

# The influence of plant diversity on the resilience of harvester termites to fire

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The harvester termites in floristically rich mallee-heath of southern Western Australia appear resilient to high-intensity fire. This contrasts with the temporary extinction of harvesters occupying a narrow food niche in floristically simple, intensely burnt spinifex *Triodia angusta* grassland in tropical Western Australia. The present study examines the effects of high-intensity fire on harvester termites *Drepanotermes tamminensis* in vegetation of intermediate floristic diversity and compares its findings with these earlier studies. We sampled 20 mounds (termitaria) in both an unburnt and (adjacent) burnt stand of *Allocasuarina campestris* shrubland. Although partially regenerated three years after the fire, 40% of mounds in the burnt area were abandoned, contrasting with 10% in the unburnt stand. No harvested chaff was found in any of the abandoned mounds. The extent of mound occupation by *D. tamminensis* was considerably lower, and ant invasion higher, in the burnt stand.

These findings are consistent with the hypothesis that high floristic diversity enhances the resilience of harvester termites to fire. The most likely mechanism is the availability of a range of plant (food) species with different regenerative responses to high-intensity fire.

The death of spinifex and the associated harvester termites after fire may be atypical. We argue, however, that temporary extinction of harvester populations in arid Australia may not be exceptional, particularly where fire coincides with drought and high livestock grazing pressure. Rigorous experimental studies are necessary to enhance our understanding of the long-term effects of fire on harvester termite populations in different vegetation types and climatic zones.

Key words: Ants, *Drepanotermes tamminensis*, Fire, Food Niche, Harvester Termites, Mound Invasion, Resilience, Plant Diversity.

## INTRODUCTION

ANIMAL populations fluctuate in response to disturbance. The term "resilience" describes their ability to return to pre-disturbance levels, and can be expressed as the probability of local extinction as a direct result of the disturbance event (Connell and Slatyer 1977). Resilience of all consumers should be enhanced by the presence of multiple pathways of energy transfer under a wide range of circumstances following disturbance (MacArthur 1955; Main 1981). High-intensity fire is potentially a catastrophic event for those species directly depending on plants for food. The degree of resilience of the populations of such species following the burn will be partly influenced by their ability to move to unaffected areas and so minimize population decline. If they are unable to move, then survival (resilience) will be determined largely by physiological requirements and by the rate of plant regeneration. Energy-frugal consumers will be advantaged, and probability of survival will be enhanced where the plant community recovers rapidly following fire. More diverse plant communities are likely to contain species which display a range of responses to fire, and hence have a higher probability of containing rapidly responding species.

Given their considerable abundance, termites in arid and semi-arid Australia fulfil an important ecological role (Stafford Smith and Morton 1990). They are a critical component in the nutrient-cycling process (Holt 1987; Noble and Tongway

1988; Tongway *et al.* 1989; Andersen and Lonsdale 1990; Holt and Coventry 1990; Lobry de Bruyn and Conacher 1990) and they provide the basis of many food chains (Greenlade 1970; Morton and James 1988; James 1991; Abensperg-Traun 1994). Biomass of termite populations have been estimated to greatly exceed that of native mammalian herbivores, and to match that of livestock in many arid and semi-arid regions of Australia (Wood and Lee 1971; Watson *et al.* 1973; Holt and Easey 1984; Watson *et al.* 1988). Because termites depend almost entirely on plants for food (Wood 1978), and because fire is frequently used in ecosystem management over large parts of inland Australia (Stocker and Mott 1981; Hodgkinson *et al.* 1984; Morton and Andrew 1987; Kealley 1991; Lonsdale and Braithwaite 1991; Andersen and Braithwaite 1992; Strehlow 1993), a clear understanding of the effects of fire on termites is necessary for sound ecosystem management.

Despite some plasticity in the types of plant material eaten by termites (Wood 1978), high intensity fire may threaten their survival by destroying a large proportion of their food resource. Wood-eating termites retain a subterranean source of food (roots) following fire. Harvester termites, in contrast, may be particularly susceptible to a high-intensity fire which temporarily destroys their principal food resource, grasses and litter, and the plants that provide them. Although colonies may initially

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survive on stored reserves, plant regeneration following fire may not keep pace with the termite's consumption of its food stores. This depletion of resources may occur during drought when regeneration is slow, or through competition with livestock for the regenerating resource, or both. In such cases, temporary extinction of harvester colonies is a real possibility (Watson *et al.* 1973). Harvester termite colonies may consist of hundreds of thousands of individuals (workers and soldiers). Estimates of annual harvests give values in excess of 100 kg of grass per ha for mound-building (*Drepanotermes*) species alone; subterranean harvester species add to that total (Watson *et al.* 1973). During prolonged periods of food shortage, plant productivity may be inadequate to sustain large colonies, threatening survival or causing population decline.

Termites of the endemic genus *Drepanotermes* are common throughout most of arid and semi-arid Australia, a fire-prone environment (Morton and Andrew 1987; Stafford Smith and Morton 1990) where they harvest primarily dry grasses, forbs, leaf and bark litter (Watson *et al.* 1973, 1988; Watson and Perry 1981; Abensperg-Traun and De Boer 1990; Park *et al.* 1993). Only two studies report fire effects on Australian harvester termites. Perry (1972) records the temporary extinction of *Drepanotermes* colonies two years after a high-intensity burn killed floristically simple spinifex *Triodia angusta* hummock grassland on arid Barrow Island, Western Australia. In contrast, harvesters *Tumulitermes westraliensis* in the floristically rich mallee-heath in the semi-arid south of Western Australia appeared unaffected by a high-intensity fire (Abensperg-Traun and Milewski 1995). Both studies were conducted two years after the fires. Plant diversity may thus have an important influence on harvester termite resilience to high-intensity fire, the most likely mechanism being differences in the availability of food plants with different regenerative powers following fire. This may have important implications for many arid and semi-arid Australian ecosystems where fire is the principal consumer of plant material (Ridpath 1985; Morton and Andrew 1987; Braithwaite 1990; Holt and Coventry 1990; Stafford Smith and Morton 1990; Griffin 1992). The present study examines the effects of a high-intensity fire three years previously on harvester termites *Drepanotermes tamminensis* in a vegetation type of intermediate floristic diversity to that of Perry (1972) and Abensperg-Traun and Milewski (1995).

## METHODS

### Study area

The study was carried out in the 81 ha East Yorkarine Nature Reserve (31°24'S, 117°39'E) 15 km north of the town of Tammin in Western Australia's central wheatbelt. The area is a wheat

and sheep farming district of low relief (< 500 m) with a semi-arid climate of hot dry summers and cool winters. Mean annual rainfall is ~ 320 mm. Summer temperatures often exceed 40°C and winter frost is common (see Saunders *et al.* 1993 for a detailed description). Prior to the high-intensity fire of March 1991, which provided the basis for the present study, the whole reserve had not been burnt for at least 25–30 years (Beard 1980; Chapman 1980).

### Vegetation description of study site

In July 1994, just over three years after the fire, we selected an area where the burn was particularly effective in its destruction of plant material (matching the effects reported by Perry 1972, and by Abensperg-Traun and Milewski 1995), with an immediately adjacent unburnt stand for comparison. The unburnt and burnt study areas measured approximately 3 ha each. The vegetation was *Allocasuarina campestris* shrubland with an understorey predominantly of the sedge *Ecdeiocolea monostachya*. This could be matched with the burnt area by the presence of dead but standing *A. campestris* shrubs, and regenerating sedge. For each termite mound that we sampled (see below), we measured five habitat variables within a 5 m radius where most harvesting activity is likely to occur (Watson and Perry 1981; Park *et al.* 1993): live shrubs > 1 m in height, live shrubs < 1 m, sedge, grass/herbs/forbs, and litter. All measures are expressed as per cent cover.

### Termite-sampling

*Drepanotermes tamminensis* is confined to the agricultural regions of southwestern Australia and is thus the only species of *Drepanotermes* restricted to an area of winter rainfall. The species is an obligate mound builder and occurs only on sites with clay subsoils (Watson and Perry 1981). The distinct conical mounds of *D. tamminensis* were destructively sampled, at random, in the unburnt and immediately adjacent burnt stand. For each of the 20 mounds sampled in each site, we recorded presence/absence of a *D. tamminensis* colony and subjectively scored each mound for occupation by the colony: 1 (abandoned), 2 (< ~ 1/3 of mound occupied), 3 (~ 2/3 occupied), 4 (> ~ 2/3 of mound occupied). We collected termite soldiers from each occupied mound to corroborate species identification.

Loss of colony vigour (e.g., diminished reproductive output) due to increased competition with other harvester colonies for declining food resources may also result in higher rates of mound-invasion by predatory ants, further reducing resilience in relation to fire (Wood and Lee 1971; Holt and Greenslade 1979; Holt 1990). We thus recorded presence/absence of ants occupying the mound, gave subjective scores for ant occupation (as for termites) and collected specimens for species identification.

Diet of *D. tamminensis* in the unburnt and burnt stand was determined by collecting harvested chaff from the galleries for microscopic examination at the laboratory. For each of the 20 mounds sampled in each area housing a *D. tamminensis* colony, the proportion (dry mass) of a sub-sample selected at random was calculated for *Allocasuarina campestris* needles, sedge *Ecdeiocolea monostachya*, grass/herbs/forbs, and "other" (fragments of bark and leaves, seeds). Each mound was also scored for total quantity of stored chaff by giving subjective rankings from 1 = low quantity to 3 = high quantity. We acknowledge that our study is based on pseudoreplication; comparable unburnt and burnt sampling sites in other native vegetation remnants were not available for investigation. Because the use of inferential statistics on pseudoreplicated data is inappropriate, data are presented as means and standard deviations.

## RESULTS

### Effects of fire on vegetation

The burnt stand contained few tall (> 1 m) shrubs, but showed a greater density of small (regenerating) shrubs than the unburnt stand (Table 1). Most *Allocasuarina* plants were killed by the fire. Unburnt and burnt stands had a similar sedge and grass/herb/forb cover, but total litter cover was greater in the unburnt stand. The litter component consisted almost entirely of *A. campestris* needles in the unburnt stand while in the burnt area the very small amounts of litter were predominantly fragments of broad leaf and other plant debris.

Table 1. Vegetation measurements (mean  $\pm$  S.D.) for unburnt and burnt stands of *Allocasuarina campestris* shrubland (all measures are percentage cover).

Vegetation	Sample areas	
	Unburnt	Burnt
Live shrubs > 1 m	3.6 $\pm$ 0.5	0.2 $\pm$ 0.3
Live shrubs < 1 m	0.7 $\pm$ 0.5	2.6 $\pm$ 0.7
Sedge	2.9 $\pm$ 1.0	2.7 $\pm$ 0.7
Grass, herbs, forbs	1.1 $\pm$ 0.3	1.0 $\pm$ 0.2
Litter	3.0 $\pm$ 0.6	1.1 $\pm$ 0.4

### Diet of *Drepanotermes tamminensis*

Harvested chaff collected (dry weight) ranged from 0.51 g to 3.60 g per mound (mean 1.39 mg  $\pm$  0.75 S.D.). Mounds in the unburnt stand contained higher levels of chaff (Table 2). None of the abandoned mounds contained any harvested plant material. Colonies harvested similar plant materials in the unburnt and burnt sample areas, consisting predominantly of *Allocasuarina* needles (Table 2).

Table 2. Total abundance (subjective scores) ( $\pm$  S.D.) of harvested chaff, and proportional composition (mean % dry weight) ( $\pm$  S.D.) in mounds of *Drepanotermes tamminensis* in unburnt and burnt *Allocasuarina campestris* shrubland.

Harvested materials	Sample areas	
	Unburnt	Burnt
Total abundance	2.5 $\pm$ 0.9	1.3 $\pm$ 1.3
<i>Allocasuarina campestris</i> needles	67.9 $\pm$ 32.7	74.6 $\pm$ 17.8
Sedge <i>Ecdeiocolea monostachya</i>	7.3 $\pm$ 23.3	2.6 $\pm$ 4.3
Grass, herbs, forbs	1.1 $\pm$ 3.2	1.8 $\pm$ 3.5
Other (leaf/bark debris, seeds)	23.7 $\pm$ 25.7	20.9 $\pm$ 19.3

### Mound occupation and ant invasion

Two mounds (10%) in the unburnt stand were abandoned by *D. tamminensis*, contrasting with eight mounds (40%) in the burnt stand. Overall, the colonies in the unburnt stand occupied a higher proportion of the mounds than in the burnt stand (Fig. 1a).

Fifty-five percent of mounds in both the unburnt and burnt stands contained ants, but ants occupied a higher proportion of mounds in the burnt area (Fig. 1b). Across all mounds sampled, we recorded twice as many ant species in mounds in the burnt stand (unburnt three spp., burnt six spp.), twice as many predatory *Iridomyrmex* ant species (unburnt two spp., burnt four spp.), and a higher incidence of occupation by *Iridomyrmex* ants (unburnt 25%, burnt 50%).

## DISCUSSION

*Drepanotermes tamminensis* harvester termites appeared to be markedly affected by the fire which occurred three years previously. This is supported by the high proportion of abandoned mounds, the lower numbers of harvesters in mounds that were occupied, and the higher extent of mound invasion by predatory *Iridomyrmex* ants, in the burnt stand. The small quantities of stored chaff in surviving mound populations, and interactions with predatory ants, may lead to further population decline within the burnt area (Wood and Lee 1971; Holt and Greenslade 1979; Holt 1990). Inadequate replenishment of its principal food resource (*Allocasuarina* needles), and ant invasion, appear to have been the principal factors in the decline of mound populations.

The exact fate of the harvester termites is unknown. We explore four potential explanations. First, harvesters perished when stores were depleted. However, there was no evidence for dead harvesters in any of the mounds that we investigated. Second, termites turned to cannibalism for survival, which is known to occur during periods of nitrogen stress (Dhanarajan 1978; Collins 1983). However, considering the large number of individual termites that are likely to have been involved, this is an unlikely explanation. Third, invading ants ate the harvester termites. However, two mounds in the

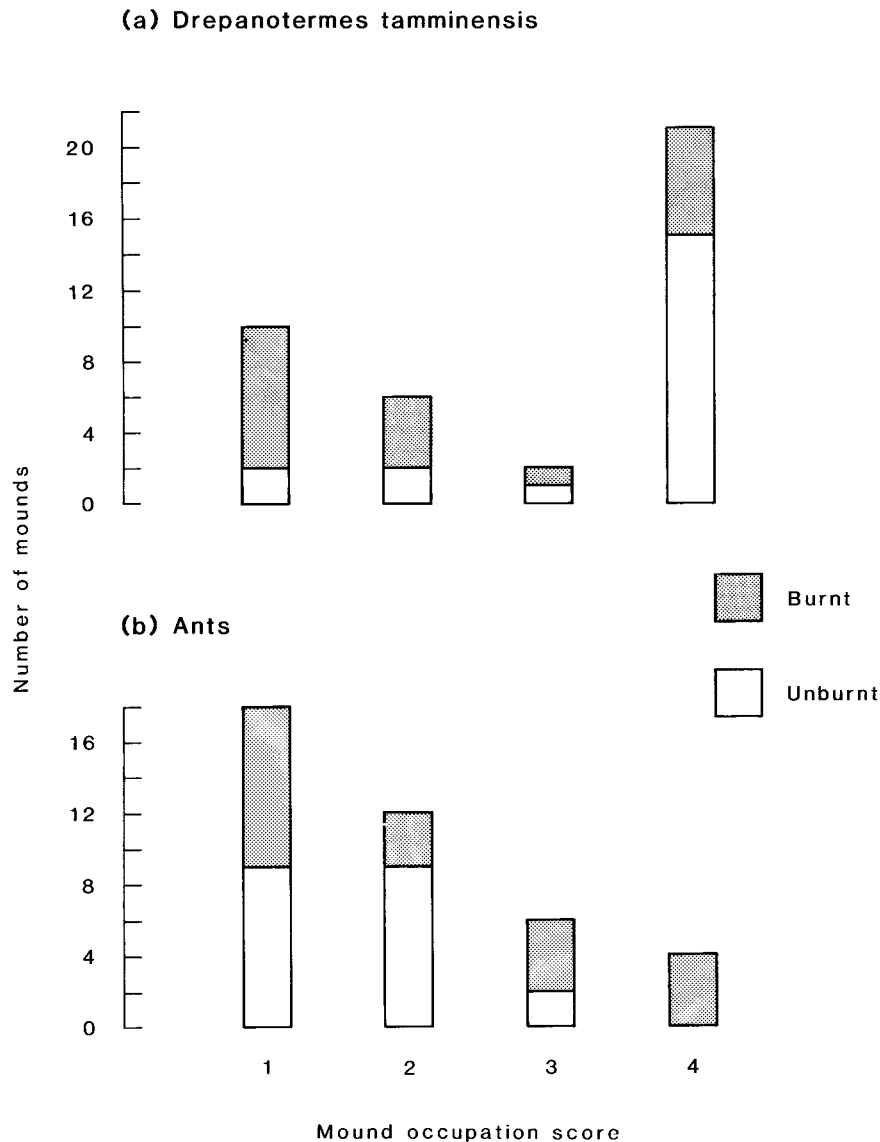


Fig. 1. Mound occupation by harvester termites *Drepanotermes tamminensis* (a) and ants (b) in unburnt and burnt *Allocasuarina campestris* shrubland in the central wheatbelt of Western Australia: 1 (abandoned), 2 ( $< \sim 1/3$  of mound occupied), 3 ( $\sim 2/3$  occupied), 4 ( $> \sim 2/3$  of mound occupied).

burnt area contained neither dead or live harvesters, nor ants. Fourth, harvesters moved into near-by mounds less affected by food shortage. Some species of *Drepanotermes* are known to be polycalic, with several mounds comprising a single colony (Holt and Easey 1985). Migration of parts of the colony (and possibly their stored reserves) into adjacent mounds less affected by the fire may enhance their survival, depending in part on plant regeneration and the ability of adjacent mounds to house the excess individuals. Whether polycalic behaviour occurs in *D. tamminensis* appears not to have been documented. Irrespective of the mechanism, whether by death or migration, mound populations of the harvester *D. tamminensis* in the burnt area declined markedly following the high intensity fire three years previously.

Table 3. Plant diversity at the family, genus and species level for the three plant communities discussed in the text: spinifex on Barrow Island (Buckley 1983), shrubland in the central wheatbelt (L. Atkins, unpublished), and mallee-heath in Fitzgerald River National Park (Newbey 1990; Aplin and Newbey 1990).

Plant taxon	Spinifex <i>Triodia</i> grassland	<i>Allocasuarina</i> shrubland	Mallee- heath
Family	18	30	34
Genus	32	61	84
Species	43	82	113+

Table 3 shows plant diversity at the family, genus and species level in the three studies discussed, and it shows a consistent increase in diversity across the three taxonomic levels. The plant diversity data for habitats dominated by *Triodia*

*angusta* on Burrow Island as given by Buckley (1983), and as presented in Table 3, covers a much wider range of landscape units than that actually sampled for termites by Perry (1972). The plant diversity data for the burnt spinifex *T. angusta* thus errs on the conservative side. We argue that an increase in plant diversity is likely to be associated with a wider range of post-fire regeneration responses. Even partial plant regeneration, ensuring sustenance (energy) for at least part of the termite population, is likely to enhance the resilience of harvester termites to high-intensity fire.

### Conservation implications

High-intensity fire in plant species-poor habitats of arid and semi-arid Australia, where harvester termites are particularly abundant, may have implications for important ecological processes, disruption or modification of nutrient and energy cycling in particular (Holt *et al.* 1980; Pianka 1986; Holt 1987; Noble and Tongway 1988; Spain and McIvor 1988; Morton and James 1988; Abensperg-Traun 1994). The energy flow in arid and semi-arid Australian ecosystems is considered to be principally one of "dead dry plant matter > termites > ants" (Greenslade 1970), and a considerable proportion of arid zone lizards are termite-specialized (Pianka 1986; Morton and James 1988; James 1991; Abensperg-Traun 1994). Spinifex (hummock grass) of the genera *Triodia* and *Plectrachne* covers > 20% of mainland Australia, and > 50% of Western Australia (Beard 1969; Griffin 1984, 1992). Wildfires in spinifex may be infrequent, once every ~ 10 years for central Australia's northern spinifex grasslands, and once every ~ 30 years for southern areas (Hodgkinson and Griffin 1982; Griffin 1984). However, a frequency of once every five years has been given for *Triodia pungens* where fire is used for range management (Suijddorp 1981), and extensive areas are often burnt. Winkworth (1967) mentions 4 000 square miles for a single burn. However, spinifex plants typically grow as islands with sizable areas of bare sand separating individual clumps. Fire is therefore often patchy, leaving many plants unaffected (Burrows *et al.* 1991) which can then be utilized by the termites. The report of Perry (1972) on the collapse of *Drepanotermes* harvester colonies in *T. angusta* attributed this to the death of the plants following the high-intensity fire, and to a lack of regeneration from root-stock two years later. Rainfall following the fire may have been inadequate for regeneration from seed. However, normally only high-intensity fire, or fire in combination with drought and livestock-grazing pressure, may kill spinifex (Jacobs 1984). Regeneration from root-stock following fire is generally quite rapid, irrespective of rainfall (Suijddorp 1981; Buckley 1983; Jacobs 1984). Except in extreme circumstances, such as those

reported by Perry (1972), harvestable materials, additional to short-lived herbaceous and graminaceous fireweeds, may again become available after fire before stored chaff is depleted.

In mulga country of arid Australia, Watson *et al.* (1973) reported the collapse of *Drepanotermes* colonies in the absence of fire, following drought and competition with livestock for scarce food resources. Watson and Gay (1970) point to a similar occurrence some 20 years earlier. These observations suggest that where fire coincides with drought and competition with livestock (and other harvester colonies) for food, death of a significant proportion of harvester termite colonies may result. Temporary extinction of *Drepanotermes* colonies (and possibly those of other harvesters such as *Tumulitermes* spp.) in arid Australian rangelands may thus occur more frequently than is thought at present.

Compared to spinifex communities of central and northern (subtropical) Australia, rainfall and hence plant regeneration in tropical Australian grasslands and savannas is relatively high and reliable (Mott *et al.* 1985). These grasslands and savannas are also often burnt annually, affecting different grass species (Haynes 1985; Mott *et al.* 1985; Morton and Andrew 1987; Andersen and Braithwaite 1992). Fire effects on harvester termites in tropical Australia, where their abundance can be expected to be particularly high (Gay and Calaby 1970; Braithwaite *et al.* 1988), is poorly understood, however (Morton and Andrew 1987). For the litter-feeding *Nasutitermes longipennis* in north-eastern Australian savanna, Holt and Coventry (1990) report a positive influence of fire exclusion on mound abundance. Benzie (1986), in his study of fire effects on harvesters *Trinervitermes* in high-rainfall northern guinea savannah of West Africa (1 100 mm rainfall/year), showed a significant short-term decline in harvester abundance after fire, and a return to pre-fire abundance levels within two years. Following high-intensity fire, the recovery of harvester populations in subtropical Australian grasslands may take considerably longer than for high-rainfall grasslands and savannas of tropical Australia.

The present study does not aim to provide a blueprint for the role of harvester termites in fire management of arid and semi-arid Australian ecosystems. This is because all studies to date were *post hoc* and short-term. Also, none were conducted in tropical Australia where high annual rainfall ensures comparatively rapid plant regeneration following fire. An important consequence of rapid post-fire regeneration in tropical Australian grasslands and savannas is that fire regimes differ from those of sub-tropical regions. Nevertheless, our findings, and those of Perry (1971), show that in the short-term (2–3 years), fire may have a considerable impact on harvester termite

populations. In plant-species poor vegetation types in low-rainfall regions, the co-occurrence of high-intensity fire with drought or livestock-grazing pressure may cause long-term effects on harvester populations. Rigorous experimental studies, in a range of vegetation types and climatic regions, are required to enhance our understanding of the long-term effects of fire on harvester termites.

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