem sections were removed from the stumps of 35 trees within a nominal 5-ha area. Each coupe therefore contributed a total of 105 trees. Although each stand carried a mixed karri-marri composition, only karri trees were sampled. The number of annual growth rings, radii to every consecutive 10th ring, and the position of fire scars (occluded charcoal or kino) were recorded (Appendix III).

Spatial data relating the position of each stem relative to its nearest neighbours were not recorded, and because the sample trees were not identified prior to logging it is impossible to conclusively identify which trees comprised the dominant cohort of trees in each d.b.h.o.b. size class. Unfortunately, comprehensive cross-matching of ring patterns between trees was not performed.

These omissions severely limit the direct comparison of tree ages within each sample location, as anomalies owing to overwood suppression, climatic perturbations (droughts), insect attacks, and possible post-fire growth pulses are complexed in the data. Nonetheless, a tentative indication of the range of trees ages within the stands was obtained by reworking the raw data in the manner described in Appendix III.

The range of tree ages within a stand results from regeneration events, the primary source of which are fire events of sufficient intensity to bare the soil in a seed-bearing year. Table 4 presents the approximate years of tree establishment and fire scarring events estimated from the ring counts of trees at each site. Although the dates are approximate, some confidence in the ring counting and dating for at least the last 50 years for trees in Beavis is provided from the coincidence in select trees of fire scars dated as 1961, a year in which Forests Department fire records indicate that this forest was burnt.

The chronologies suggest that a multi-aged forest structure occurred at each site. However, the effect of scale on the interpretation of pattern in structural diversity must be qualified when interpreting Table 4 (West 1984; Bradshaw 1992). The chronology presented for each site is an aggregate from 35 trees randomly selected over an area varying from 3 to 6 ha.

Considerable spatial variability in gap size would have existed, and at a smaller scale of, perhaps, 0.5 ha only a portion of the fire and regeneration events recorded for any particular site may have occurred. Unfortunately, the absence of further information on the exact position of the trees relative to one another and the lack of cross-dating of the original ring counts, precludes further analysis of pattern and frequency at these smaller scales.

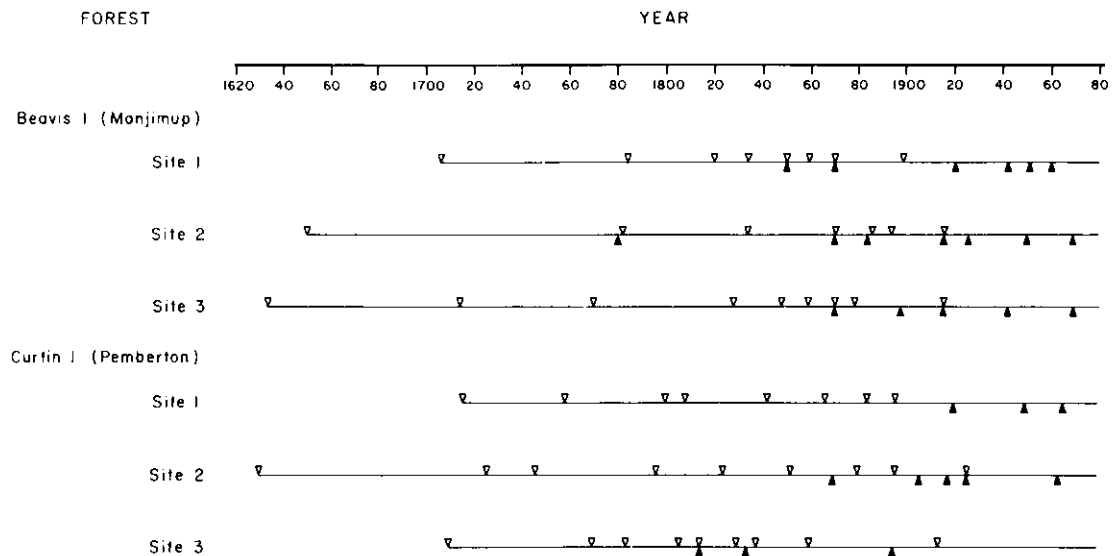
Information on the relative frequency of stem numbers in each age class is necessary to interpret the relative importance of the regeneration events. The chronologies could be interpreted, for example, to indicate an old, even-aged stand breaking down over time with mild fires generating intermediate age classes. There would be relatively high numbers of trees in the old age classes if this were the case. Alternatively, fewer regeneration events may have created 'cohorts' of even-aged regrowth resulting from the passage of high intensity fires. Unfortunately, the sampling framework does not enable the derivation of d.b.h.o.b. class frequency distributions from the raw data. Similarly, the absence of regeneration events recorded on each site since the early 1900s is probably an artifact of the sampling method: most smaller stems in the stand would have been removed or smashed during the logging operations.

The correlation between fire scars and some tree establishment events listed in Table 4 infer that fire events were a source of regeneration (e.g. 1780 and 1870 in Beavis 1). However, the almost complete absence of fire scars recorded pre-1850 at each site is difficult to interpret. Given the rate of fuel accumulation recorded in old-growth karri stands (Grove and Malajczuk 1985) and the periodic occurrence of lightning strikes during summer thunderstorms within these forests (Churchill 1968; Underwood 1978) it would seem highly unlikely that fire-free periods of up to 220 years (Beavis 1 Site 3, Curtin 1 Site 2) would have actually occurred. A possible reason for the low frequency of fire scars recorded for pre-1850 might be that the few large, old trees included in the sample at each site had simply escaped scarring because of limited fuel in their vicinity.

Alternatively, the presence of fungal decay in the centre of sections from many of these larger trees may have obliterated any evidence of fire scarring in the younger years of the tree. The most probable reason, however, is that

Table 4

Chronology of tree establishment (Δ) and fire event (\blacktriangledown) years for six sites in virgin old-growth karri forest. Dates for each site are approximate (determined solely from ring counts) and represented an aggregation of 35 trees from a nominal 5 ha area. Within each forest, the stands were located 1-3 km apart.



frequent, low intensity fires occurred which did not cause scarring above stump height. Christensen and Annels (1985), for example, suggest that fires were relatively frequent in the karri forest. Based on the fire survival adaptations of the forest flora and fauna they inferred that fires of comparatively low intensities occurred in most vegetation types at intervals of between 3 to perhaps 10 to 20 years.

The relative frequency of fire events is of considerable management importance. However, dendrochronological data can rarely provide a complete picture of fire frequency as not all fires will be of sufficient intensity to inflict scarring on surviving trees. The sensitivity of the lower bole of a tree to fire scarring will vary with such factors as tree size, proximity of fuel to the lower bole, the time since the last fire and the amount of fuel consumed (Burrows 1987). For example, Bell *et al.* (1989) suggest that fire intensities below about 600 kW m⁻¹ are unlikely to inflict cambial damage on single stems of jarrah, while large trees might tolerate intensities several times this level without experiencing bole damage. Karri has thinner bark than jarrah and is therefore more susceptible to thermal damage at an equivalent level of fire intensity (McCaw 1986). Table 4, for example, suggests that the fuel reduction burns undertaken in Beavis 1 during 1961 and 1969 were of sufficient intensity to induce fire scars on some trees. As well, historical fire frequency data will vary with the scale of the area being investigated, as local changes in topography, fuel accumulation and fire ignition probability may occur over short distances in these forests.

Although fire intensity may not be sufficient to induce scarring on boles, depending upon the quantity of fuel consumed and nutrient mineralization a 'growth pulse' may be evident from an increase in ring width following a fire (Banks 1982). Ash bed effects have been demonstrated to markedly influence karri growth (Loneragan 1961; Loneragan and Loneragan 1964; Grove 1987), and it is likely such pulses may be observed in karri ring studies. Such pulses provide a further pointer when cross-dating to improve chronology accuracy, and their detection and sequencing in the data for Beavis 1 and Curtin 1 would have greatly assisted the interpretation of stand history for these forests.

Factors influencing the range in tree ages within other virgin stands: an interpretation

The species composition of virgin karri stands ranges from pure to mixed karri in varying proportions with marri, jarrah and other species. The present distribution, species composition, and their spatial extent have been determined by a complex interaction of climatic and edaphic factors (Loneragan 1961; Churchill 1968; McArthur and Clifton 1975; Beard 1981; Bradshaw and Lush 1981; Churchward *et al.* 1988; Inions 1990). The current age and species status within any stand will, however, be an historical artifact of a series of such interacting events as storm, insect or pathogen attack, but most commonly fire. In particular, the frequency of regeneration events and the gap structure of the stand existing at that time will determine the relative success of seedling development through to maturity following germination.

The complex interaction between fire frequency and the phenological cycle of karri (which is climate dependent) suggests that no single age distribution of trees within a stand would be representative of the entire virgin forest. The data for Beavis 1 and Curtin 1, for example, were obtained from mixed karri-marri-jarrah stands which were among the oldest sampled to date, suggesting that younger stands may have fewer age classes within them.

The species composition, area, and age structure of virgin karri stands can change rapidly over short distances in response to changing edaphic, topographic, and climatic influences. A mosaic of stand and tree ages therefore exists, and the interpretation of pattern depends upon the scale of observation. The accurate interpretation of any forest therefore requires sufficient spatial data to interpret gap dynamics and hence patch size.

Massive conflagrations originating from summer lightning events have been proposed as the likely origin of many of the virgin even-aged stands which pre-date European settlement (White and Underwood 1974). The area of such stands will reflect the fuel and fire conditions prevailing at the time, as well as the availability of seed in the karri overstorey (Loneragan 1979).

The area of predominantly even-aged stands regenerated by a wildfire event may vary from tens to thousands of hectares. Where a wildfire was of sufficient intensity to kill all overstorey trees, a completely even-aged regrowth stand would develop, as in a 10 ha stand regenerated in 1854 in Warren Block or a 30 ha stand regenerated in 1852 in Carey Block. Typically, however, a proportion of the overstorey survives to persist as severely fire-damaged veterans among the resulting even-aged regeneration. Stands carrying this structure, and exceeding 1000 ha in extent, date from the 1937 and 1951 wildfires in the Walpole region. In contrast, limited regeneration established among surviving old-growth stems following a wildfire in the Brockman National Park in 1985, partly because of the limited availability of seed in the overstorey during that year.

Where a second age class establishes among the older stems the subsequent development of the younger trees would depend upon the gap structure and size of the older trees. Over time, several age classes may have developed in a stand but the ability to accurately determine tree age/regeneration dates from ring counts of the trees within the stand will depend upon all the factors previously listed.

FUTURE INVESTIGATIONS

Dendrochronology and stem analysis provide efficient, cost effective means of gathering growth data and of reconstructing stand histories. Properly conducted dendro-ecological studies can provide considerable information on

the historical frequency of stand disturbances arising from both natural and anthropogenic causes. The development of accurate annual growth ring chronologies can also assist the interpretation and validation of generalized growth and yield models for all stand structural types.

The integration of each of these data requirements within future studies requires prior consideration of the following factors.

Sampling

Future dendrochronological work in karri must incorporate the measurement of spatial data to assist the interpretation of stand dynamics. The location of all species on a site, including woody understorey species, should be mapped, and crown mapping is particularly informative. Photography augments interpretation and provides an invaluable historical record of stand structure at the time of felling. At the least, a sample of all species should be dated, particularly the marri component in mixed stands. Accurate ring counts of marri within regenerated 55-year-old karri-marri stands have been obtained (Rayner, unpublished data).

Where definition of the range in tree ages is a primary objective of the study, sample trees must be selected prior to felling. Preliminary stand mapping and analysis of gap size in old-growth stands provides an indication of likely dominants in each size class. Inspection of candidate sample trees prior to felling is also necessary to detect visible evidence of past suppression or abnormal crown history. Full stand enumeration within defined boundaries is necessary to enable the relative frequencies of each species within size classes to be computed and used in the interpretation of stand history.

Even when the determination of stand age is the primary objective, consideration should be given to collecting additional data on tree attributes of likely interest for other values, such as the frequency and size distribution of nesting-hollows for select fauna species.

Measuring and annual growth ring counting

The preparation of accurate annual growth ring chronologies requires strict adherence to proper measurement technique. Cross-dating of sample trees, which involves both ring counting and ring-width pattern matching, is essential. The identification of specific pointer sequences such as narrow drought rings provides a means of obtaining consistent dating between workers over time. The possibility of false and partially complete rings in some karri sections means that where possible stem cross-sections should be intact and the entire surface of the section should be planed and counted in preference to simply planing and counting on select stem radii.

A major constraint on comparing the accuracy of data collected in different studies has been the absence of master chronologies for the species concerned. Greater emphasis must be placed on the development and subsequent publication of master chronologies for these species.

ACKNOWLEDGEMENTS

The data presented herein were collected by various research and inventory officers of the former Forests Department and the present Department of CALM. They include Messrs Annels, Armstrong, Breidahl, Rayner, Rotheram, and Schuster. I thank F.J. Bradshaw, P. Hewett, L. McCaw, G. Wardell-Johnston and Drs P. Christensen and J. Banks for helpful review comments on the manuscript. Paul Davies prepared the final copy of the figures and Leanne Kingston typed the manuscript.

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Appendix I

Stem analysis data used for determining the accuracy of tree age estimations

Data type:	Stem analysis of trees in regrowth and old-growth stands.
Purpose:	Stand age estimation for development of site index relationship, tree taper and volume function calibration, and stand volume estimation.
Study Location:	Throughout the karri zone. Rayner (1991) details the complete sample framework.
Date of collection and officer responsible:	1916-1978 (various), 1979-1981 (Rotheram), 1982-1983 (Armstrong), 1984-present (Rayner).
Method of ring counting and dating:	
Pre-1984	Visual counts with hand lens on entire planed surface. Three independent assessors.
Post-1984	Visual counts with hand lens on entire planed surface. Three independent assessors. X-ray testing of accuracy of ring counts. Cross-matching performed for three sample trees per site using fire and drought pointer years.
Present analysis:	d.b.h.o.b. and total tree age data extracted for each tree, stand site index computed using formulation in Rayner (1991).

Appendix II

Inventory data used to investigate the range of stand ages in virgin old-growth jarrah

Data Type: Management Level Inventory of old-growth stands.

Purpose: Stand volume estimation for harvest planning.

Study Location: Throughout karri zone.

Date of collection and officer responsible:

1973-1985 (Inventory Branch).

Present Analysis: d.b.h.o.b. distributions extracted within Aerial Photo Interpretation strata for virgin stands. Site representation was arbitrarily selected to ensure the geographic and age range was represented. Emphasis in the selection was to include the largest trees observed in the database for the area. Girth and imperial values were converted to metric d.b.h.o.b. for ease of comparison. Frequency distributions standardized to a per hectare basis for each sample line and tabulated by forest strata.

Appendix III

Analysis of dendrochronology data collected in Beavis 1 and Curtin 1 forest blocks

- Data Type: Annual growth ring counts of trees sampled from two old-growth stands.
- Purpose: Estimation of the range of tree ages within a stand.
- Study Location: Beavis 1 and Curtin 1.
- Date of collection and officer responsible:
1979 (Schuster).
- Method of ring counting and dating:
Visual ring counts along three radii by three independent assessors using a hand lens.
- Present analysis: Each location (35 trees) was examined separately. Stump height varied from 0.5 to 1.1 m. D.b.h.o.b. estimates were derived from the stump diameter measurements using taper functions derived by Rayner (unpublished) while d.b.h.o.b. values (for direct comparison with data presented in Figure 2 (p. 8) and Table 3 (p. 9) were derived from regression relationships in WAFD (1981) and WAFD (1983). Tree dominance or vigour class was inferred from the diameter measurements relative to trees of comparable age (number of rings) within each location. Some calibrating of counts was possible using fire scar records for the various sections.
- A number of large veteran trees lacked a solid core, necessitating proportional estimation of tree ages for missing sections. It is likely in some instances the accuracy of the counts for such veterans may exceed the figure of ± 5 per cent suggested by White (1971).

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