Age structure of the karri forest: 1. Defining and mapping structural development stages

F.J. Bradshaw and M.E. Rayner

Department of Conservation and Land Management, Manjimup, Western Australia 6258

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Summary

Even-aged stands of karri (*Eucalyptus diversicolor*) develop through distinct stages of development - *Establishment, Juvenile, Immature, Mature* and *Senescent.* This paper describes a study in which *Immature, Mature* and *Senescent* stages were interpreted from aerial photography. The age range of these stages was estimated by sampling diameters of dominant trees for which regressions of diameter and age had been established. The stage and age of uneven-aged stands was based on the biologically dominant cohort - the oldest cohort with a crown cover exceeding 25%. The results confirm that broad structural development stages can be mapped from API, and that the stages, defined from stand dynamics and silvicultural characteristics, correlate well with the age of the dominant cohort. Data for stages derived from interpretation and from historical records were combined to produce a map of development stages for the karri dominant forest in the south west of Western Australia. This was part of a broader study to model the development of forest age structure into the future.

Introduction

Karri (*Eucalyptus diversicolor* F. Muell.) occurs as a dominant tree in tall open (wet sclerophyll) forest in the extreme south west of Western Australia. As one of the tallest hardwoods in the world, its spectacular size and relatively limited distribution give it considerable value for recreation and conservation as well as for its timber resource and associated industry. Approximately half of the publicly owned forest is available for timber harvesting and the other half is managed for nature conservation. Almost all of the public forest is managed by the Department of Conservation and Land Management (CALM 1992).

One of CALM's management objectives is the maintenance of an appropriate representation of each of the recognisable stand development stages of the forest (CALM 1992). This is required in the context of both sustained timber production and sustained habitat representation. The objective applies to the whole public forest, regardless of tenure and land use.

To meet this objective requires a knowledge of the present distribution of stand development stages, their age and the way that they might change over time. This study was undertaken in two parts. Part 1 reported here describes the factors influencing the distribution of the karri forest, its response to fire disturbance, the characteristics of the structural development stages, and the techniques used to map those stages. We

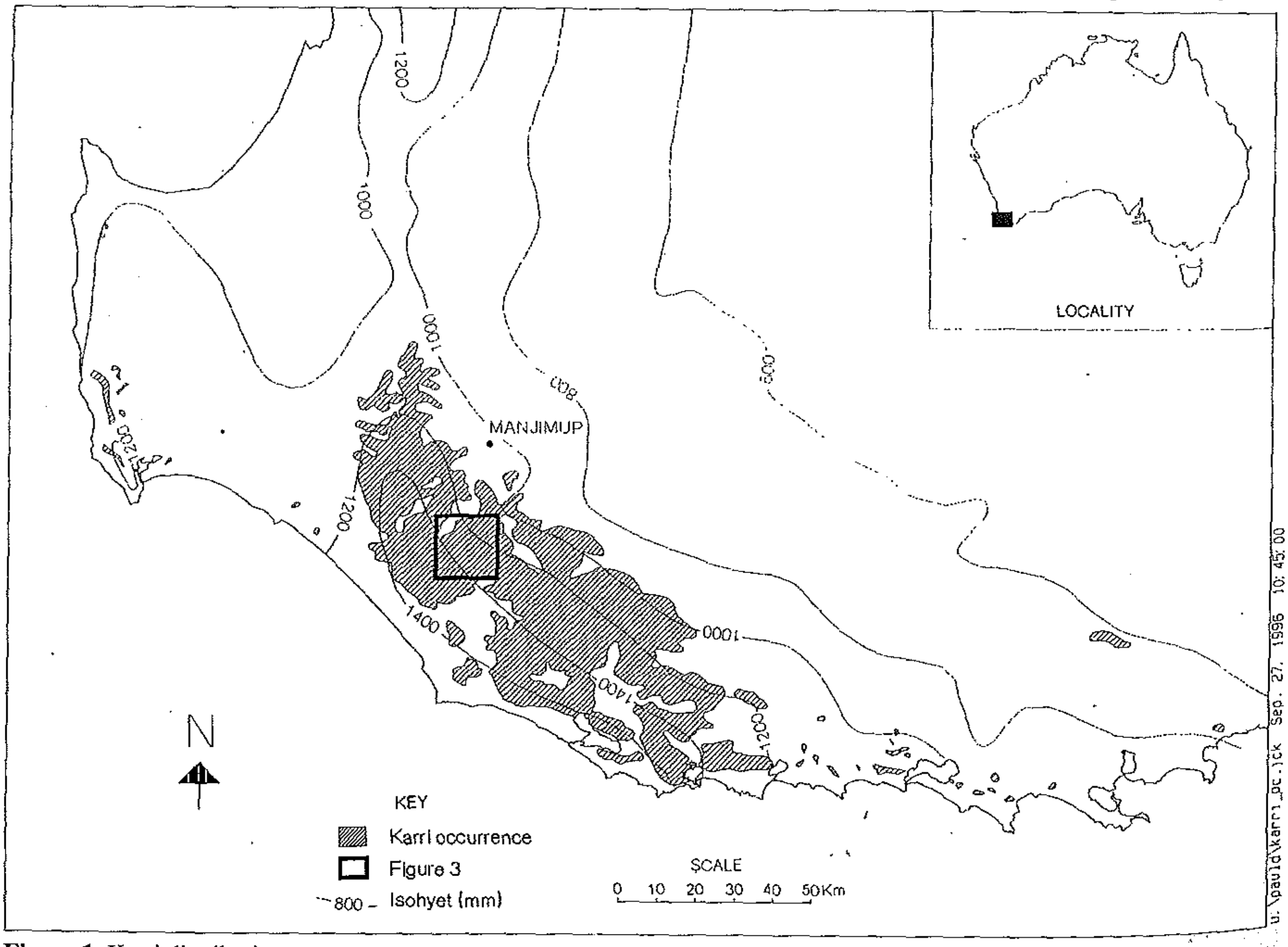

Figure 1. Karri distribution

confirm the relationship between age and development stage and map the location of the existing stand development stages in the main karri belt. Part 2 of the study (Bradshaw and Rayner 1997b) estimates the present age distribution of the forest, makes a projection of age and development stage into the future and considers the implications for management.

Background

Description of the karri forest

Karri occurs in three broadly discrete areas - the 'main karri belt' and two outliers on the west and the south coast (Figure 1). The climate is distinctly Mediterranean and the forest occurs generally in areas that receive 1000 to 1400 mm of annual rainfall with a summer (driest quarter) rainfall exceeding 70 mm per month.

Within the climatic zone suited to karri, distribution is determined by soil type (McArthur and Clifton 1975, Bradshaw and Lush 1981). Karri occurs within a mosaic of other forest types and, within the main karri belt, karri dominant forest occurs in more than 2000 discrete patches, 30% of the area occurring in patches of less than 100 ha. Karri commonly occurs in mixture with marri (*Corymbia calophylla*) and less commonly with jarrah (*E. marginata*). In the southernmost part of the distribution it also occurs in mixture with red tingle (*E. jacksonii*) and yellow tingle (*E. guilfoylei*) (Wardell-Johnson and Coates 1996).

Although it is a wet sclerophyll forest there is an absence of the cool, temperate rainforest elements common to many wet sclerophyll forests of the east coast of Australia (Ashton 1981, Christensen 1992).

The Mediterranean climate of the south west ensures that weather conditions conducive to fire occur every summer. In the driest part of the year, when the Soil Dryness Index (Mount 1972) exceeds 50, there are approximately 110 rain-free days. This contrasts with about 165 rain-free days for the dry sclerophyll jarrah forest and about 80 rain-free days for the wet sclerophyll *E. regnans* forest in Tasmania. McCaw [1] (unpublished data) suggests that ignition is possible on about 70 of the 110 rain-free days in the karri forest.

The present age distribution reflects natural disturbance events such as fire and cultural disturbances such as harvesting and abandoned agricultural clearing. Harvesting began in 1913 in the main belt using at different times both clearfelling and group selection systems (Bradshaw and Lush 1981).

This study applies to the publicly owned karri dominant forest within the main karri belt (138,000 ha) of which 63,000 ha is virgin forest. (Virgin forest is unlogged but has had a history of fire disturbance of varying frequency and intensity.)

Stand development stages

The maintenance of an appropriate representation of development or seral stages is a common requirement in forest management plans and is seen as one means of providing and maintaining a broad level of diversity throughout the forest. In the absence of detailed knowledge about the relationships between these stages and other organisms, it can act as a surrogate for bio-diversity - the 'coarse filter' approach (Harris 1984, Hunter 1990). To be useful for this purpose, development stages need to have easily recognised and quantifiable physical attributes that facilitate mapping. They also need to reflect the dynamics of the stand throughout its life, and should be relevant to habitat requirements.

Even-aged stands of karri develop through several distinct stages from establishment to senescence and therefore fit the first two of the requirements mentioned above. Although these stages describe key structural changes in the forest we make no assumptions concerning specific habitat which may be associated with these stages. Our purpose is to provide a spatial and a temporal framework on which any of these particular values may be extrapolated from the stand to the forest as a whole.

Five development stages are recognised in the overstorey of even-aged karri forest (CALM 1992). These are the *Establishment, Juvenile, Immature, Mature* and *Senescent* stages. These are described in detail in Appendix 1.

The role of fire in stand initiation and structural variation

The establishment stage of karri begins with disturbance, usually fire, that exposes mineral soil and provides the opportunity for germination. Regeneration will occur if seed is present at the time of disturbance and will persist if there is vacant space in the canopy of sufficient size to allow it to become established (Breidahl and Hewett 1995). Large gaps will give rise to even-aged stands which will develop through the distinct stages described in Appendix 1. Progression through the whole series of stages will only occur where there is no significant subsequent disturbance to the overstorey during this period. Such a situation would be rare since most stands will have been affected by fire, the most common form of disturbance, to some degree during that time.

Fire may result in a number of different outcomes. If it is severe it may kill a large proportion of the overstorey, truncating the cycle and providing the opportunity for regeneration. The regenerating patch size will vary widely depending on the severity of the disturbance and the development stage (and hence fire sensitivity) of the stand. Following intense wildfires a substantial proportion of the overstorey may be killed and patches of regeneration will be larger and more frequent. While stand-replacing fires do occur, the large contiguous areas of many hundreds or even thousands of hectares described for many conifer forests of north America or the Mountain Ash in Australia (Attiwill 1994) are not observed in karri forest. Severely affected areas of several hundred hectares are known, although totally single-aged patches of greater than twenty hectares are uncommon. Observation suggests that a single severe fire event will seldom cause complete stand replacement, though it may result from multiple severe fire events.

Milder fires produce smaller gaps in the original canopy, as will other disturbances such as storms or simply old age, even down to the loss of a single tree. Very small gaps are unlikely to regenerate successfully unless the surrounding overstorey trees have reached maturity and are no longer able to extend their crowns to occupy the vacated site. Where small patches are occupied with a new cohort of regeneration, a multi-aged stand is produced and the structural phases described in Appendix 1 become somewhat blurred and overlapping (Mackowski 1984).

[1] L. McCaw, Department of Conservation and Land Management, Manjimup, WA.

Further complexity will develop where karri grows in mixture with other tree species. Since all of these species are periodic seeders, regeneration will tend to favour the species that is most heavily in seed at the time of the fire. Two associated species, jarrah and marri, are also capable of regenerating via a lignotuber (Jacobs 1955) which gives them an added advantage, especially in areas where fire is more frequent and less intense. In this study we have confined our attention to those forest types dominated by karri.

Fire in the understorey

The karri forest understorey is dominated by legumes. Almost 90% of the shrub cover is made up of fire sensitive species that regenerate from seed. The remaining 10% are fire tolerant sprouters (Christensen and Kimber 1975). Common species include *Trymalium floribundum, Bossiaea laidlawiana, Acacia urophylla, Chorilaena quercifolia,* with *Acacia pentadenia, Lepidosperma tetraqetrum* and *L. effusum* in southern parts of the forest (Christensen 1992). At any one site, only one or two species predominate. The understorey shrub layer is dense and may reach a height of about 5 metres.

Fires initiate a new succession in the understorey. This event, however, is repeated much more frequently because while most fires will not kill the overstorey almost any fire is intense enough to kill the understorey shrub layer and initiate another shrub cycle. Thus there may be many independent and variable cycles of understorey development during the life of the overstorey. It is possible therefore to have a 'regrowth' overstorey associated with an 'old growth' understorey and vice versa. For many vertebrate and invertebrate forest species the understorey development phase will be more important than that of the overstorey (Christensen 1992).

Christensen and Annels (1985) suggest that natural fire frequency in the karri forest may have been relatively high, in the order of 20 years, based on the species composition of the understorey, the absence of late successional mammal species, the incidence of lightning strikes (Underwood 1978) and the use of fire by Aborigines (Hallam 1975). However the observations of early settlers and explorers suggest that this frequency was also very variable (Talbot 1973).

The varied intensity of the fires will also have very different impacts on the forests. While fire at 250 kW/m will burn the litter and understorey, 5,000 kW/m may kill some trees and extreme fire intensity of 60,000 kW/m will kill all trees (Underwood and Christensen 1981).

Other factors have influenced fire frequency and intensity in more recent times though it is not clear to what extent. These include the burning practices of early European settlers in the latter part of last century when they regularly fired the forest between their inland farms and their coastal grazing leases; the cessation of Aboriginal burning from about the same time; and the introduction of both fire suppression measures and prescribed burning (to any significant extent in the karri forest) from about the 1960s.

Method

Defining a stand

Broadscale mapping of development stages within the forest required us to define the minimum patch size to be recognised and mapped as a stand, and to identify the cohorts to be recognised in mixed age stands.

Two hectares was selected as the minimum patch size for classification as a separate stand. Patches of this size are sufficient to contain about 50 mature trees. This was consistent with the patch size recognised for species and structural delineation first mapped from 1:15,840 air photo interpretation (API) in the 1960s (Bradshaw *et al* 1997), and was subsequently adopted as the base resolution of the data in CALM's raster-based GIS database. It is also the minimum area that is mapped and managed as even-aged forest in routine forest management.

Because most stands are not totally even-aged, but may have two or more cohorts of different age constituting different proportions of the stand, stands were classified according to the development stage and the age of the oldest dominant cohort. This required a definition of structural dominance.

Rotheram (1983) determined the magnitude of the influence of dominant mature karri trees on regrowth and concluded that evenly distributed mature trees with a crown cover of 20% would effectively dominate the site, causing some suppressing effect on all of the regrowth. Alternatively it has been suggested that the site is dominated at 30% of gross potential crown cover, that is, at about 25% crown cover in tall open eucalypt forest (Institute of Foresters of Australia 1991). This is similar to the level suggested by Woodgate *et al* (1994 p 61). In this work we have selected 25% crown cover as the level at which it may be said that the oldest cohort dominates the stand and as such would be the cohort that represents the age of the stand. This is the 'dominant' cohort. Younger cohorts with more than 25% crown cover have the potential to dominate the stand in the future and are considered 'significant' cohorts. Cohorts representing less than 25% crown cover were not considered for stand ageing purposes.

Mapping stand development stages

Mapping karri development stages involved three sources of information: records of harvesting, air photo interpretation from previous projects and air photo interpretation designed specifically for this project.

The extent of even-aged regeneration originating from harvesting, abandoned farmland and wildfire from 1875 to the present was already recorded in CALM's GIS database. These records were based on routine monitoring of regeneration operations, aerial photo interpretation (Armstrong 1984) and ring count sampling of some older stands. In these datasets regrowth was defined as even-aged if the veteran overstorey was less than 15% crown cover. Veteran overstorey up to this level was common in stands regenerated until about 1970 after which time silvicultural practices resulted in more uniform stands. This mapping therefore covered almost all of the areas dominated by cohorts in the establishment, juvenile, and immature stages of development.

New aerial photo interpretation was undertaken over the remaining areas of karri forest to delineate the mature and senescent stages and any immature stands that may not have been detected in earlier mapping. Both virgin and previously logged stands were interpreted in this way; 1993 colour print photography at a scale of 1:25,000 was used for the interpretation. This scale and format provided adequate definition of patch and crown size but limited definition of individual crown condition.

Stands were categorised according to the 'dominant' cohort i.e. as either Immature (I), Mature (M) or Senescent (S). The actual crown cover of the cohort was interpreted and recorded in 10% classes. The size of the patches of different stages that were discriminated was typically about 10 ha.

Immature stands were recognised by the size (< 20 m diameter) and the texture of the individual tree crowns. The distinction between mature and senescent stages based solely on crown degradation proved too subjective and unreliable. Senescent stands were therefore defined as those in which stand decline had reached the point where gaps had developed in the original canopy and provided the opportunity for regeneration to persist. This definition has the advantage of representing a distinct structural change in the stand that is more objective and recognisable. The senescent category therefore includes stands where the original canopy is declining due to old age as well as some stands where the crown degradation and reduction in site domination is due to severe fire damage of a younger dominant cohort.

Field reconnaissance undertaken during the program enabled photo interpreters to calibrate their interpretation. The interpretation data was entered into the GIS database and cross-checked where appropriate against the structural mapping of the 1960s aerial photo interpretation (API) and other related map themes (Bradshaw *et al* 1997).

Ageing of the dominant cohort

Various options were considered to estimate the age of the dominant cohort in a stand, all of which involved the selection of sample trees and determination of their age by counting the number of annual growth rings. The most reliable method to determine the range of tree ages in the dominant portion of the stand would be to fell and ring-count all dominant stems, but the logistics and destructive nature of such an approach precludes extensive use. Sampling stem cores to age the trees was rejected due to the inherent difficulties in ensuring the centre rings are adequately sampled on trees of this size and that false rings are properly detected on very small sections from large trees, and because of the difficulty of coring large hardwood trees.

An indirect approach was adopted in which a tree diameter / tree age relationship was used to estimate tree age within stands. Previous work (Rayner 1992a) had shown that the relationship between diameter at breast height and age was strongly linear for dominant trees within unlogged stands, and that the slope of the relationship would vary across site qualities. This work extended the previously published relationship by determining the effect of site quality on the tree diameter / tree age relationship. This relationship for dominant karri was then used to estimate the age of sample trees in significant cohorts across each of the photo-interpreted development stages.

Determining the tree diameter / tree age relationship

Tree diameter / age data was available for 27 trees from earlier studies (Rayner 1992a). Twelve further sample stands (all previously unlogged) were selected to ensure that the range in geographic location, site variation and development stage within the unlogged forest was adequately represented. Within each stand at least three mature, dominant karri trees, including the tree of largest diameter, were felled after recording the tree diameter and bark thickness at breast height, total and bole height, crown width and condition.

Tree age was determined by counting the annual growth rings under a hand lens (x 10 magnification) on an intact, whole breast-height section. The ring counting on planed, moistened, whole stem sections was cross matched for sequences within a site to help correct for false or missing rings. Adjustment was made for age to basal section, assuming the trees grew 1.3 m by age 2; and where rot or hollows made ring counting impossible the distance from solid wood to the estimated tree centre (cm) was recorded for later adjustment of age. The total number of tree rings and periodic 5-yearly diameter, was recorded. Measurements were taken along a radius at breast height.

Table 1 provides details of the sample trees in the combined dataset used in this study. The range in tree diameters within this sample covered the range of sizes recorded during routine inventory of the mature virgin (unlogged) karri forest (see Table 3, Rayner 1992a). The oldest karri tree sampled was estimated to be 350 years, with an overbark diameter at breast height of 240 cm.

Each tree was allocated to one of three site quality classes on the basis of total tree height. The classes used were API classes because these provided a pre-existing mapped basis for extrapolation of results (Bradshaw *et al* 1997). The three classes were KA (> 50 m) KB (40-49 m) and KC (<40 m), but the small number of observations in KC class meant they were combined with KB to make two site categories only in subsequent analysis. Where senescent trees had had their crown broken out, an estimate of their former mature height was required to determine site potential. In these instances the site potential was allocated on the basis of the mean height of the mature dominant trees measured for that area during previous routine inventory.

Sampling for the age of the significant cohorts

A stratified random sample of plots was established in stands across the geographic range of the mapped categories (Immature, Mature and Senescent) within the main karri belt. At each sample site, three dominant or codominant trees within the dominant cohort (i.e. the oldest cohort occupying at least 25% crown cover) were randomly selected and measured for tree height, crown class and breast height diameter. Site class (API) and the derived Site Index (Rayner 1991) were also recorded. Individual tree ages were then calculated using the diameter/age relationship for dominant trees and the three ages averaged to determine stand age. In a similar fashion, the age of any younger significant cohorts with the potential to occupy the site in the future (crown cover 25% or more) under the dominant cohort was also determined. These could not be identified during the interpretation if the two cohorts were from the same development stage.

Table 1. Minimum-Mean-Maximum values of tree attributes for the combined dataset used in deriving tree diameter / tree age relationship for karri. d denotes diameter at breast height over bark, h denotes total tree height.

Site Class	n	d (cm)	h (m)	Tree Age (Years)
KA	35	88 - 159.5 - 245.1	50.5 - 61.1 - 76.0	131 - 220 - 350
KB	23	68 - 101.8 - 152.5	40.0 - 45.0 - 49.5	106 - 149 - 230

Table 2. Minimum-Mean-Maximum values of stand attributes for stands sampled to determine the age of the oldest dominant cohort within each development stage. Stands were karri dominant, but may contain up to 50% by stocking of other tree species. d denotes diameter at breast height over bark, H denotes stand top height.

	Dominant cohort only			
Development Stage	n	d (cm)	H (m)	Stand Age (years)
Immature	27	21.7 - 63.2 - 99.8	33.6 - 44.1 - 68.1	23 - 68 - 112
Mature	62	75.6 - 138.0 - 216.0	28.1 - 56.5 - 75.9	108 - 184 - 283
Senescent	32	130.1 - 206.4 - 307.0	36.2 - 57.5 - 77.2	178 - 291 - 378

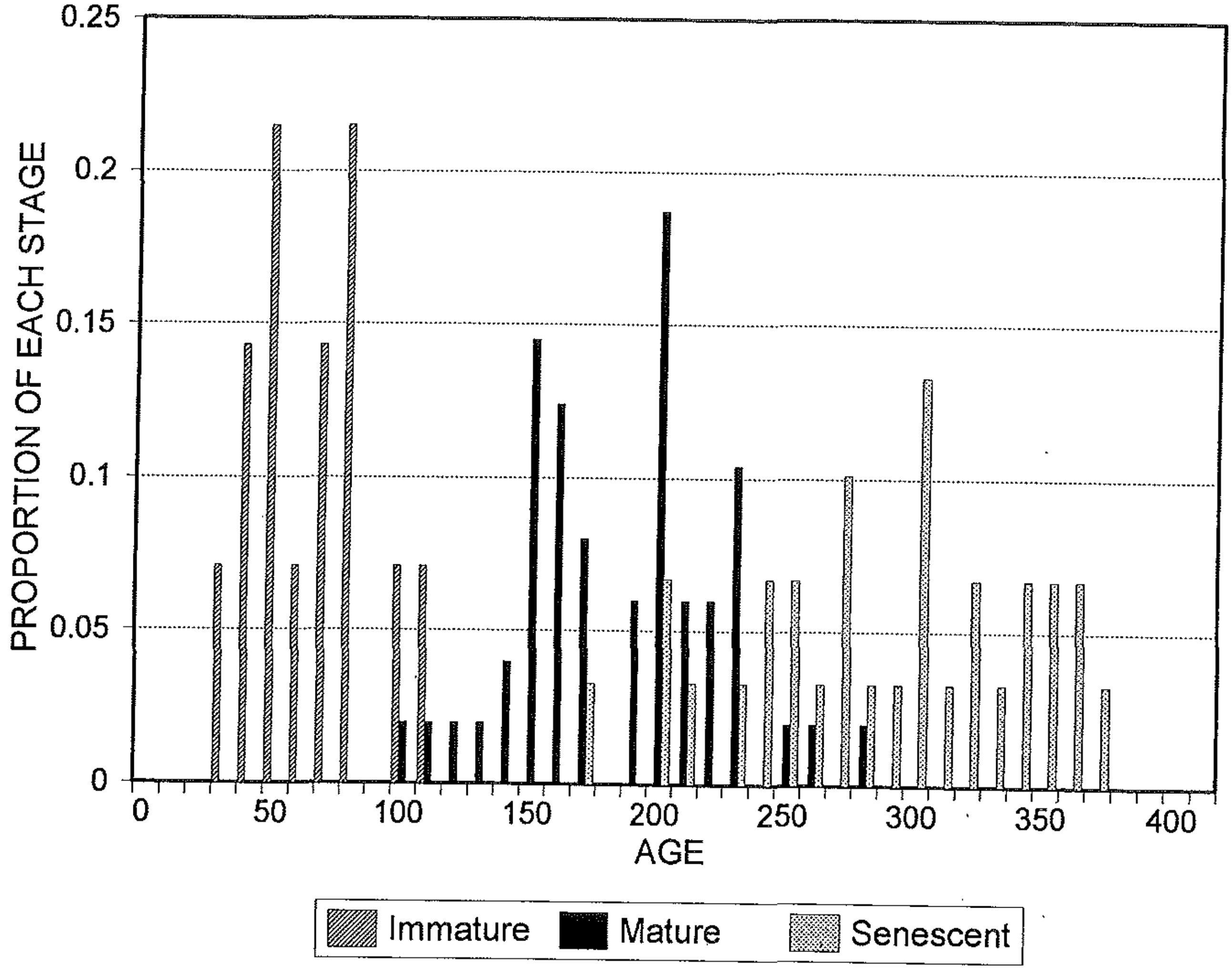

Figure 2. Sampled age distribution within each interpreted development stage in virgin forest.

Results

Age/size relationship for dominant trees

Graphical analysis of the diameter versus age relationship for each site class confirmed the linear relationship for trees older than approximately 50 years. Previous work had demonstrated the non-linear nature of the relationship for younger ages, and it was therefore decided to restrict linear regression analysis to trees older than 50 years. Linear regression confirmed that the slope of the linear relationships differed between site classes. The following transformed versions of the regressions were used to estimate tree ages:

age = (d - 26.2) / 0.61 for dominant trees in KA sites [1]
{ $n = 46, R^2 = 0.68, MSE = 25.5$ }

$$\text{age} = (d - 42.8) / 0.4 \quad \text{for dominant trees in KB sites [2]}$$
$$\{ n = 21, R^2 = 0.49, MSE = 14.4 \}$$

Due to the possibility of changing dominance during the period of strong competition, equations [1] and [2] may underestimate tree age to a small extent. Estimates of tree age from tree diameter for trees less than 50 years were made using an adjusted form of equation 6 in Rayner 1992b.

Age of development stages

Table 2 summarises the range of stand parameters measured within the sample.

Estimates of the age of the dominant strata ranged from 23 to 112 years for stands interpreted as Immature, 108 to 283 for Mature stands and 178 to 378 for Senescent stands. These estimates are generally within the age ranges anticipated, confirming that development stages could be interpreted from aerial photography with an adequate degree of confidence. These data suggest that all stands are senescent by 300 years but that senescence may be induced earlier. (Table 2, Figure 2). Early senescence is likely to be as a result of fire damage.

It was not possible to distinguish reliably, from aerial photo interpretation alone, the difference between the younger and the older stands within the mature stage.

Table 3. Area of each development stage on publicly owned karri dominated forest within the main karri belt in 1995 (hectares).

Harvest History	Establish.	Juvenile	Immature	Mature	Senescent	Total
Unlogged (Virgin)	0	0	9200	50,700	2,900	62,800
Previously Logged	12,900	28,400	19,200	14,400	400	75,300
Total	12,900	28,400	28,400	65,100	3,300	138,100

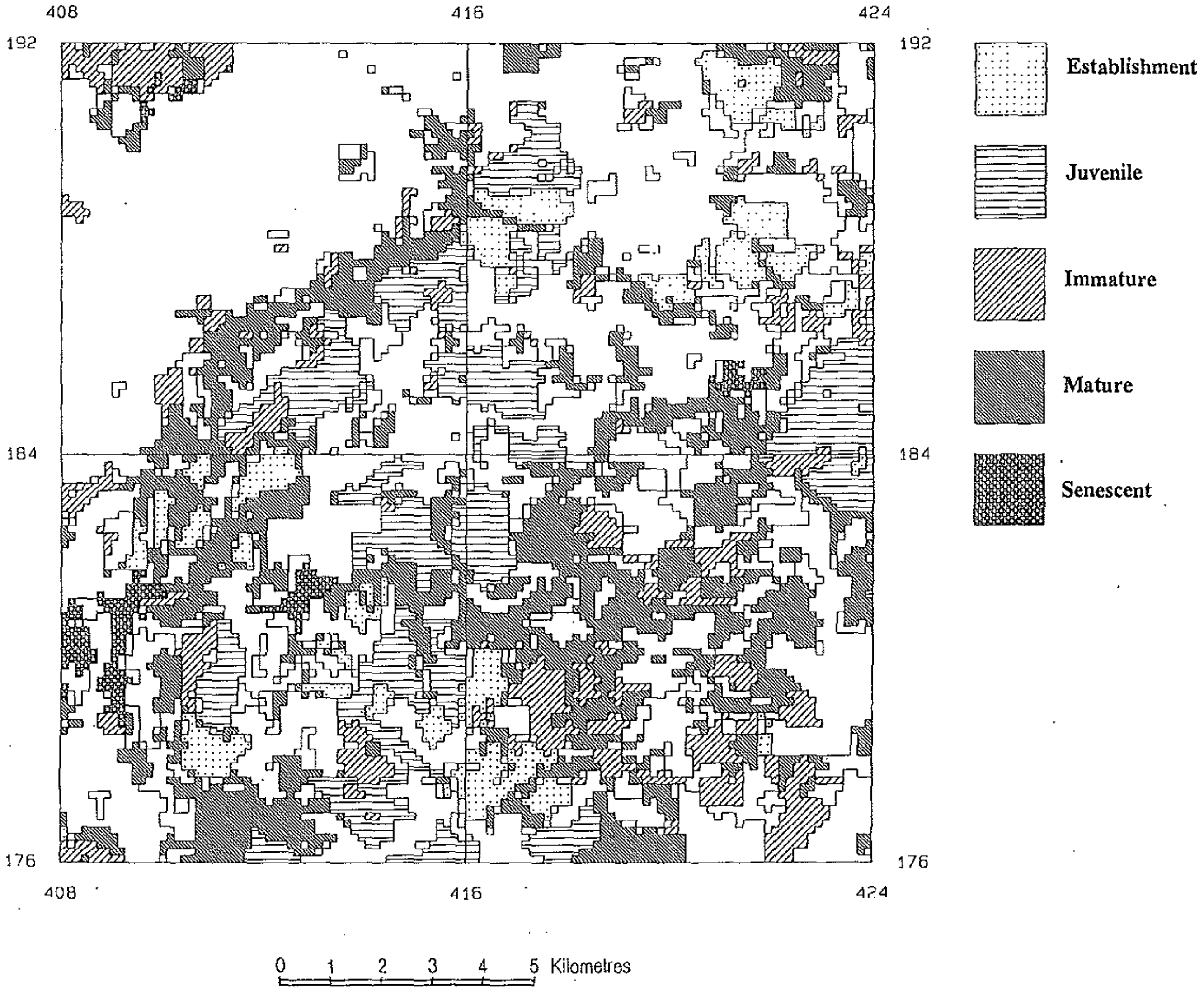

Figure 3. A portion of the map of development stages in the karri dominant forest.

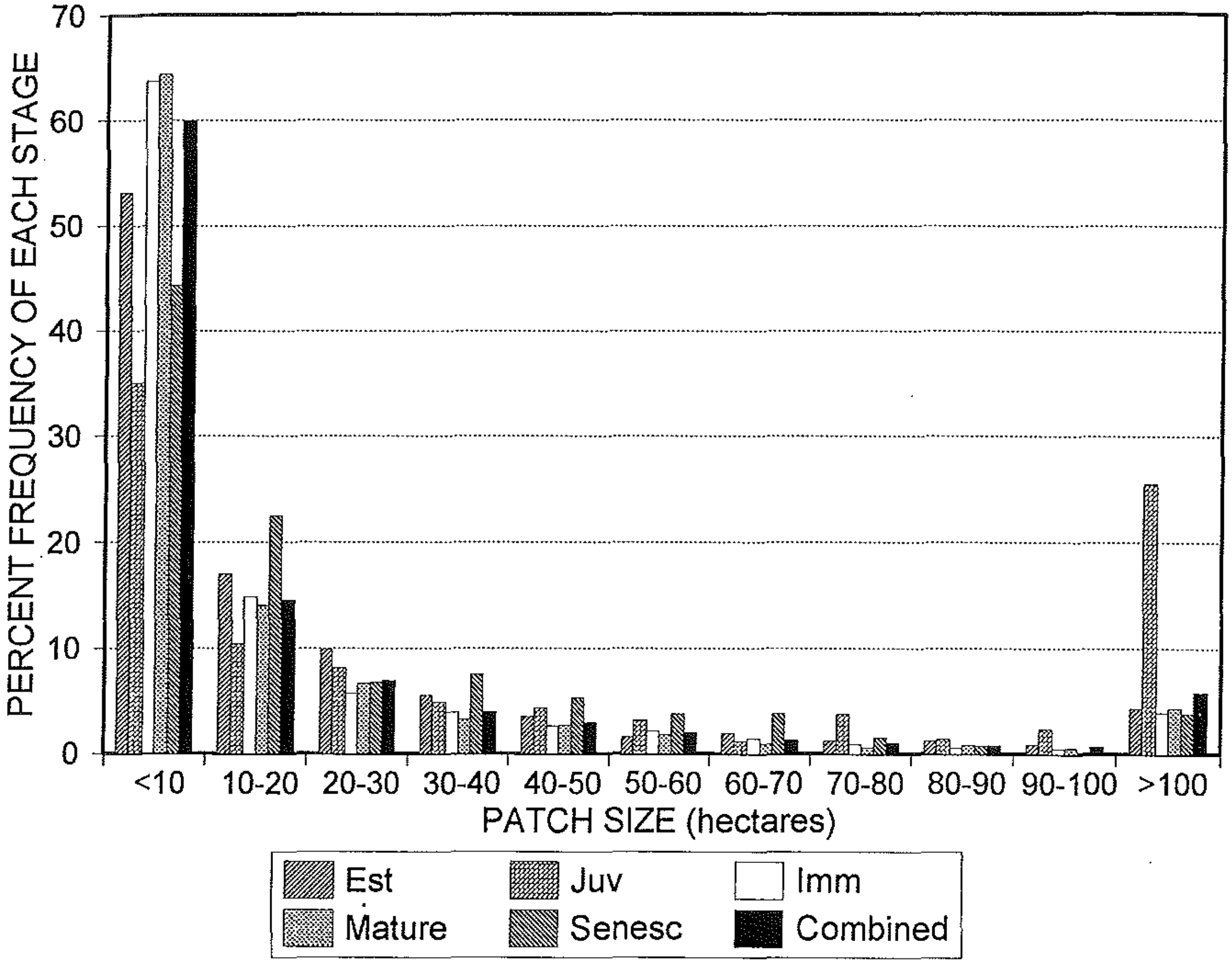

Figure 4. Frequency of patch size within each development stage in karri dominant forest.

Distribution of development stages

Map data for the interpreted development stages were added to that from existing records to prepare a map of the karri dominant forest by development stages. A portion of this map is shown in Figure 3. The area of each development stage within the main karri belt is shown in Table 3. Analysis of patch size for each of the development stages shows that there are about 4,500 discrete structural patches, the majority of which are less than ten hectares in extent (Figure 4). This pattern is true of each development stage. The relatively higher proportion of large patches of *Juvenile* forest is a consequence of the concentration of harvesting and regeneration in some areas as part of a deliberate regional (Figure 2) fire protection strategy (Bradshaw and Lush 1981). This will revert to a more typical distribution over the next ten years as some areas pass into the *Immature* stage.

Discussion

There have been several systems developed previously for the classification and description of seral stages and those commonly used in the northern hemisphere have been summarised by Oliver and Larsen (1990). These systems are mainly applicable to forests which will regenerate with tolerant climax species in the long absence of disturbance.

In Australia, the mapping of growth stages has previously been attempted in Victoria (Woodgate *et al* 1994) and New South Wales (RACAC 1996) but these studies were designed with an emphasis on the proportion of the stand in older development stages. As such they are not directly comparable to this study in that they did not assign dominance to a particular development stage, nor did they attempt to assign a 'stand' age.

In this paper we have described development stages in the karri forest which are readily recognised on the ground. These stages are based on the tree growth stages described by Jacobs (1955) as juvenile, sapling, pole, mature and overmature, but places them in the context of even-aged stand dynamics. Three of these stages (Immature, Mature and Senescent) have been mapped from aerial photography and the expected age range of these stages has been validated using tree diameter sampling and diameter/age relationships.

The approach has been adapted to uneven-aged stands with a wide variety of structure using the concept of 'significant' and 'dominant' cohorts. In this study we have chosen to designate and age stands on the basis of the dominant cohort, defined as the oldest cohort with more than 25% crown cover. In a study of stand age in north America, Lesica (1996) based stand age on the age of the cohort having the greatest basal area. Our approach places emphasis on biological rather than statistical dominance and will have the effect of indicating a higher proportion of older stands compared with Lesica's technique.

We believe that the approach developed here is appropriate for forests such as karri which regenerate as a result of both stand replacing events and small gap regeneration and which do not involve a late succession species change. Furthermore it acknowledges fire as a normal part of the dynamics of the karri forest which may give rise to a variety of structural changes in the both the understorey and the overstorey.

The relationship which has been established between stage and age of the overstorey will provide a base for the projection of these stages into the future.

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Appendix 1

Description of stand development stages

Stands of karri develop through several distinct stages from establishment to senescence.

In order to describe the stages in their simplest form we will discuss the development of distinctly even-aged stands and avoid the complexities of site and species mixtures. These descriptions are expanded versions of those previously described by Butcher [2] in CALM (1992). Figure A1 provides a diagrammatic illustration of the structure and key features of these stages.

Establishment

In a natural forest the establishment stage begins with the death of a tree or a group of trees in the original overstorey of such a size that the space that is vacated is not 're-occupied' by the surrounding trees (Breidahl and Hewett 1995)

If the conditions for establishment are suitable (primarily an exposed mineral soil seed bed and a source of seed) then the 'unoccupied' space will become occupied by seedlings. These seed-bed conditions are most commonly created by fire of varying intensity and as a result the early phases of establishment are characterised by strong inter-specific competition from the understorey species that regenerate at the same time. Rapid growth of the seedlings ensures dominance over the understorey and the establishment stage ends with canopy closure of the saplings at about eight years of age. By this age competition has reduced numbers from perhaps 1,000,000 germinants to 5,000 saplings per hectare and the saplings are about 6 - 10 metres tall.

Net nutrient demand is highest during this period (O'Connell and Menage 1982).

Juvenile

The juvenile stage begins with crown closure and is characterised by a period of intense intra-specific competition which results in the emergence at the end of this stage of about 400-500 dominant and co-dominant trees from an original 5000 individuals at the start of the period. Current annual volume increment peaks towards the end of this period.

The juvenile stage ends when the stand is about 25-30 years old and the crown shape of the dominant and co-dominant trees has begun to alter from the previous conical form to a more rounded shape. This is due to the retention of branches

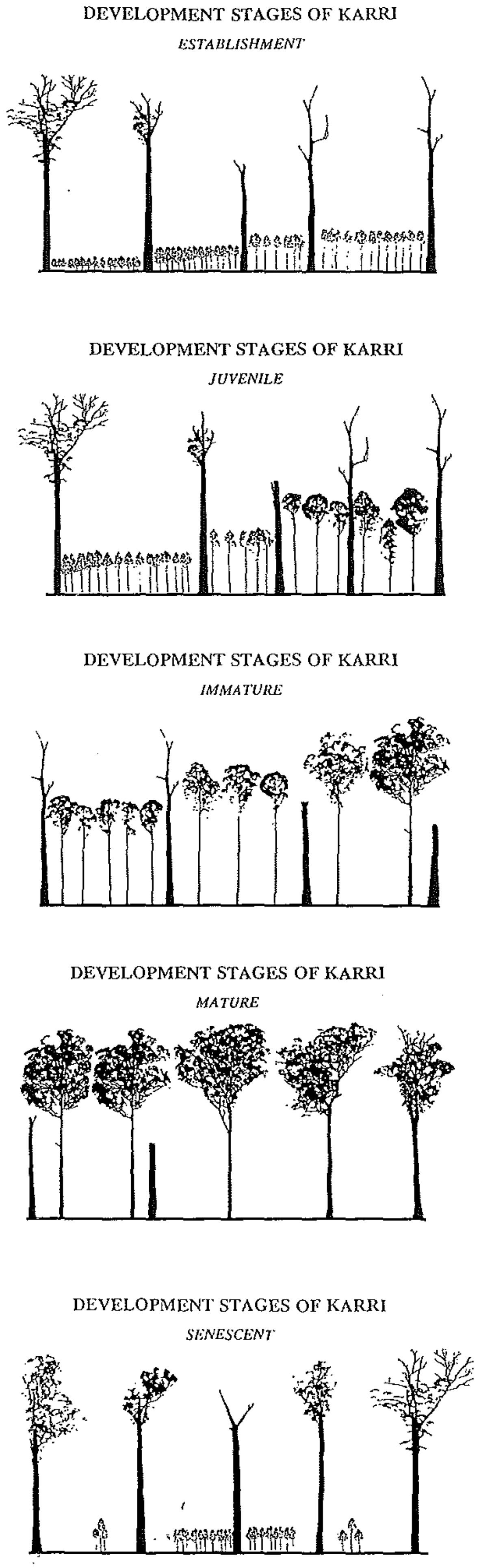

Figure A1. Diagrammatic representation of the structure of karri development stages.

at the base of the crown as they become too large to be shed cleanly from the bole. The appearance of the stand changes at the end of the period due to the shedding of the lower dead branches causing the stand to take on the more open appearance of the 'pole' stand.

By the end of the juvenile stage and without further fire disturbance the understorey also changes in character. Much of the short lived 'fire weed' species have died and together with the leaf litter and coarser debris, form a partially suspended, well aerated dead litter layer which is still accumulating. There is a sparse mid-layer of green understorey canopy at about 4 metres. Changes in understorey composition over time have been illustrated by Christensen (1972).

Immature

Competition continues throughout the immature stage though at a less rapid rate than in the juvenile stage. Dominants and co-dominants reduce from about 300 to 150 stems per hectare. Small gaps in the canopy resulting from the death of individual trees are quickly re-occupied by the vigorously growing adjacent trees. Net basal area increases till about 50 years of age from which time it fluctuates about a plateau according to the limitations of the site and periodic mortality events (Rayner 1992a).

Height growth continues at a slower rate but the dominants achieve 90% of their final height by the time they are 60-70 years old (Rayner 1992b).

Although bole length continues to increase, the lower dead branches are no longer shed cleanly. The dead branches are now shed by first breaking off several centimetres from the bole and then either rotting away or being overgrown as the bole diameter increases (Jacobs 1955). There is opportunity for the development of hollows to be initiated at this stage where larger branches are involved. The 'shaping' branches become larger and more persistent towards the end of the stage.

This stage ends when individual tree crowns have reached the size above which they are no longer capable of expansion, regardless of the space available. This occurs at about 120 years of age.

In the absence of further fire disturbance the understorey becomes more open. The highly suspended litter of the juvenile stage has broken down, a few long lived individuals of shrub species (such as *Chorilaena quercifolia)* remain, and dry matter (<25 mm) accumulation has stabilised at levels in excess of 50 tonnes per hectare (McCaw unpublished). The situation beyond 65 years is a matter of speculation since this is the longest (documented) unburnt site known to the authors.

Mature

The rapid growth stage ends as the physical limitations of each individual are reached. They can neither occupy more of the site nor increase their crown dimensions; only tree diameter will steadily increase. Intra-specific competition is much reduced and the stand enters a period of relative stability.

The crown has reached its maximum size (about 20-25 metres diameter) and permanent or shaping branches form the outline of the crown. As the extremities of the primary crown become less efficient, epicormic shoots develop within the crown (Jacobs 1955). The branches will periodically break, resulting in replacement through epicormic development without changing crown dimensions (Mackowski 1984). Individuals will slowly decline in vigour, although the growth rate of a dominant tree is largely maintained (Rayner 1992a). Where an individual tree dies, the remaining trees are unable to take up the available growing space, leaving a break in the canopy and allowing regeneration to occur. In many other non-eucalypt forest types this equates to the time when the regeneration of tolerant species will be released and begin to develop (Oliver and Larsen 1990).

The majority of hollow development in crowns is probably initiated early in this stage as large shaping branches break and larger branch stubs overgrow. As with jarrah (Inions *et al.* 1989), their development will be accelerated by wildfire.

The end of this stage occurs when the stand is about 200-250 years old.

Senescent

This is the stage of rapid decline in health, vigour and the number of original trees. The trees have a reduced control over the site. The process of crown renewal slows and, as major branch components are lost, they are replaced by epicormics lower on the branch or bole of the tree. This damage also provides entry points for fungi, which further weaken the tree's structure. In effect, the trees are in decline and will slowly break up. How much of this decline is due simply to the ravages of age and how much to the probability that trees of this age have been subjected to a greater number of damaging events is difficult to determine. However, even relatively young trees may become 'senescent' if severely injured and unable to support their existing structure following such an event.

Previous studies of tree ages (Rayner 1992a) have shown that few living individuals are known to exist beyond 350 years. The age distribution of large living individuals in the forest indicates a rapid decline in numbers between 200 and 280 years, followed by a more gradual reduction till there are only a few rare individuals recorded at 350 years.

Opportunities for regeneration increase as the control of the site by the overstorey diminishes with the increasing death rate of individuals in the stand. In the absence of severe 'stand replacing' disturbance this may result in small patches of regrowth becoming established in small gaps in the canopy if suitable regeneration conditions exist. This may then result in the development of a multi-layered forest. This is the beginning of a new establishment stage overlapping with the senescent stage.

In contrast with some forests, karri has no tolerant climax species waiting to eventually replace it in the absence of disturbance. Furthermore, life-long absence of disturbance from fire is inconceivable in this climate (Underwood 1978). This model is based on the presumption that fire at least of an intensity to create seed bed conditions will occur several times during the natural life span of karri. In the final phase of development there is therefore no late seral phase of alternate species but simply old karri forest which given even modest fire disturbance at that stage will be replaced by a new generation of karri forest.

2 G. Butcher, Department of Conservation and Land Management, Hayman Road, Como, WA