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A Review of the Fire Ecology of Forest Containing Red Tingle, Yellow Tingle, and Rate's Tingle

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Summary

The three species of tingle, Red Tingle (*Eucalyptus jacksonii*), Rate's Tingle (*E. brevistylis*) and Yellow Tingle (*E. guilfoylei*) have a restricted distribution near the south coast town of Walpole. They are mainly associated with granite hills and grow on freely drained brown gravelly soils. This area has the wettest and least seasonal climate in Western Australia. The presence of these and several other relictual plant, and animal, taxa in the vicinity of Walpole are presumed to be due to a combination of climatic and geological factors.

At the local scale the three tingles, as co-dominants, typify community types in association with each other or with Karri, Jarrah and Marri. These communities, the Karri/Red Tingle, Jarrah/Marri/Yellow Tingle and Jarrah/Marri/Rate's Tingle community-types have a similar suite of understorey species to nearby forest on similar soils which lack tingles. None of the plant taxa restricted to eastern Australian rainforest communities is found in the southern tall forests probably because of the summer drought and consequent higher incidence of fire in the Western Australian formation.

The Karri/Red Tingle is thought to have had a similar pre-European fire regime to the Karri forest as a whole, and that fire periodicity ranged from 6 to perhaps 30 years over most of the southern tall forests. The longer unburnt areas most probably occurred on south facing slopes and along valleys. There is general agreement that there was an interlocking mosaic of different ages since fire in the southern tall forests, depending on the level of Aboriginal activity and lightning strikes with the passage of summer thunder storms. Limited dendrochronological evidence from tingle trees indicates that fires severe enough to cause scarring have occurred at intervals of 20 to 80 years since 1840. Other fires, too mild to cause scarring may also have occurred.

All of the tingles have thick bark and after the early sapling stage recover from crown scorch by epicormic sprouting. Yellow Tingle is regarded to be the most fire hardy, while Red Tingle is vulnerable to "hollow butting" caused by fire entering the tree at the interface between the trunk and the roots. Yellow Tingle flowers prolifically and is well adapted to regeneration after fire. The sporadic flowering of Red Tingle is considered to make it best suited to regenerating in gaps caused by fallen trees. However, Red Tingle may also regenerate after catastrophic fire and there is evidence of "pulses" in the stand structure of Red Tingle which are consistent with this.

All of the understorey species of the tingle forest, for which this information is known, have commenced flowering by five years after fire. The minimum planned interval for fire in forest with tingles as a significant component is 8 years. The proportion of fire-killed understorey species with soil-stored seed in the Karri/Red Tingle and Jarrah/Marri/Yellow Tingle communities is intermediate between those

published for Karri and Northern Jarrah forest. The three "fire sensitive" plant taxa sometimes present in tingle forest are more commonly found in open forest or woodlands and shrublands with relatively high fire frequencies.

More research is required into the post-fire recovery and regeneration of Red Tingle and Rate's Tingle. Research is also needed into the distribution, taxonomy and phenology of invertebrate taxa associated with deep litter in tingle forests.

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1.0 Introduction

The three species of tingle have a patchy, restricted distribution in open forests and tall open forests between Walpole and Denmark (Wardell-Johnson & Coates, 1996). This area has Western Australia's wettest and least seasonal climate. Despite their common name none of the tingles is particularly closely related, although Red Tingle (*Eucalyptus jacksonii* Maiden) and Rate's Tingle (*E. brevistylis* Brooker) both belong to the *Eucalyptus* subgenus Monocalyptus whereas Yellow Tingle (*E. guilfoylei* Maiden) is placed within Symphomyrtus, where it is the only member of the sub-section Guilfoyleanae (Wardell-Johnson & Coates, 1996).

The tingles are notable for their association with well-drained soils on the slopes of granite hills. Some of these hills, particularly Mt Lindesay, are local centres of endemism and may have acted as refugia during marine transgressions (Wardell-Johnson *et al.*, 1995). As well as providing refugia and being centres of endemism for several plant species, the tall southern forest of the Walpole-Denmark region has apparently preserved several relict spider species which have changed little since they evolved in the rainforests of Gondwana 65 million years ago (Main, 1987).

Yellow Tingle is the most abundant and widespread of the tingles and Rate's Tingle the most restricted although all populations of the latter are in conservation estate (Table 1).

Table 1. Total area and distribution by tenure of the three tingle species.

Species	National Park/Nature Reserve (ha)	State Forest (ha)	Private Property (ha)	Total Area (ha
Rate's Tingle	1900	0	0	1900
Red Tingle	5000	600	400	6000
Yellow Tingle	8400	19300	8000	35700

The object of this review is to summarize the ecological knowledge, particularly in regard to fire effects on the vegetation of the tingle forests.

2.0 Plant Communities

There have been three main floristic surveys covering the open forests and tall open forests in which the tingles occur. The most broad-scale of these, that by Inions *et al.* (1990) did not separate the communities in which the tingles are a significant component from Karri forest on similar soils. A survey of the Walpole-Nornalup National Park (Wardell-Johnson *et al.*, 1989) also did not place "tingle forest" in a separate community. However another survey in the Walpole-Denmark area which included additional open forest and tall open forest sites did result in community-types partly distinguished by the presence of one or more of the tingles (Wardell-Johnson *et al.*, 1996).

The floristic classification of regenerated Karri forest (Inions *et al.*, 1990) placed Yellow Tingle in the Stoate community-type and Red Tingle within the Wallace community-type. The climate where these community-types occur was found to be significantly colder and to have a higher summer precipitation than other Karri community-types. Soils were also significantly more acid than those of other Karri communities and were at the lower end of the scale of soil fertility.

Within Walpole-Nornalup National Park Red Tingle is found within, the *E. diversicolor* (Karri) forest community (Wardell-Johnson *et al.*, 1989). This community, typically occurs on light-brown gravelly duplex soils and red and yellow earths over granitic rock in hilly terrain. Rate's Tingle and Yellow Tingle are also found in the *E. diversicolor* community within Walpole-Nornalup National Park (Smith *et al.*, 1990). Compared to other communities within the National Park the *E. diversicolor* forest community had a low number of species (only non-herbaceous species were included in the study) and little between site variation (Wardell-Johnson *et al.*, 1989). As well as being found within the *E. diversicolor* forest community Yellow Tingle is also present in the *Agonis parviceps* shrubland/*Bossiaea webbii* forest ecotone community (Wardell-Johnson *et al.*, 1989). This community ranges from closed-scrub to open-forest (Specht, 1981a) and is found in hilly terrain on yellow duplex soils with a high gravel content.

A survey of the "tingle mosaic", an area of 3700 km^2 covering the Walpole, Denmark, Redmond and Torbay 1:50000 map sheets resulted in three community groups partly defined by the presence of tingle (Wardell-Johnson *et al.*, 1995). The Jarrah/Marri/Yellow Tingle open forest to tall open forest community and the Karri/Red Tingle tall open forest community were both found on brown gravelly freely-drained upland soils, with the Karri/Red Tingle soils being substantially more fertile than the Jarrah/Marri/Yellow Tingle soils. The average annual rainfall for the Karri/Red Tingle (in which Yellow Tingle is common) and Jarrah/Marri/Yellow Tingle community-types is 1275-1330 mm. Jarrah/Marri/Rate's Tingle open forest was found on similar soils but in the medium rainfall zone (1130-1200 mm/yr).

Analysis of the ordination data indicates that the Jarrah/Marri/Yellow Tingle forest is similar in vegetational composition to the Jarrah/Marri open forest on the same soil-type and that the Karri/Red Tingle tall open forest is close to one of the Karri tall open forest community-types. Most of the Jarrah/Marri/Rate's Tingle open forest was quite close in species composition to adjacent Jarrah/Marri/Yellow Tingle forest and Jarrah/Marri forest on similar soils. This similarity in overall species composition between forest containing tingle and nearby forest on the same soils where it is absent confirms the results of the Walpole-Nornalup National Park survey (Wardell-Johnson *et al.*, 1989).

3.0 Fire ecology

3.1 Fire in tingle forest

3.1.1 *Fuel accumulation*

There is a rapid accumulation of fuel in the Karri/Red Tingle community-type. Wardell-Johnson (1996b) measured about 28 tonnes/ha of fuel 6 years after fire, almost 2.5 times the quantity in the same forest type 2 years after fire. This rate of accumulation is similar to that given for Karri forest by Sneeuwjagt & Peet (1985). After 48 years there was about 44 tonnes/ha of fuel in Karri/Red Tingle forest of which about half was litter. Over 40% of Karri/Red Tingle forest has not been burnt for between 25 and 50 years and only 16% of this community has been burnt in the last 5 years.

The species composition of the various forest community-types where the tingles are co-dominants have been shown to be quite similar to nearby Karri or Jarrah/Marri forests on similar soils. Therefore it reasonable to assume that they experienced a similar range of fire frequencies to those community-types. That is, fire was probably less frequent in damper areas or rocky areas with discontinuous fuel and more frequent in drier areas.

3.1.2 *Pre-European fire frequencies*

Before the arrival of Europeans the main causes of fire were Aborigines and lightning strike (Underwood, 1978). Pre-European fire frequency within the Karri forest is thought to have been less than that in the Jarrah forest because of the lower proportion of resprouters and the shorter season when the Karri forest will burn (Christensen & Annels, 1985). Dendrochronological evidence suggests that severe fires were infrequent in Karri forest before 1850 when the activities of European settlers increased their frequency (Rayner, 1992). In fact several Karri trees were well over 200 years old before they experienced their first fire severe enough to cause scarring.

It has been proposed that the low numbers of fire scars observed in the stems of old trees was because mild fires occurred relatively frequently in the Karri forest, perhaps at intervals of between 3 and 20 years (Christensen & Annels, 1985). Underwood (1978) believes that the highest frequency of fires was in the order of 6 to 10 years. It is argued that relatively frequent fires would have caused little scarring above stum height and thus would not show up in the annual growth rings (Rayner, 1992). Burrows *et al.* (1995), in a study of dendrochronological evidence for fires in the Jarrah forest came to a similar conclusion. Aboriginal burning practices in the shrublands along the coast and in the woodlands to the north and east of the tall forest would have been the source of most of these fires. Some pockets of forest undoubtedly remained unburnt for 30 years or more and these most likely occurred along river systems and on southern aspects (Underwood, 1978).

A limited number of trunks of the three tingle species have also been assessed for age and fire frequency (Wardell-Johnson & Coates, 1996). These counts showed that all three species could attain an age of 350 - 400 years. This data has not been published but reference to the original field sheets shows that moderate-high intensity fires have been moderately frequent (intervals of 20 - 80 years) in parts of the tingle forest over the last 150 years. Other, milder fires, of too low intensity to cause scarring may also have occurred between these events. A 330 year-old Yellow Tingle from private property north west of Walpole experienced fires intense enough to cause scarring in or around 1951, 1876, 1856, and 1845. The approximate dates of intense fires for several other trees are given below[1];

Rate's Tingle, *c.*163 years-old (London Block): 1984, 1969, 1910, 1884, 1844
Rate's Tingle, *c.*170 years-old (London Block): 1951, 1872, 1859
Red Tingle, *c.*100 years-old (Loc 10179): 1985, 1957, 1951

The age of peak flowering or of seed production of understorey species can give some indication of "natural" fire frequencies. The hard seeded legume species *Acacia browniana, A. divergens A. myrtifolia* and *Bossiaea linophylla*, which are characteristic of the Jarrah/Marri and Jarrah/Marri/Yellow Tingle community (Wardell-Johnson *et al.* 1995) reach peak seed production by 5 or 6 years after fire. In contrast, *Trymalium floribundum*, a thin-barked, soft-leafed species typical of the Karri and Karri/Red Tingle communities, increased its seed production up till 8 years after fire (Skinner, 1984).

Christensen (1992) has proposed that the absence of a suite of mammals with k-selective traits (i.e. longevity, low sexual maturity, low fecundity) from the southern tall forests is a result of frequent fire. This is in contrast to the tall wet sclerophyll forests of eastern Australia where fire is less frequent. The higher frequency of fire in the southern tall forests of Western Australia is also suggested by Christensen (1992) to be the reason why cool temperate rainforest elements, which are sometimes present in the tall wet sclerophyll forests of eastern Australia, are absent from the flora.

3.2 Fire response of the tingles

3.2.1 *Bark thickness*

All of the tingles have rough, persistent bark which insulates the cambium and provides them with the ability to survive 100% scorch of their crowns and regenerate foliage from epicormic shoots. Measurements taken by Wardell-Johnson (1996) show that Red Tingle and Yellow Tingle have thick bark (> 20 mm) while the bark of Rate's Tingle is moderately thick (11-20mm) and in the same category as Karri and Jarrah. The average bark thickness of a number of species from the Walpole area is shown in Table 2.

[1]Based on original field sheets, Department of Conservation and Land Management, Manjimup.

Table 2. Average bark thickness of several shrub and tree species of the forests and woodlands near Walpole (Wardell-Johnson, unpublished)

Very Thin (< 5 mm)	**Thick (11-20 mm)**
Trymalium floribundum	*Eucalyptus brevistylis*
Banksia attenuata	*E. diversifolia*
Acacia pentadenia	*E. marginata*
Thin (6-10 mm)	**Very Thick (> 20 mm)**
Agonis flexuosa	*E. calophylla*
Banksia grandis	*E. guilfoylei*
	E. jacksonii

3.2.2 *Regeneration and resprouting*

Wardell-Johnson (1996a) investigated the response of immature and mature tingle to defoliation by moderate to high intensity wildfires. Amongst the tingles, Yellow Tingle showed the greatest resilience by regenerating new foliage from epicormic buds and flowering within 2 years of the defoliation of a mature tree. Yellow Tingle flowers within 8 years of seedling establishment and at 10 years of age is able to recover from intense fire and produce a crop of seed.

In contrast Red Tingle does not flower for at least 30-40 years after seedling establishment, is sporadic in its flowering and showed limited resprouting ability at the sapling stage. Nevertheless, 4 year/old, 4 -5 m high Red Tingle examined by Wardell-Johnson (1996b) had survived a fire of moderate-high intensity and had abundant epicormic sprouting. This indicates that Red Tingle saplings are more fire-resistant than Karri at a similar age (Peet & McCormick, 1971).

There is evidence of "pulses", perhaps linked to catastrophic fire events, in the regeneration of Red Tingle (Wardell-Johnson, 1996b). These pulses of regeneration (i.e. even-aged cohorts) may be the result of mass establishment of seedlings after severe fire has killed large numbers of mature trees.

Wardell-Johnson (1996b) considers Yellow Tingle the equivalent of Jarrah and Marri in regard to its ability to "handle" fire prone environments. However, the tendency of large Red Tingle to "hollow-butt" and to burn-out and fall over after even mild burns may indicate that this species is not as well adapted to relatively frequent fire (Wardell-Johnson, 1996b). There have been limited opportunities to make observations on the post-fire recovery of Red Tingle and Rate's Tingle during research to date and further study of the establishment of these species is warranted (Wardell-Johnson, 1996b).

3.2.3 *"Hollow butts" and fire access*

Wardell-Johnson *et al.* (1995) found that a much higher proportion of Red Tingle than Karri more than a metre in diameter were hollow-butted. Red Tingle has shallow roots, with the stem-root interface often being within the humus layer (which is deepest at the base of the trees). This characteristic was considered to make the tree vulnerable to the entry of fire into the highly flammable, decaying heartwood of older individuals of this species. Another reason may be that the fibrous bark of the

Red Tingle, which burns readily, provides a pathway for fire to run up the trunk and into any dead limbs or hollows, whereas fire does not generally carry up the trunk of a Karri (R.Smith, pers.observ.).

The buttressing of Red Tingle and Rate's Tingle were also a "weak" point where fire could enter the tree. In addition, the less dense, fibrous wood of Rate's Tingle and Red Tingle were more likely to catch fire and sustain fire than Karri (Wardell-Johnson, 1996b).

3.2.4 *Species dominance*

Wardell-Johnson (1996) proposed that relatively frequent fires would advantage Yellow Tingle, Jarrah and Marri to the detriment of Red Tingle and Rate's Tingle because of the ability of the former species to more rapidly refoliate and produce a seed crop. Although mature Rate's Tingle and Red Tingle generally survived a wildfire, their sporadic flowering sharply reduced the chances of them being able to distribute seed into an ashbed. They appear to be adapted to regenerating from seed dispersed into gaps caused by dead or fallen trees.

3.3 Fire and other plant species in tingle forest

3.3.1 *Fire and flowering*

The longest interval between fire and the commencement of flowering in understorey species of the Karri/Red Tingle forest is 57 months for *Cryptostylis ovata* (Slipper Orchid) and 54 months for *Trymalium floribundum* and *Acacia pentadenia*. However most understorey plants commence flowering within 24 months (Table 3). The current minimum interfire period for fuel reduction burns in Karri/Red Tingle is 96 months (8 years) which means that *C. ovata, T. floribundum* and *A. pentadenia* have 3 - 4 years of seed production before the next prescribed burn. No understorey species of the southern tall forests are known to have an interval between fire and first flowering of longer than 5 years.

Table 3. Time to first flowering of understorey species of the Karri/Red Tingle community. This interval is not known for a number of species.

Time to first flowering	6 - 11 months	12 - 23 months	24 - 35 months	36 - 47 months	48 - 53 months	54 - 66 months
Number of species	15	41	15	1	0	3

3.3.2 *Regeneration strategies*

Data has been collected on the regeneration strategy and time to first flowering after fire of most plant species that occur in the two community groups that contain the tingles within Walpole-Nornalup National Park (Smith *et al.*, 1990). This data has been used to prepare Table 4 which shows the proportion of species in the four main regeneration categories. The proportions given for jarrah and karri forest by Christensen and Annels (1985) are also shown for comparison.

Table 4. The percentage of understorey plant species by regeneration strategy in the two main tingle community-types (Wardell-Johnson et al. 1995) compared with figures for Jarrah and Karri forest given by Christensen & Annels (1985).

Regeneration strategy	Karri/Red Tingle	Jarrah/Marri/ Yellow Tingle	Jarrah	Karri
Resprouters	58.5	61.6	68.6	42.0
Seeders (soil stored)	27.7	28.2	16.2	49.5
Seeders (on plant storage)	2.1	2.3	8.6	0
Short-lived herbs	10.6	7.9	4.8	8.6

It can be seen from Table 4 that both Karri/Red Tingle forest and Jarrah/Marri/Yellow Tingle forest have a lower proportion of understorey species in the "fire sensitive" seeder categories than the "Karri forest" of Christensen & Annels (195) and are similar to Jarrah forest in the proportion of resprouters. It must be stressed however that this data is only in regard to species numbers and does not give an indication of the contribution of the various species (or regeneration strategies) to the vegetation cover. The data given by Christensen & Annels (1985) showed that shrubs with soil-stored seed contributed 83% of vegetation cover even though they represented only 50% of total species. In addition all species which occurred within the two tingle forest types were included in the analysis even though some of them occurred infrequently.

Unpublished work by Wardell-Johnson (Table 5) shows that the Karri/Red Tingle community-type has a similar ratio of fire killed taxa/reprouters to the other "damp" community-types, the shrublands occurring in peat swamps and minor valleys and the non-forest around granite outcrops. If the proportion of obligate seed regenerators is used as an index of relative fire frequency (e.g. Keeley and Zedler, 1978; Bell *et al.*, 1984) then fire has occurred substantially less frequently in these community-types than in the heathlands on drier sites and the shrublands and heathlands of the coastal dunes.

Table 5. Proportion of fire-killed taxa with soil-stored seed to reprouters for selected communities near Walpole. Also shown is whether the number of obligate seeders is higher or lower than would be expected (by chi-squared analysis) considering their proportion of total species numbers (Wardell-Johnson, unpublished).

	heathland	recent dune vegetation	peat swamp/minor valley shrublands	karri/red tingle forest	non-forest granite outcrop vegetation
Ratio of seeders/sprouters	0.28	0.29	0.60	0.61	0.55
Number of obligate seed regenerators	lower than expected	lower than expected	higher than expected	higher than expected	same as expected

3.3.3 *"Fire sensitive" species*

Of the 12 known "fire sensitive" species identified by Smith *et al.* (1990) for Walpole-Nornalup National Park, (i.e. where the mature plant is killed by 100% scorch and which have on-plant seed storage), 3 are found in communities that contain tingles (Wardell-Johnson *et al.*, 1995). Two fire sensitive species, *Hakea lasianthoides* and *Petrophile diversifolia*, which commence flowering by 3 years after germination, are predominantly found in Jarrah/Marri open forest, including the Jarrah/Marri/Yellow Tingle and Jarrah/Marri/Rate's Tingle communities. Another fire sensitive species, *Hakea oleifolia*, is found at low levels in the Jarrah/Marri/Yellow Tingle and Karri/Red Tingle communities but is much more common in woodland and shrublands on sandy soils. The juvenile period of *H. oleifolia* is not known.

If the recommendation of Gill & McMahon (1986) is followed and twice the juvenile period is required between fires for sufficient seed to be accumulated for parent replacement then 6 years is should be the minimum fire rotation for communities containing *H. lasianthoides* and *P. diversifolia*.

3.3.4 *Species richness and change in species composition with time since fire*

Wardell-Johnson (1996b) examined the change of species composition since fire in the Karri/Red Tingle community-type. The ages were 2, 6 and 48 years since the last fire. The total number of plant species was greatest in the 6 years since fire quadrats, with the 2 year-old and 48 year-old quadrats having similar numbers of species. However these differences were minor, only 32 species occurred in the 6 year-old burn quadrats and 27 in the 48 year-old burn. The highest number of unique species (7), that is species found only within a particular burn age, also occurred in the 6 year-old burn quadrats. Only four species were confined to the long unburnt area. There was a roughly equal number of obligate seeders and resprouters among the unique species of the three burn ages.

3.4 The "Gondwanan element" in tingle forest vegetation

It is generally considered that plant species (or genera) largely restricted to temperate rainforests as found in the eastern states of Australia are absent from the tall open forests of the wetter areas of Western Australia (Christensen, 1992). This is confirmed by a perusal of the common genera of temperate, closed forest from eastern Australia (Specht, 1981a), the only genera that the karri/tingle forests and the southern rainforests have in common are also found in dry sclerophyll forests elsewhere in Western Australia. However, Wardell-Johnson & Coates (1996) have recently questioned this. They cite the evidence of several undescribed plant (and fungus) taxa found within the "tingle mosaic" as relicts which establish an ancient link to the warm, perhumid climate of Gondwana (Powell, *et al.* 1981).

The issue here appears to be not that the species have links to Gondwana; the great majority of genera in many south west Australian plant formations, including those of mallee shrublands and dry sclerophyll forests are either endemic to Australia (and thus evolved from Gondwanan ancestors) or are shared with the other Gondwana-derived southern continents (Specht, 1981a). No subtropical-tropical Gondwanaland flora, which have evolved least since the break-up of that continent (Specht, 1981b), are found in the southern tall forests that have not also adapted to the drier open forest formations (e.g. *Podocarpus, Pittosporum*). Rather, the issue is that these taxa have evolved in habitats where fire may not have been frequent (e.g. among granite outcrops, along streams and under the canopy of Red Tingle forest) because high moisture levels have shortened the "fire season" or prevented the spread of fire.

3.5 Relict animal species

Main (1987, 1993) documents the existence of several relict spiders of Gondwanan origin which have persisted in various damp, shady habitats in southern Western Australia. One of these, *Moggridgea*, is restricted to the Stirling Range and tingle forest near Walpole. *Moggridgea* is considered to be vulnerable to bushfires because the burrows are shallow and the spider is killed by heat (Main, 1993). Although Main (1987) considers that taxa such as *Moggridgea* evolved in fire-free habitats, she believes the season where fire is of <u>lowest risk</u> to them is early autumn "when they may still be in retreat in the lower litter/humus layers or buried in the soil. This is the time when prescribed burns in tingle forest are generally carried out.

Another taxon, *Chasmocephalon*, a tiny spider found in eroded buttresses of trees and other damp, shady habitats in long unburnt forest near Walpole probably does not retreat to deeper layers of litter (Main, 1987). This species lays dormant during summer on exposed moss or debris. Main argues that such spiders need to be protected from fire in selected, planned refugia and that large scale fires with no allowance "for saviour patches would destroy such relics".

Such taxa as the spider *Moggridgea* and the understorey shrub *Trymalium floribundum* (which has thin bark, soft leaves and a long interval between fire and flowering) have retained some characteristics which are typical of temperate rainforest species and do not suit them to frequent fire. Nevertheless they have survived large scale fires and climate changes in the area over a long period (Churchill, 1968). As recently as 1937 a wildfire reportedly burnt through most of the tingle forest. *Trymalium floribundum* (Karri Hazel), in fact, is one of the most widespread of understorey species in the southern tall forest.

Main (1987) contends that the phenology of the vertical movements of relict spiders needs to be studied in order that their vulnerability to fire at different seasons can be confirmed. Wardell-Johnson (1996a) proposed that small vertebrates and invertebrates are better indicators of community and vulnerable species responses to fire than large vertebrates which have persisted through some severe climatic bottlenecks in the south west.

3.6 Suggestions for further research4

1. More information is required on the post-fire recovery of young Red Tingle and Rate's Tingle.

2. More information is required on the reproduction of Red Tingle and Rate's Tingle, in particular the links between flowering and environmental factors.

3. Nutrient uptake studies to shed more light on the proposed reliance of Red Tingle on deep litter.

4. Factors which influence the regeneration success of Red Tingle and Rate's Tingle.

5. Studies on the taxonomy, distribution and phenology of deep litter invertebrates in the tingle forest.

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Summary of Major Points from Review of Tingle Forest Fire Ecology

- The three tingle species are all associated with a particular forest community-type but overall species composition of these types is generally quite similar to nearby forest on the same soils where tingles are absent.
- The short dry season, cool temperatures and steep near coastal granite hills near Walpole have produced a flora which has a high level of local endemism.
- The rate of accumulation of fuel in Karri/Red Tingle forest is similar to that published for Karri forest in general.
- Growth ring counts indicate that all three tingles may live for more than 350 years.
- Limited evidence on the occurrence of fire scars show that moderate-high intensity fire has occurred in some tingle forest at intervals of 20 - 80 years since about 1840.
- Relatively frequent fire in the past, because of the dry summers in south west W.A. is the reason why plant genera restricted to cool temperate rainforests are absent from the southern tall forests.
- All the tingles have thick or very thick bark and have the ability to recover from fire at a young age (> 4 - 5 years) by resprouting.
- Red Tingle has shallow roots and the root/stem interface is often within the litter layer which provides a "weak" point for entry of fire into the tree.
- The rough, fibrous bark of the tingles may provide a pathway for fire up the tree, whereas fire does not travel up the trunk of Karri so readily.
- The previous two points are probably the reason why a much larger proportion of old tingles than karris are dry-sided or hollow-butted.
- Red Tingle and Rate's Tingle are less able to withstand frequent fire than Yellow Tingle.
- The sporadic flowering of Red Tingle puts it at a disadvantage compared to Yellow Tingle in regard to regeneration after severe fire.
- Red Tingle appears to be better adapted to regeneration following isolated tree falls rather than mass fire deaths.
- The proportion of total species numbers in tingle forest dependant on soil stored seed for regeneration is intermediate between that published for Karri forest and Northern Jarrah forest.
- In the Walpole area, based on the ratio of obligate seeders to resprouters the Karri/Red Tingle forest, the shrublands of peat swamps and granite outcrop vegetation have evolved under a lower fire frequency than have dry heathlands and the woodlands of recent dunes.
- There was a higher species richness in Karri/Red Tingle forest 6 years after a fire than in forest free from fire for 48 years.
- Some plant and animal species in the tall southern forests have retained characteristics which do not suit them to frequent fire, nevertheless, they have survived for millions of years in a fire prone environment.
- The time of lowest risk for the relictual spider *Moggridgea* in regard to time since fire is in autumn because it has retreated to deeper liiter or into the soil.