Fire Regimes and Biodiversity

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Abstract

Biodiversity, or the diversity of life, is largely influenced by climate, soils and topography. Fire is also an important environmental factor influencing the composition, distribution and abundance of living organisms in bioregions which experience seasonal or periodic drying. Although many studies have been conducted in a variety of ecosystems, knowledge of the temporal and spatial effects of fire and of fire regimes (frequency, intensity and season) is imperfect. This is due in part to the complexity of ecosystem processes, spatial and temporal variability and to the poor taxonomic knowledge of numerous organisms, particularly invertebrates and microflora.

Reducing the undesirable impacts of wildfire without regard for the preservation of biodiversity is, technically, relatively straight forward with measurable outcomes. However, land management agencies often have moral and legal obligations to protect community assets (life, property, commercial resources, etc.) from damage by wildfire and to preserve biodiversity (genetics, species and ecosystems). As a management objective, the preservation of biodiversity is a laudable concept, but practically is somewhat nebulous and largely immeasurable in space and time beyond measuring changes to known or charismatic taxa, which may be as few as 5% of the total number of species. This, together with limited ecological knowledge and a variety of practical constraints, has given rise to a variety of fire management approaches which include; do nothing until more is known, let nature take its course, go for diversity of fire regime, mimic nature by reconstructing historical fire regimes, and single species management. Any of these strategies may be appropriate for a given set of circumstances.

In sclerophyllous forests and woodlands of south-west Australia, the dual fire management objective is to protect human life and assets from damaging wildfires and to maintain biodiversity. The region experiences a Mediterranean-type climate with defined seasons of cool wet winters and warm/hot dry summers, giving rise to an annual "fire season". The tripod of fire management is a good detection system, an efficient suppression force and prescribed burning. In the absence of comprehensive long term fire effects data, fire regimes which strive to achieve protection and biodiversity objectives are devised, implemented and modified based on a combination of historical evidence and a growing knowledge of fire behaviour, fuel accumulation rates, fire ecology and life history attributes of key floral and faunal elements. The latter includes post-fire regeneration strategies and flowering phenology of vascular plants, and habitat requirements and post-fire response patterns of selected vertebrate and invertebrate fauna. Based on this information, the important features of managed fire regimes in parts of the jarrah (*Eucalyptus marginata*) forest are; a) prescribed ranges of fire intensity, scale and patchiness, b) determination of minimum sustainable fire frequency and c) variation in frequency and season of fire.

Introduction

Biodiversity is usually referred to in terms of the diversity of genotypes, species and ecosystems or habitats. Diversity at the species level is the most widely accepted level at which to consider or characterise whole organism diversity. It is at the species level that evolutionary mechanisms are focussed and it is the origination and extinction of species which ultimately controls or determines biodiversity (Groombridge 1992). Biodiversity can be considered at various scales from biogeographic scales of thousands of square kilometers to local scales of less than several square km (Davis *et al.* 1990).

The natural occurrence, diversity, abundance and geographical distribution of wildlife (species and communities of plants and animals) is largely controlled by geology, topography and climate. Where climatic conditions give rise to seasonal or occasional dry periods, fire is a natural environmental factor which can either decrease, maintain or enhance biodiversity depending on the nature of fire regime (frequency, intensity, season) and the ecosystem properties.

Preserving biodiversity has emerged as a major scientific, management and political issue over the last two decades (e.g., see Wilson and Peter 1988; Groombridge 1992). There are very laudable reasons for managing natural ecosystems to preserve biodiversity including commercial, scientific, ethical and aesthetical reasons, but the notion of maintaining or enhancing biodiversity *per se* is a relatively new one. Historically, mankind has deliberately managed ecosystems to favour species which are of direct benefit. For example, in parts of Australia, Aborigines fired the land regularly to promote and maintain grasses which attracted game such as kangaroos, valuable for meat and other products (Jones 1969; Hallam 1975; Pyne 1991). In other situations, Aborigines protected certain vegetation types from fire so that they could procure the right type of wood for making tools and weapons (Start 1986). Early European settlers also used fire to promote palatable grasses and other fodder on which to graze their stock. In these situations, fire was used deliberately to promote desirable species rather than to preserve or promote biodiversity.

Today, conservation and land management agencies have a legal and moral obligation to mitigate the damaging effects of wildfire and to preserve or enhance biodiversity in natural ecosystems. In many ecosystems, including the sclerophyll forests of south-west Western Australia, the deliberate use of low intensity fire applied on a rotational basis to manage the build-up of flammable fuels (prescribed burning) is the cornerstone of wildfire control, together with efficient detection and suppression systems (Underwood *et al.* 1985). However, this practise is controversial with opponents claiming that such fire regimes are ecologically damaging and threaten biodiversity. The challenge for land management agencies therefore is to develop fire regimes which achieve an acceptable level of wildfire protection while preserving biodiversity.

Setting fire regimes to manage fuel build-up without regard for biodiversity is technically relatively straight forward and is based on a knowledge of fire behaviour, fuel accumulation rates and a systematic analysis of wildfire threat (see Sneeuwjagt this volume). The capacity of an agency to implement fuel reduction regimes is usually constrained by practical rather than scientific factors such as limited resources, weather, smoke pollution issues, etc. On the other hand, determining the most appropriate fire regime to preserve biodiversity can be very complex.

In the first instance, to preserve biodiversity implies a knowledge of this diversity or a knowledge of what is to be preserved. It is most unlikely that at the management scale (hundreds or thousands of hectares), this will ever be known. For example, in the jarrah (*Eucalyptus marginata*) forests of south-west Western Australia alone, a single interim bioregion of Australia) there are estimated to be more than 15 000 species of insects, 9 000 species of fungi, 2 500 species of vascular plants 180 species of soil invertebrates (Majer and Abbott 1989), 150 species of birds, 60 species of frogs and reptiles, 29 species of native mammals, and 4 species of native fish (Nichols and Muir 1989). The vast majority of invertebrates and fungi are poorly described and are yet to be discovered, but Abbott and Christensen (1995) estimate that insects and fungi probably make up 99% of all species present in south-west Australian forests. Taxonomists continue to separate species as sophisticated techniques such as isozyme analysis and DNA fingerprinting techniques become available. Therefore, at the species level, knowledge of biodiversity beyond charismatic taxa (vertebrate fauna and vascular plants) is poor and knowledge of biodiversity at the genetic level is even poorer. Another limitation with managing for species diversity is that it does not take account of species abundance. Management activities or other perturbations, may not threaten biodiversity, but may alarmingly decrease or increase populations of organisms.

Taken literally, managing fire to preserve all levels of biodiversity implies both a knowledge of this biodiversity and of its responses to fire. The ecological effects of fire are many and complex and it is highly unlikely (and probably unnecessary) that this will be well understood for all organisms and ecosystems.

In the absence of perfect knowledge, there are a number of management approaches which can and have been adopted to determine the most appropriate fire regime to preserve biodiversity. These include "doing nothing" and letting nature take its course. This may be appropriate in some instances, but in most cases, proactive management is necessary for a raft of reasons. A similar approach is to mimic nature by attempting to reconstruct and implement pre-historical fire regimes, or fire regimes which were believed to have persisted prior to European settlement. This includes lightning and aboriginal sources of fire, the notion being that existing ecosystems evolved under this regime, so, *a priori*, should be preserved by this regime. There is some validity to this argument, but also some pitfalls. In most instances, natural ecosystems are extant, existing in highly fragmented landscapes interspersed with farmland, towns and settlements, commercial forests, and densely populated centres. In addition, disturbed ecosystems are now vulnerable to invasions by exotic fauna and flora which can significantly impact on native organisms. There is also the risk that attempts to reconstruct pre-historic fire regimes may inaccurately reflect temporal and spatial variability of fire within and across biogeographic regions. For example, there is historical evidence that frequent firing by Australian Aborigines maintained a grassy understorey beneath tuart (*Eucalyptus gomphocephala*) and jarrah forests along the coastal plain and foothills of the Darling Scarp in south-west Western Australia (Hallam 1975; 1985). However, it would be unwise to assume broader application of this regime such as to the hill forests east of the plain if the management objective for these forests is to preserve or enhance biodiversity.

Another approach is to simply apply a fire regime which is variable in season, intensity and frequency, based on a "best bet" and following the ecological axiom that "diversity is good". A common approach to fire management is to attempt to exclude fire or to be very cautious with the use of prescribed fire until more is known about fire ecology. Such management actions are often implemented under the guise of the poorly defined "precautionary principle", even though it is highly likely that fire has played a key role in the evolution of the ecosystem in question, particularly in climates of seasonal wetting and drying, or of periodic drought. This is usually accompanied by a belief that ecosystems are delicate and fragile. However, most ecosystems in fire and drought prone environments, are quite resilient to fire and drought. While it is of course important to continue to research and gather fire ecology information by the scientific method, fire and land management agencies who are charged with the moral and legal responsibility of managing these lands, cannot wait until scientists deem that enough is known before they must take some form of management action, either to protect values at risk from wildfire, or to apply fire to regenerate habitat. In fire-prone environments, under-management by way of the "do nothing" or "let nature take its course" options, in most circumstances will be very damaging to both community and conservation values.

This paper presents a practical rather than a theoretical or conceptual approach to managing fire to maintain biodiversity. The jarrah forest of south-west Western Australia is used as a case study of how key biological indicators can be used to devise appropriate interim fire regimes in complex ecosystems.

Biological Indicators and Sustainable Fire Regimes

Using biological indicators to predict post-fire responses in natural ecosystems is not new. For example, Noble and Slatyer (1980) developed a conceptual model based on life history attributes to predict post-fire responses in plant communities. In a detailed review of semi-arid vertebrates, Friend (1993) suggested that the responses of mammal species to fire could be predicted reasonably well from their life history parameters. However there are few examples of where these concepts have been applied to manage fire or to devise appropriate fire regimes at an operational level, especially where there is the added complication of the need to minimise the impact of wildfires on human life and property values.

In the absence of comprehensive long term fire effects data, a useful and practical approach to devising fire regimes which strive to satisfy wildfire protection and the maintenance of biodiversity is to use readily measurable biological indicators (bioindicators). These include:

- The identification of plants with thin bark, long juvenile periods and which depend on canopy-stored seed for regeneration (fire sensitive taxa).
- The determination of the juvenile period of these plants, the regeneration strategies of individual species and of plant communities and the post-fire floristic and structural changes of plant communities.
- Fuel (phytomass) accumulation rates.
- The identification of fauna which have specialised habitat requirements (food, shelter and breeding) (Friend 1993), which have a long juvenile period, a low reproductive capacity and which show high site fidelity (fire sensitive taxa).
- The post-fire response patterns of fire sensitive fauna.

The jarrah forest

Jarrah forest is a general description given to forested areas of south-west Western Australia in which the dominant overstorey species is jarrah or a mixture of jarrah and marri (*Corymbia calophylla* formerly *Eucalyptus calophylla*). The climate of the region is Mediterranean-type, with cool wet winters and warm/hot dry summers (Figure 1). Average annual rainfall across the range of the main forest belt varies from about 650 mm to 1300 mm of which 80% falls over the winter months. Summer and early autumn are warm to hot and dry and bushfires are common. The long association between climate, fire and vegetation has ensured that jarrah forest ecosystems have evolved a wide range of physical and behavioural adaptations to persist in this drought- and fire-prone environment (e.g., Gardner 1957; Christensen and Kimber 1975). Jarrah forests are widely distributed throughout south-west Western Australia, occurring on a range of geomorphological units. Prior to European settlement, jarrah was scattered over some 5.3 million ha, but today is restricted to about 3.3 million ha (Dell and Havel 1989). The jarrah tree reaches its best development in the high rainfall zone (1 100 - 1 300 mm annum^{-1}) along the Darling Scarp where it grows on lateritic soils and can reach mature top heights of 30-40 m. Further to the east, and as rainfall decreases, the mature trees are shorter (15-25 m) and the forest more open. The understorey varies across the range but upland forests in the northern and east parts of its range normally have a low open (10-30% cover) understorey of mixed woody shrubs and herbs to about 1.5 m. On moisture gaining sites, riparian zones and the southern portion of the main forest belt the understorey is structurally more complex, denser (60-100% cover) and taller (up to 2 m). Plant species composition is largely determined by soil type, rainfall and topography (Havel 1975). The jarrah forest is managed for multiple uses including timber, water production, conservation and recreation.

Fuel accumulation rates

The intensity or severity of a bushfire in terms of suppression difficulty and extent of physical damage, is a function of the amount of live and dead vegetation (fuel) which burns, weather and topography. Of these variables, only fuel quantity can be managed. This can be managed by physical removal or modification of the fuel, or by the use of prescribed fire to “burn off” the fuel. The frequency with which fuel reduction prescribed burns need to be implemented in order to manage fuel build-up depends on the rate of fuel accumulation, and the appraised risk of damage by wildfire (the risk of ignition, likely fire behaviour, detection and suppression capacity and values threatened - see Sneeuwjagt this volume). The number of days during summer and autumn when fires can be controlled, decreases with increasing fuel load. For much of the jarrah forest, experience has shown that when litter fuels on the forest floor accumulate over about 7 to 8 t ha^{-1}, then wildfire suppression becomes almost impossible under all but mild weather conditions. Therefore, fire managers aim to keep fuel loads to less than 7-8 t ha^{-1} throughout most of the forest. In situations where extremely high values are at risk, such as near townships, commercial tree plantations or known populations of particularly fire sensitive fauna or flora, then fuel levels in surrounding areas may be maintained at less than 4-5 t ha^{-1}. In other areas where there are no major values at risk, it may be acceptable to allow fuels to accumulate beyond 7-8 t ha^{-1}. A systematic analysis of wildfire threat is undertaken to determine the appropriate level of wildfire mitigation (Sneeuwjagt 1985, Sneeuwjagt this volume).

A knowledge of fuel accumulation rate is important for planning fuel reduction burning programs. For jarrah forests, fuel accumulation rate is a function of annual rainfall and overstorey canopy cover or tree basal area, as shown below in Figure 2 (from Burrows 1994). If litter fuels are to be maintained below about 4-5 t ha^{-1} or 7-8 t ha^{-1}, then based on a knowledge of fuel accumulation rate, the fire frequency will need to be 3-5 years and 6-8 years respectively, depending on rainfall and canopy cover.

FIGURES 1 AND 2 HERE

Vegetation response to fire

Unlike many northern hemisphere conifers, mature jarrah trees are resilient to even the most intense fires (Burrows 1987). Following scorch or defoliation by fire, jarrah quickly re-sprouts from epicormic shoots buried beneath thick protective bark and within several years, has replaced its crown. About 70% of all understorey species on drier, upland sites re-sprout following fire with the remainder regenerating from seed stored in the soil or in woody fruits in the canopy (Christensen and Kimber 1975; Bell and Koch 1980; Burrows *et al.* 1995). On seasonally moist sites (e.g., creek lines) the proportion of obligate seed species is often higher, varying from 40-60%. Generally, re-sprouting woody trees and shrubs are long lived, whereas obligate seed species tend to be shorter lived. For example, some species of *Acacia* which regenerate profusely from soil-stored seed following summer wildfire usually die within 7-10 years. This species depends on highly durable seed ("hard" seed) stored in the soil for regeneration (Peet 1971; Shea *et al.* 1979). As well as being important in their own right, leguminous taxa such as *Acacia* species are also important for maintaining the nutrient status of the forest (Shea and Kitt 1979).

With the predominance of resprouters and fire-induced seed germinators, the jarrah forest does not conform to the classical ecological species succession model following disturbance by fire. Bell and Koch (1980) showed that a single fire had little long term effect on floristic composition of the northern jarrah forest, which was mainly determined by edaphic and climatic factors. However, they found that species richness was greatest 3-5 years after fire then declined to pre-fire conditions as relatively short lived obligate seed species and herbs declined, only to persist in the seed bank (Figure 3). In the jarrah forest, seedling germination and successful establishment is very rare in the absence of fire. Long periods of fire exclusion could result in a permanent decline in plant species richness if the interval between fires exceeds the "shelf life" of soil-stored seed for some species.

Studies of more than 300 upland jarrah forest understorey species showed that all species reached flowering age within 3 years and 4 years of fire for high rainfall (1 150 mm annum^{-1}) and low rainfall (750 mm annum^{-1}) forests respectively (Burrows *et al.* 1995; Burrows and Friend in prep.) (Figure 4). Observations by the author of some relatively restricted species which occur on creek lines or wet broad valley floors in parts of the jarrah forest (e.g., *Lambertia rariflora, Melaleuca viminea*) show that these species can take 6-8 years to flower after fire. The former relies on soil-stored seed while the latter relies on canopy-stored seed to regenerate after fire (although occasionally some plants resprout). Time to first flowering after fire (juvenile period) is clearly important for determining minimum fire intervals, especially for obligate seeders with canopy-stored seed such as *M. viminea* and some species of *Hakea* and *Banksia* (fire sensitive species).

Juvenile period is not necessarily an indication of seed set and does not indicate the amount of seed stored either in the canopy or in the soil. For example, although *M. viminea* may flower 6-8 years after fire, flowering and hence seed set is very light in the early years post-fire. Gill and Nichols (1989) suggest that, if floristic biodiversity is to be maintained, then the minimum interval between fires should be double the juvenile period of the slowest maturing species to allow sufficient replenishment of seed banks (soil and canopy) following fire. Flowering phenology studies by other workers (e.g., Benson 1985; Auld and Myerscough 1986; Bradstock and O'Connell 1988) also suggest that seed production is poor in the first few years after first flowering. Therefore, a minimum, sustainable fire frequency for upland jarrah forests, based on time to first flowering of understorey species, is about 6 and 8 years for high rainfall and low rainfall forests respectively. Based on this criterion, low lying areas, creek lines and broad valley floors should not be burnt more frequently than 12-16 years, depending on presence or absence of fire sensitive species (species with long juvenile periods, which are obligate seeders and which store seed in the canopy). Occasional fires at shorter intervals are unlikely to be harmful to species richness while there exists a viable *in situ* or *ex situ* seed bank.

The rate of post-fire recovery of vegetation biomass and structure is yet another bioindicator of the productivity of the site, of habitat recovery, and therefore of fire interval to retain a specific habitat quality. As well as being important in its own right, vegetation provides important habitat elements such as food and shelter for animals. The structure of the vegetation is largely determined by site factors (geological and climatic), and the age of the vegetation (time since last fire). An example of the post-fire development of a jarrah forest understorey (biomass increment) on gully and midslope sites is shown in Figure 5. Habitat requirements for jarrah forest mammals varies for each species, with some preferring low open vegetation and others preferring tall, dense mature vegetation.

Season of fire can influence vegetation by impacting on biological processes which are seasonally queued, such as reproduction, and by the physical impact of fire. Many jarrah forest understorey species are queued to germinate by the products of combustion including heat and smoke. Seedling regeneration and survival was found to be significantly higher after a moderate intensity (500-1,000 kW/m) summer/autumn fire set under dry soil conditions than after a low intensity (<250 kW/m) spring fire set under moist fuel and soil conditions. Very few seedlings regenerate in the absence of fire (Burrows and Friend in prep.) (Figure 6).

FIGURES 3, 4, 5 AND 6 HERE

Response of Birds to Fire

The effect of a single fire on jarrah forest bird communities depends on the extent to which fire changes the structure (habitat) of the vegetation and how rapidly the vegetation regenerates to its former structure (Christensen *et al.* 1985). In general, resident forest birds can be segregated into guilds, depending on where in the forest profile the birds prefer to forage and nest. While some birds are generalists, most can be classified as a) ground foragers, b) mid-storey foragers and c) canopy leaf gleaners (Christensen *et al.* 1985). The extent to which birds are affected by fire largely depends on the extent to which their preferred habitat has been affected by fire. Fire intensity (Byram 1959), or flame height, is the major factor determining the impact of fire on the structure of vegetation, therefore on forest birds. Fire causes temporary short term changes in the species composition and numbers of resident birds, commensurate with the level of damage to the vegetation and the rate of post-fire recovery of the vegetation structure. Christensen *et al.* (1985) found that both the number of birds and the number of species increased in the first three years after a low to moderate intensity prescribed fire then returned to pre-fire conditions within about three years. High intensity wildfire causing total defoliation of the jarrah forest over a large area had a significant negative impact on the density and species diversity of resident birds (Christensen *et al.* 1986) (Figure 7).

FIGURE 7 HERE

Response of Mammals to Fire

The response of forest mammals to fire can be predicted to some extent by understanding their post-fire responses and life histories (Friend 1993, Whelan 1995). Almost without exception, the impact of fire on jarrah forest mammals depends on the habitat requirements, life history of the animal and on the intensity, scale and patchiness of the fire, or the extent of habitat fire damage. As with birds, mammals can be roughly grouped according to their general habitat type (Table 1). There is a group of mammals which prefer mature, tall and dense vegetation normally associated with seasonally moist sites such as along creeks, swamps and broad wet valleys where the dominant fuel is elevated live and dead scrub. Similarly there is another group of mammals which prefer more open vegetation usually associated with midslopes and ridges. The position in the landscape (ridge, midslope, creekline etc.) and soil properties affect the floristics, structure and biomass of vegetation associated with the habitat types shown in Table 1. These characteristics also affect the flammability or fuel properties of these habitat types. The fuel on upland sites consists of a continuous layer of surface litter shed from overstorey *Eucalyptus* trees which dry faster and therefore earlier than the mainly elevated shrub fuels in wetter lowlands. The difference in fuel structure and drying rates between upland and lowland fuels is the basis for the flammability differentials in Table 1.

The large and more mobile macropods such as the Western Grey Kangaroo and the Brush Wallaby, are most abundant in the first few years after fire (Christensen and Kimber 1975) (Figure 8). These highly mobile animals feed on the new succulent post-fire regrowth and take advantage of the open conditions to move freely about. If the area burnt is relatively small (about <500 ha and < 1,000 ha in high and low rainfall forest respectively), then these animals can have a very significant grazing impact (Per Christensen personal communication). The impact of fire on mammals which inhabit seasonally moist or wet sites which carry dense vegetation such as swamps, creeks and valley floors, depends on the scale and intensity of the fire. These animals are severely impacted upon by large and intense fires which consume entire swamp complexes or valley systems and may take many years to reach pre-fire abundances (Christensen and Kimber 1975) (Figure 8). However, a low intensity fire which burnt out about 30% of a swamp containing Quokkas had very little impact on Quokka numbers (Christensen and Kimber 1975). Quokkas grazed on the burnt area but were not resident in this area, preferring the dense cover of adjacent long unburnt vegetation. It takes about 10-15 years before creek vegetation in jarrah forests is suitable as habitat for Quokkas (Per Christensen, personal communication). Similar observations have been made for other valley floor fauna such as the Tammar Wallaby (Christensen 1980,1982).

The Southern Brown Bandicoot (*Isoodon obesulus*) is also found in thick vegetation along creek lines in most parts of the jarrah forest. Providing there is adequate vegetation cover, this omnivorous marsupial is able to utilise a wide range of post-fire stages from recently burnt to long unburnt vegetation, preferring an interlocking mosaic of vegetation at different seral stages (Braithwaite 1983). As with many medium sized mammals, large and intense fires have an acute and often severe impact on local populations. The author observed high mortality rates of Southern Brown Bandicoots immediately following a high intensity (3,500-6,000 kW m^{-1}) wildfire which totally defoliated the forest including a 1.2 km section of a creek system. Two days after the fire, the author collected 11 burnt Bandicoot carcasses along the section of defoliated creek. However, the high reproductive rate and the generalist diet of these animals enables them to readily re-colonise an area provided the burnt area is not large (say < 2,000 ha) and they are not heavily predated by the introduced European Fox (*Vulpes vulpes*).

Honey Possums are similarly severely affected by large and intense fires which result in complete or near complete landscape burn-out (Richardson and Wooller 1991). Unlike the Southern Brown Bandicoot, this small marsupial is relatively sedentary, has a specialised diet of pollen and nectar and is most abundant in mature vegetation (10-15 years since fire). They nest in elevated vegetation and are either killed by the fire or are predated or starve within a few days of the fire. In the presence of introduced predators such as the fox and the feral cat (*Felis catus*), these animals face the possibility of local decline following large and intense fires. However, if fires are patchy and relatively small, then they can recolonise relatively quickly from unburnt patches. Idealised post-fire response patterns for several species of mammals which inhabit dense vegetation along creek lines and in swamps are shown in Figure 8. The reduction in numbers of Tammar and Quokka after about 25-30 years after fire reflects habitat senescence, reduction of cover and subsequent decline in populations.

A space-for-time survey (Burrows *et al.* 1996) of the density of Brush-tail and Ring-tail possums in eastern (low rainfall) jarrah forest in relation to time since fire revealed that the densities of both species was greatest in sites which were burnt 5-10 years previously (Figure 8) and least in forests which were long unburnt (up to 45 years) and very recently burnt. It is possible that foliar nutrient levels decline in long unburnt vegetation, so the carrying capacity falls. The survey also revealed that predation by the fox was the main factor affecting possum densities in these forests. Significantly higher possum densities occurred in forests where the fox had been controlled. That is, highest possum densities were found in forests where fox control had been carried out and which were last burnt 5-10 years previously by low intensity prescribed fires.

TABLE 1 AND FIGURE 8 HERE

Fire intensity and scale or patchiness of fire critically affects the capacity of arboreal mammals, such as Possums and Phascogales to persist and re-populate after fire. For example, a small scale (100 ha) experimental burn in woodland east of the main jarrah forest belt had very little long term impact on populations of Red-tailed Phascogale (Burrows and Friend in prep.) (Figure 9). Animals within the burnt area and which were directly affected by the heat of the fire were severely impacted upon, with about 30% being killed directly by the fire. However re-colonisation from adjacent unburnt woodlands resulted in a rapid recovery of animals and within several months, the number of animals known to be alive in the burnt and unburnt grids was similar. In the same experimental fire, another species, the Little Long-tailed Dunnart, showed a different response to the same fire. In the first two months or so after fire, the population remained steady, but then fell significantly, as did the population in the unburnt control. For the first 18 months after fire, the populations in the control and the burnt plot fluctuated, but numbers in the burnt plot remained consistently below those in the control for about 24 months. Being able to shelter in burrows and having a more general diet enabled these animals to persist on the burnt site, albeit in reduced numbers. Unlike the Red-tailed Phascogale, the Little Long-tailed Dunnart population increased due to both dispersal and *in situ* breeding. While there are no data available for these species, it is highly likely that they would take much longer to recover after a large and intense summer or autumn fire because of their limited capacity to survive *in situ* during and after an intense fire, and their dependence on recolonisation. On the other hand, experimental evidence (Burrows and Friend in prep.) shows that impacts of low intensity, small or patchy fires are relatively small and short lived.

FIGURE 9 HERE

Response of frogs and reptiles

Frogs mostly burrow deep in the soil during dry periods when fires are likely to occur so evade the acute impacts of fire (Friend 1993). Having a generalist invertebrate diet also enables most frog species in dry sclerophyll forests and woodlands to be little affected by fire (Bamford 1986, 1992). A jarrah forest frog (*Neobatrachus pelobatoides*) studied by Friend (1993) was not affected by a single fire and frog capture rates were mostly influenced by seasonal rainfall. Some species such as tree dwellers (e.g., *Littoria cyclorhychus*) are likely to be directly affected by intense fires burning under dry conditions, but there are no published data on this (Friend 1993).

Reptiles, especially lizards are more resilient to fire than mammals because of their physiological adaptations to arid conditions (Friend 1993). Most reptiles are burrowers with generalised invertebrate diets and strongly seasonal activity and breeding patterns. Survival may be relatively high during a fire, but predation and starvation may be significant in the early post-fire period (Newsome *et al.* 1975, Friend 1993). Species which inhabit jarrah forest leaf litter and feed on leaf litter invertebrates (e.g., *Morethia obscura*) were affected for up to two years by a high intensity summer/autumn (dry conditions). This species is less likely to be affected by patchy, low intensity fires. Generally reptile species richness and abundance are greater in recently burnt vegetation than in long unburnt vegetation (Friend 1993, Bamford 1986). Bamford (1995) working in Banksia woodlands in south-west Australia found that the greatest changes to reptile populations occurred in the first few years after fire and was largely limited to short term changes in population structure with some species increasing after fire and others decreasing. He suggested that the absence of a long term fire response was probably a function of survival of adult animals during the fire and the relatively rapid post-fire regeneration of the vegetation.

Response of invertebrates

In south-west Australian ecosystems, invertebrates typically decline immediately after fire, but most species/groups return to pre-fire abundances and species diversity levels within 1-2 years (Abbott 1984; Majer 1984; Strehlow 1993; Friend and Williams 1996). While there are no published long term studies, Abbott *et al.* (1984), in a space-for-time study found that repeated low intensity fires in upland jarrah forest had little effect on the diversity and abundance of soil and litter invertebrate fauna. The level of taxonomic resolution influences the interpretation of results of fire impact studies because individual species may be markedly affected, but at the Order level these important observations and trends will be obscured. Studies of the response of ground dwelling spiders in woodland vegetation east of the main jarrah forest belt (Strehlow 1993) showed that invertebrate post-fire succession does not necessarily return to the pre-fire state but instead to a new transient state also occupied by undisturbed communities.

Invertebrate population responses are highly variable in space and time and seasonal factors such as rainfall often outweigh any effects due to fire (Friend and Williams 1996). Some invertebrate groups are more sensitive to fire than others. For example, long-lived sedentary animals such as the trap-door spiders (Myglamorphs) are vulnerable to fire and if extant animals are killed by fire, the species could become locally depleted for a period of time (Main 1987).

An Interim Fire Regime to Preserve Biodiversity

In most of the world's fire prone environments, managers will always be faced with the dilemma of a) prescribed burning for fuel management to mitigate the threats of wildfire and b) implementing fire regimes (which may include fire exclusion for long periods) to preserve biodiversity. At the extreme, these objectives are not compatible in most habitat types. That is, persistent rotational burning at very short intervals, or at frequencies less than the juvenile period of the slowest maturing obligate seed species (i.e. <3 years in high rainfall jarrah upland forests), and over large areas will significantly reduce the risk of wildfire damage, but is likely to increase the risk of local decline in biodiversity over time. On the other hand, attempts to exclude fire from large areas will inevitably lead to large and intense wildfires, large tracts of old, senescing vegetation, reduced variability of post-fire seral stages at the local scale and accompanying reduction in biodiversity.

The difficulty with managing for biodiversity *per se*, is that at the regional or local scale, it is probably impossible to define, even at the species level, and it is highly unlikely that the effects of fire on all species and communities will ever be completely known. Lack of knowledge can be a good reason or an excuse for lack of management action in a fire prone environment. Inaction, or a decision to take no action, can threaten biodiversity because it is likely to result in uncontrolled fire regimes particularly in environments prone to arson, or unplanned fires. The consequences of this are often infrequent but large and intense wildfires causing substantial environmental and social damage. In the absence of long term data, baseline data about fuel accumulation rates, vegetation regeneration strategies, post-fire response patterns and life histories of faunal elements can be used as a basis for devising an appropriate fire regime (fire frequency, season, intensity and patchiness) which can be modified as more information becomes available (adaptive management).

Setting fire frequency using bioindicators

When litter fuels in jarrah forests accumulate beyond about 7-8 t ha^{-1} then there is an unacceptable number of days when fires will burn with such intensity as to be uncontrollable and very damaging (Underwood *et al.* 1985; Sneeuwjagt 1989;

Sneeuwjagt this volume). Therefore, based on a knowledge of fuel accumulation, it would be desirable from a wildfire mitigation perspective to prescribe burn the jarrah forest at intervals no longer than about 6-8 years (see Figure 2). Clearly if prescribed burning were to be conducted more frequently (say every 2-3 years) then the level of protection against wildfires would be improved but biodiversity would probably decline. As discussed above, the sustainable minimum interval between fires based on age to first flowering and seed bank replenishment is 6-8 years for upland sites and 12-16 years for creek lines, swamps and non-forested, seasonally wet lowlands. These fire frequencies also satisfy vascular plant species richness requirements (Figures 3, 4 and 5), and cater for the post-fire response patterns of vertebrate and invertebrate fauna described above. Higher populations of valley floor/riparian zone mammal fauna (e.g., Quokka, Tammar Wallaby and Bandicoot, see Table 1) can be maintained by longer intervals between fire but in the absence of predation by the introduced fox it may be possible for less mature vegetation to provide suitable cover for these animals. On the other hand, excluding fire for long periods leads vegetation senescence and to a decrease in both plant and animal diversity. Thus, in terms of the frequency component of fire regimes to maintain biodiversity in jarrah forests, the bioindicators suggest that very frequent (<3 years) and very infrequent (>30 years) fire intervals are likely to result in a reduction in biodiversity.

Therefore, even at the local scale (thousands of ha) within a broad forest type, there is a requirement for differential fire frequencies based on the habitat type and position in the landscape (Table 1); a frequency of 6-8 years being adequate for uplands, but the lowlands requiring at least double this for the preservation of biodiversity.

Setting fire season, intensity and patchiness (scale) using bioindicators

In Mediterranean-type climates particularly, season reflects the extent of landscape dryness and therefore the proportion of the landscape which will burn. This in turn affects both the patchiness and intensity (therefore damage to vegetation/habitat) of fire. Setting prescribed fires under mild weather conditions early in spring when fuel moisture content (therefore flammability) is variable across the landscape will usually result in a low intensity and patchy fire. Most of the drier ridge and midslope areas will burn, but important riparian and swamp habitat will not burn because it will be too moist at this time of year. Likewise, large hollow logs and old trees with hollows, both of which are important faunal refugia, are unlikely to catch alight or burn away under these conditions.

However fires which burn following extended dry periods in summer and autumn when there is little or no moisture (flammability) differential across the landscape will burn intensely and will generally burn out the entire landscape including riparian zones and a higher proportion of hollow trees and logs. Such fires are more intense and burn substantially more live and dead vegetation, or habitat, than early spring fires. Scale and patchiness of fire are crucial elements of a fire regime which impact on the diversity of fauna particularly. The above examples show that the rate of recolonisation of several species is facilitated by the relatively small size or the patchiness of the burn. The special riparian habitats of mammals such as Quokka, Mardo, Bandicoot and Tammar Wallaby can be protected or maintained by setting fire under cool, moist conditions in spring when the ridges and midslopes are dry enough to carry low intensity fire (<350 kW m^{-1}), but creeks and sparsely forested valley floors are too moist to carry fire or fuels are too light to burn under cool moist conditions. Burning under such conditions provides refugia for animals which occupy these habitats. If these habitat types were burnt regular by large summer or autumn fires they would soon be depleted of these mammals and of many species of fire sensitive plants. However, an occasional fire under dry soil conditions in summer or autumn is necessary to regenerate the habitat (Christensen 1982; Christensen and Maisey 1987). Larger mammals such as Quokka and Tammar Wallaby will decline as their habitat senesces. Creeks and wetland systems should only be partially burnt in any one prescribed autumn fire event to allow for the potential of recolonisation from adjacent long unburnt habitats. Individual low intensity spring burns which are patchy (60-70% burn) and do not burn creeks and lowlands, should not exceed about 3-5 000 ha in area. Autumn/summer prescribed burns which result in complete landscape burnout should not exceed about 1-2,500 ha. If prescribed burns are interspersed to form an interlocking patchwork of forest blocks (each 1 000 - 5 000 ha) at different stages of post-fire development, this will ensure a mosaic at both local and regional scales of habitat diversity. A capacity to implement such prescribed fires requires reliable fire danger, fire behaviour and fire weather forecasting systems.

While low intensity, patchy spring burns reduce fuels on upland sites, retain important habitats, and cause minimal physical damage to habitat and commercial tree species, both the season of fire and the interval between fires should be varied to maintain biodiversity. Season of fire *per se* does not appear to be important to the fauna described above but it does affect the density, survival and vigour of seedling regeneration. Low to moderate intensity fires (350-1,000 kW m_{-1}) under dry soil and fuel conditions stimulates the prolific regeneration and survival of many obligate seed species and of overstorey tree species which take advantage of fire-prepared seed beds (e.g., Shea *et al.* 1979; 1981; Burrows *et al.* 1990). As well as being important in their own right, many obligate seed species form fire-induced thickets which are important for habitat. Often many are leguminous, so are important for ecosystem nutrient status (Shea and Kitt 1979).

Conclusion

Fire is an important environmental factor influencing the composition, distribution and abundance of living organisms. Knowledge of the temporal and spatial effects of fire and of fire regimes (frequency, intensity and seasonallity) is imperfect due in part to the complexity of ecosystem processes, spatial and temporal variability and to the poor taxonomic knowledge of the numerous organisms which comprise natural ecosystems.

Fire regimes which strive to achieve protection and biodiversity objectives can be devised at the local and regional scale in the absence of comprehensive long term data based on a combination of historical evidence and a growing knowledge of fire behaviour, fuel accumulation rates, fire ecology and life history attributes and post-fire response patterns of key floral and faunal elements. Case studies in the jarrah forests of Western Australia show that patterns emerge from these data sets which enables the derivation of appropriate fire regimes. Important fire regime components and bioindicators for setting these are:

> Minimum interval between fires to sustain biodiversity: This can be estimated from the juvenile period of the slowest maturing vascular plants (especially obligate seeders) and from the post-fire response patterns of fire sensitive taxa of fauna and flora.

- Minimum interval between fires for wildfire control: Estimated from fuel accumulation and fire behaviour models, and wildfire threat analysis.

- Maximum interval between fires to sustain biodiversity: Estimated from plant species richness with time since fire, seed bank quantity and durability (shelf life), vegetation/habitat biomass increment and structural changes with time, post-fire response patterns and habitat requirements of key fauna.

- Fire intensity: This will determine the level of acute physical impact of fire on vegetation, on habitat and on individual organisms. Generally, the greater the intensity, the gretaer the impact on habitat.

- Scale and patchiness of fire: Estimated from habitat requirements, life histories and post-fire response patterns of key fauna.

As a general rule of thumb, jarrah forest fauna are favoured by small to medium sized (1 000-3 000 ha), low intensity (<350 kW m^{-1}), patchy fires and are disadvantaged by large (>3 000 ha), intense and uniform (complete landscape burnout) fires. In the face of predation by introduced predators, some species may decline locally following large intense wildfires or very frequent fires (less than the juvenile period of slowest maturing plant species). Seasonal and topographical moisture differentials existing across landscapes at certain times can be exploited to prescribe and implement fires which are low intensity, patchy and meet protection objectives.

Occasionally, vegetation or habitat regeneration fires are necessary. Often these need to be set under dry conditions which result in burn-out of the entire landscape. Providing the scale and frequency of such fires is limited, then such variation in fire season will enhance biodiversity.

These elements are contained in the fire regime illustrated in Figure 10. Based on the bioindicators, this interim fire regime for jarrah forests demonstrates the compatibility of managing fire to satisfy wildfire protection requirements and to maintain biodiversity.

Figure 10 Here

Acknowledgments

This paper is not a review, but refers to the published findings of many workers. In particular, it draws on and is an expansion of a paper being prepared for publication by Gordon Friend and me. I thank Bruce Ward and Alex Robinson for their invaluable assistance and contribution to jarrah forest fire ecology research and Per Christensen for his pioneering work in forest fire ecology in south-west Australia.

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Table 1: Broad grouping of some jarrah forest mammals based on landform/vegetation types and flammability of habitat.

Common Name	**Scientific Name**	**Preferred habitat type and flammability**
Quokka	*Setonix brachyurus*	Tall, dense, mature understorey vegetation in creeks, swamps and valleys. Low flammability in winter and spring, but extremely flammable in summer and autumn.
Mardo	*Antechinus flavipes*	
Quenda	*Isoodon obesulus*	
Honey Possum	*Tarsipes rostratus*	
Pygmy Possum	*Cercatetus concinnus*	
Bush Rat	*Rattus fuscipes*	
Numbat	*Myrmecobius fasciatus*	Low open understorey vegetation, ridges, midslopes and broad valleys. Low flammability in winter, moderate in spring and highly flammable in summer and autumn.
Ring-tail Possum	*Pseudocheirus peregrinus*	
Echidna	*Tachyglossus aculeatus*	
Chuditch	*Dasyurus geoffroii*	
Brush-tailed Possum	*Trichosurus vulpecula*	
Brush Wallaby	*Macropus irma*	
Western Grey Kangaroo	*Macropus fuliginosus*	
Woylie	*Bettongia penicilata*	
Tammar	*Macropus eugenii*	Tall, dense thickets with grassy ground cover along broad valley floors. Very low flammability in winter and spring, highly flammable in summer and autumn.
Brush-tailed Phascogale	*Phascogale tapoatafa*	Recorded in a wide range of habitat types including ridges, midslopes, creek lines and swamps
Red-tailed Phascogale	*Phascogale calura*	
Fat-tailed Dunnart	*Sminthopsis crassicaudata*	
Dunnart	*Sminthopsis murina*	

CAPTIONS FOR FIGURES

Figure 1: Mean monthly rainfall and daily maximum temperature for the Perth, Western Australia, illustrating the annual fire season experienced in the region which experiences a strong Mediterranean-type climate.

Figure 2: A model of surface litter fuel accumulation in jarrah forests with time since fire (Burrows 1994).

Figure 3: Vascular plant species richness with time since fire in a northern jarrah forest (adapted from Bell and Koch 1980).

Figure 4: The proportion of upland jarrah forest understorey species to have flowered with time since fire for various rainfall zones.

Figure 5: Understorey shrub biomass increment for a) midslope and b) creekline sites in a jarrah forest near Nannup, Western Australia.

Figure 6: Seedling density and species richness measured about 12 months after spring and autumn fires in a jarrah forest.

Figure 7: Bird density and species richness measured in jarrah forests a) unburnt for 14 yrs, b) 6 months after a low intensity (<350 kW m^{-1}) prescribed fire and c) 12 months after a high intensity wildfire (Christensen *et al.* 1985).

Figure 8: Idealised post-fire response patterns for a range of mammals which occur in jarrah forests.

Figure 9: Response of Red-tail Phascogale (*Phascogale calura*) populations to a small and patchy experimental fire in woodlands in south-west Western Australia.

Figure 10: A managed fire regime for jarrah forests developed from biological indicators for the dual purpose of ameliorating the threat posed by wildfire and for maintaining biodiversity.

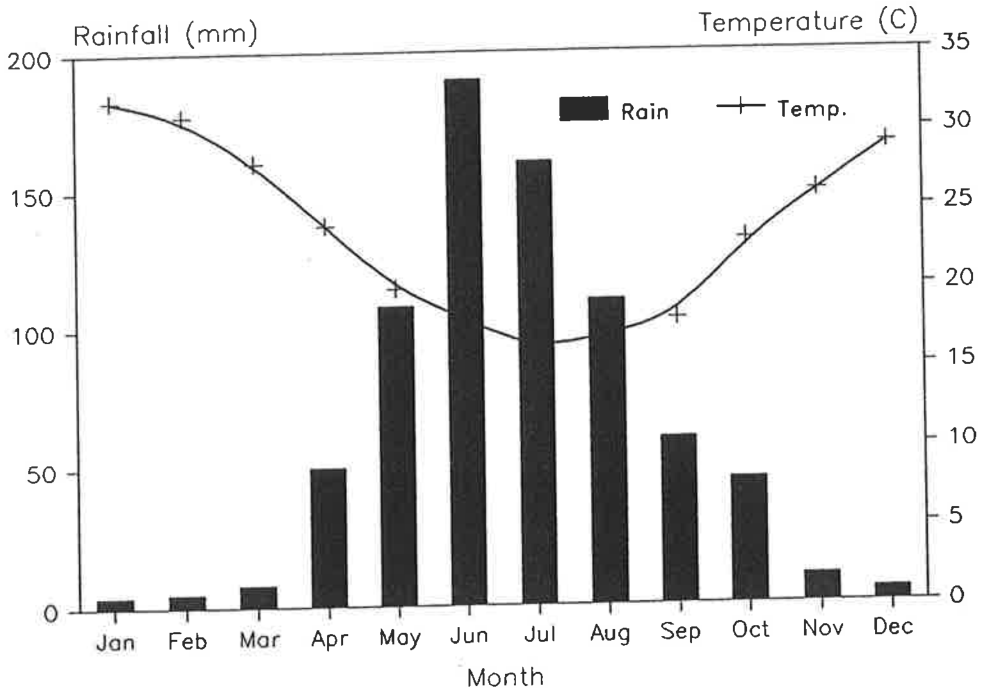

Rainfall (mm)
Temperature (C)
200
150
100
50
0
35
30
25
20
15
10
5
0
Rain
Temp.
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Fig. 1

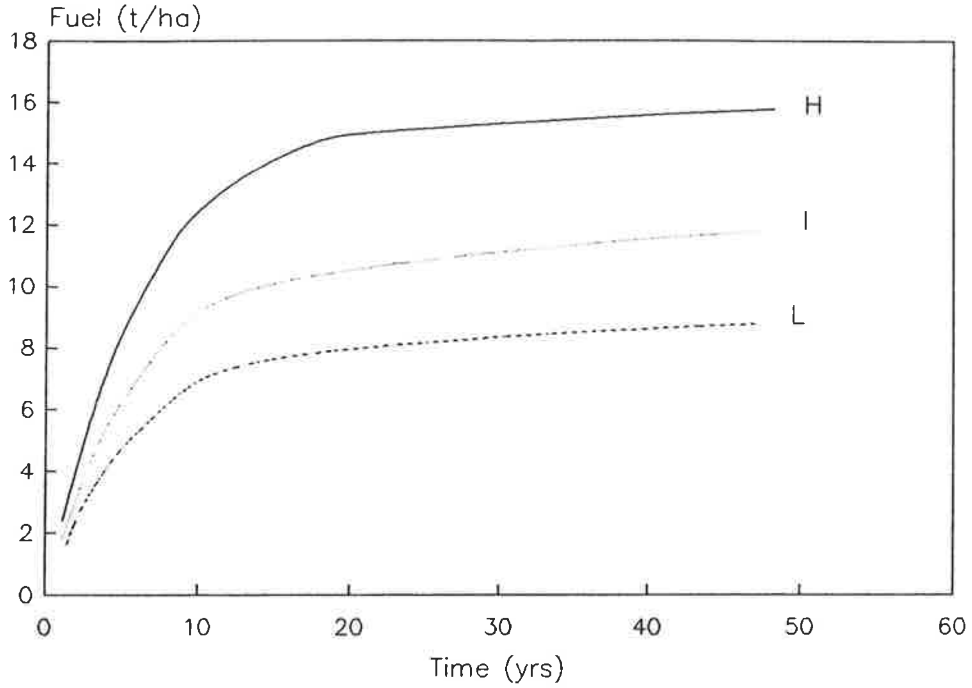


Fig. 2

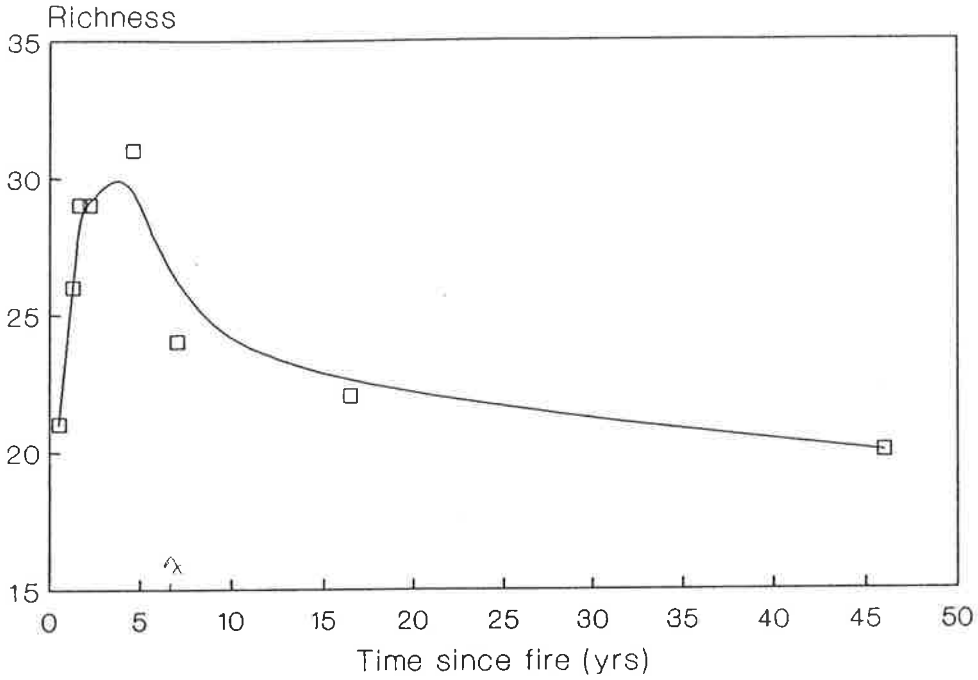

Richness
35
30
25
20
15
0
5
10
15
20
25
30
35
40
45
50
Time since fire (yrs)

Fig. 3

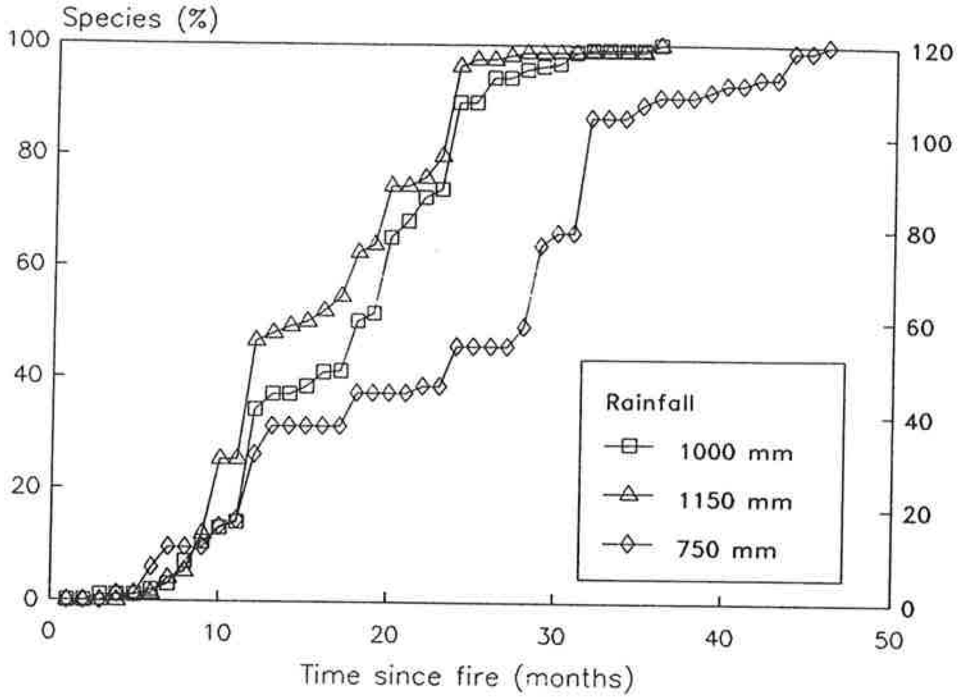

Species (%)
100
80
60
40
20
0
120
100
80
60
40
20
0
0
10
20
30
40
50
Time since fire (months)
Rainfall
1000 mm
1150 mm
750 mm

Fig. 4

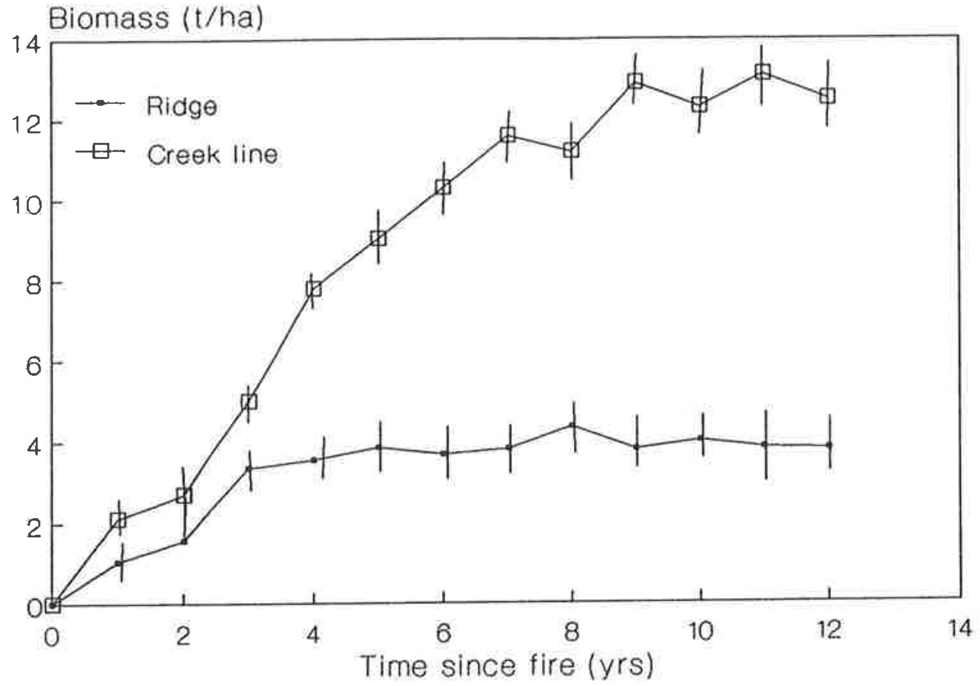

Biomass (t/ha)
14
12
10
8
6
4
2
0
Ridge
Creek line
0
2
4
6
8
10
12
14
Time since fire (yrs)

Fig 5.

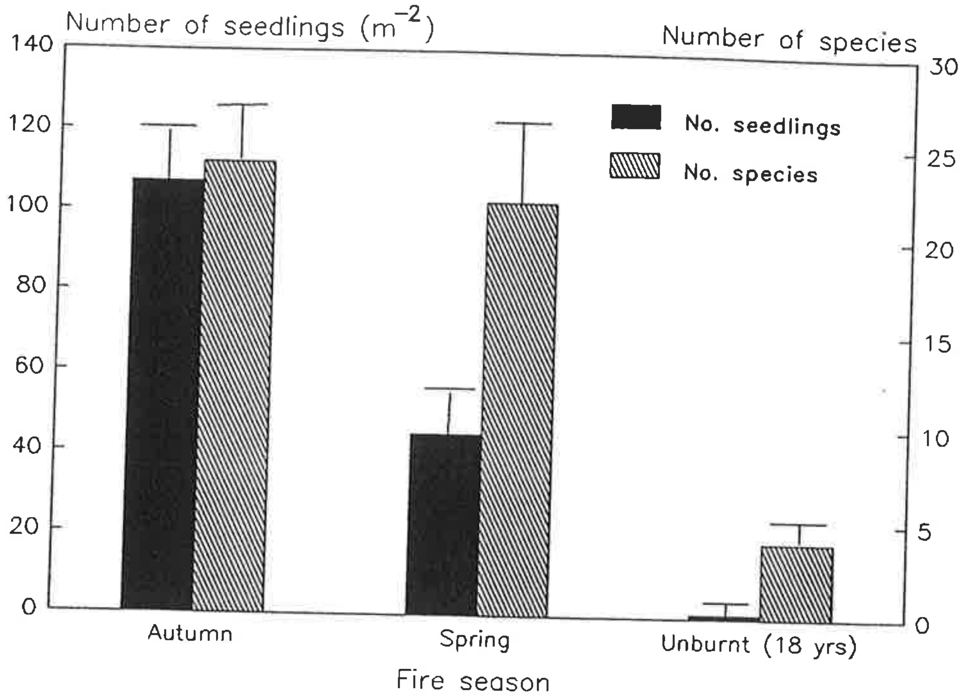

Number of seedlings (m^{-2})
Number of species
140
120
100
80
60
40
20
0
30
25
20
15
10
5
0
No. seedlings
No. species
Autumn
Spring
Unburnt (18 yrs)
Fire season

Fig. 6.

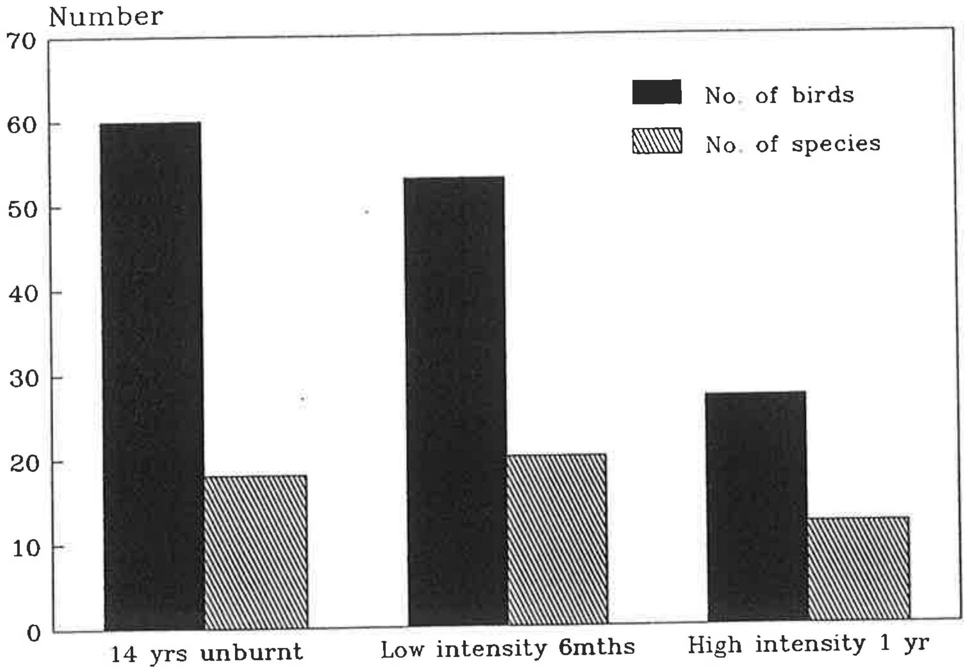

Number
70
60
50
40
30
20
10
0
No. of birds
No. of species
14 yrs unburnt
Low intensity 6mths
High intensity 1 yr

Fig. 7.

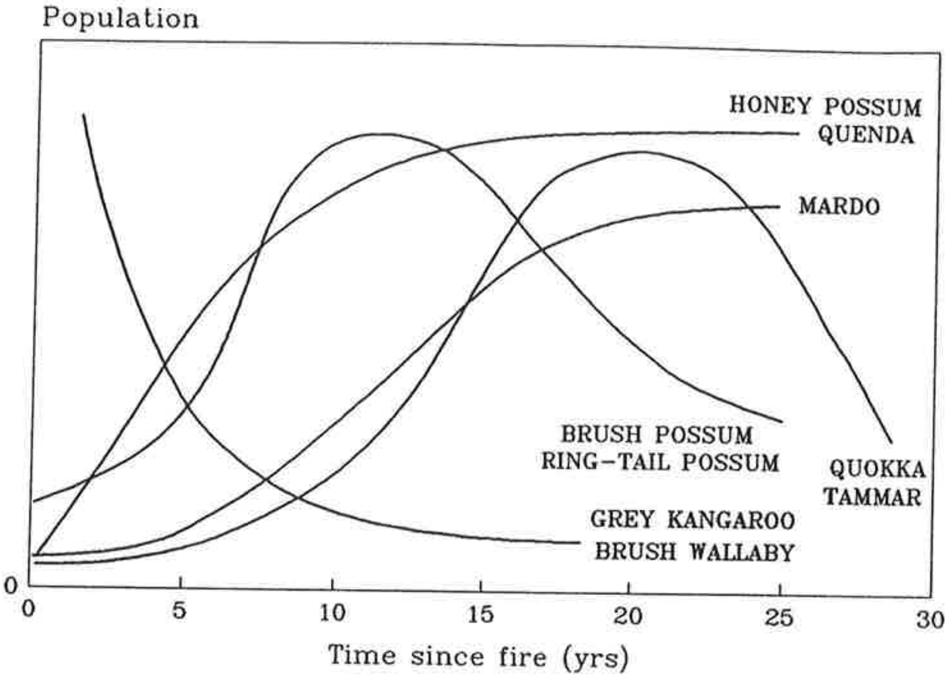

Population
HONEY POSSUM
QUENDA
MARDO
BRUSH POSSUM
RING-TAIL POSSUM
QUOKKA
TAMMAR
GREY KANGAROO
BRUSH WALLABY
0
0
5
10
15
20
25
30
Time since fire (yrs)

Fig 8.

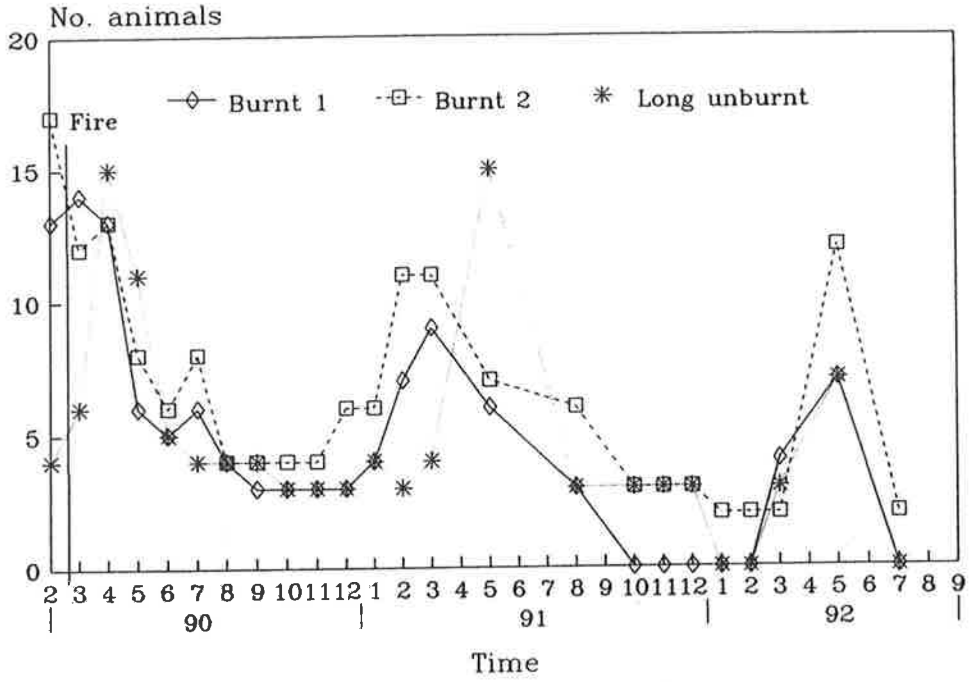
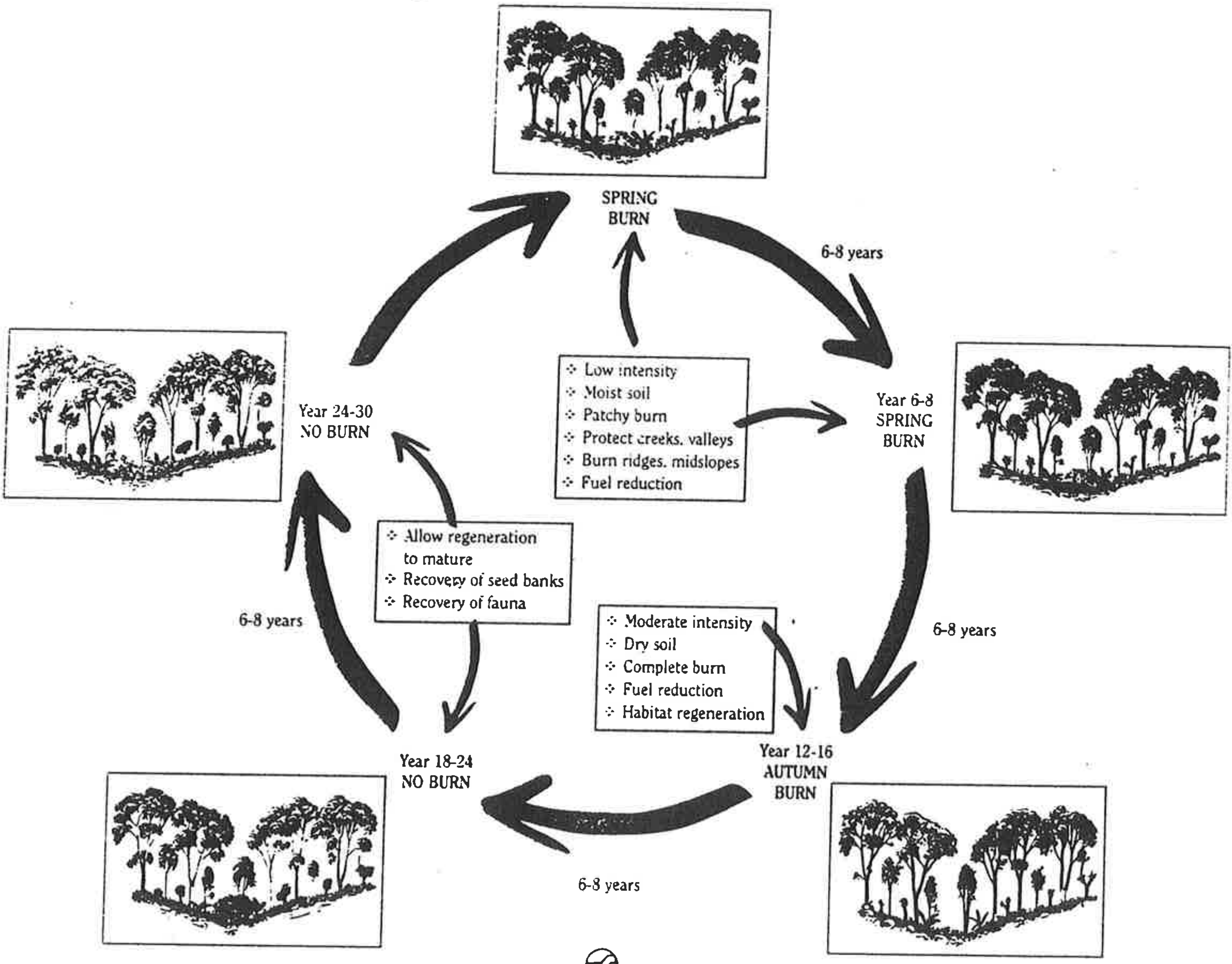

No. animals
20
15
10
5
0
Burnt 1
Burnt 2
Long unburnt
Fire
2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9
90
91
92
Time

Fig. 9

A MANAGED FIRE REGIME FOR JARRAH FOREST



DEPARTMENT OF CONSERVATION AND LAND MANAGEMENT

Fig. 10.