PLANT ANIMAL INTERACTIONS

Savanna fires increase rates and distances of seed dispersal by ants

C. L. Parr · A. N. Andersen · C. Chastagnol · C. Duffaud

Abstract Myrmecochory (seed dispersal by ants) is a prominent dispersal mechanism in many environments, and can play a key role in local vegetation dynamics. Here we investigate its interaction with another key process in vegetation dynamics—fire. We examine ant dispersal of seeds immediately before and after experimental burning in an Australian tropical savanna, one of the world's most fire-prone ecosystems. Specifically, our study addressed the effects of burning on: (1) the composition of ants removing seeds, (2) number of seed removals, and (3) distance of seed dispersal. Fire led to higher rates of seed removal post-fire when compared with unburnt habitat, and markedly altered dispersal distance, with mean dispersal distance increasing more than twofold (from 1.6 to 3.8 m), and many distance dispersal events greater than the pre-fire maximum (7.55 m) being recorded. These changes were due primarily to longer foraging ranges of species of *Iridomyrmex*, most likely in response to the simplification of their foraging landscape. The significance of enhanced seed-removal rates and distance dispersal for seedling establishment is unclear because the benefits to plants in having their seeds dispersed by ants in northern Australia are poorly known. However, an enhanced removal rate would enhance any benefit of reduced predation by rodents. Similarly, the broader range of dispersal distances would appear to benefit plants in terms of reduced parent–offspring conflict and sibling competition, and the location of favourable seedling microsites. Given the high frequency of fire in Australian tropical savannas, enhanced benefits of seed dispersal by ants would apply for much of the year.

Keywords Ants · Burning · Seed dispersal · Disturbance · Dispersal distance

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Introduction

Myrmecochory, the dispersal of seeds by ants, is a widespread and common process throughout the world, involving plants from more than 80 families (Beattie 1983; Gómez and Espadaler 1998). It involves ants collecting and transporting seeds with elaiosomes: nutrient-rich tissue attached to the seed that is unnecessary for germination or growth of the plant (Beattie 1985). Ants carry seeds with elaiosomes back to their nest where the elaiosome is consumed, and the seed is either left underground or deposited outside the nest (Beattie and Culver 1981; Westoby et al. 1982). Several advantages of myrmecochory have been suggested, including avoidance of seed predation by rodents (O'Dowd and Hay 1980; Bond and Slingsby 1984; Auld and Denham 1999), dispersal to nutrient-rich nest sites (Culver and Beattie 1978; Davidson and Morton 1981), protection from fire (Beattie 1985; Hughes and Westoby 1992), and reduced parent–seedling competition

due to distance dispersal (Westoby et al. 1982; Andersen 1988a; Boyd 2001) (see also Giladi 2006). Myrmecochory has been shown to play a key role in local vegetation dynamics (Christian 2001).

In the southern hemisphere, seed dispersal by ants is particularly prominent in sclerophyll habitats (Giladi 2006). Fire is another ecological process that is particularly important for vegetation dynamics in these habitats (Cowling 1992; Bond and van Wilgen 1996; Keith et al. 2002), and can potentially have a major influence on seed dispersal by ants. Seed dispersal by ants is influenced proximately by biotic factors such as vegetation structure, ant community composition, nest density, and competition for resources (Andersen 1988a; Ness et al. 2004; Gómez et al. 2005), as well as abiotic factors such as temperature (Ness and Bressmer 2005). All of these factors are potentially influenced by habitat disturbance (see Majer 1980; Andersen 1988a; Andersen and Morrison 1998; Ness 2004).

Fire is known to influence ant abundance, diversity and assemblage composition across a wide range of habitat types throughout the world, both in the short- and longer term (Andersen 1988b; York 1999; Farji-Brener et al. 2002; Parr et al. 2004). However, the potential for either individual fire events or long-term fire regimes to influence myrmecochory is unknown. This issue is especially relevant to Australia, where myrmecochory is a particularly prominent seed dispersal syndrome (Berg 1975), and fire has played such a dominant role in the continent's evolutionary history (Bradstock et al. 2002).

Here we describe the immediate effects of fire on distance dispersal by ants in an Australian tropical savanna. The tropical savannas of northern Australia are among the most fire-prone ecosystems in the world, with up to half or more of regional savanna landscapes being burnt each year, and fire being a key management tool for biodiversity conservation (Russell-Smith et al. 1998; Andersen et al. 2003). As such, fire frequency has been shown to have a major effect on local ant communities in these ecosystems (Andersen 1991; Hoffmann 2003). The specific aims of this paper are to examine the immediate impact of fire on: (1) the composition of ants removing seeds, (2) rates of seed removed, and (3) distance of seed dispersal.

Materials and methods

Study site

The study was carried out at the Territory Wildlife Park (TWP), located 40 km south-east of Darwin (12°42′S 130°59′E) in the Northern Territory. Mean annual rainfall is approximately 1,700 mm (nearest station Darwin airport, Bureau of Meteorology), and heavily concentrated in a summer wet season between November and April. Temperatures are high all year round, with a mean daily maximum of 31.9°C and minimum 23.2°C (Bureau of Meteorology).

The study forms part of the Bushfire Cooperative Research Centre's Burning for Biodiversity experiment at the TWP, where a series of 1-ha experimental burn plots has been established to investigate the effects of fire frequency and time-since-fire on biodiversity and ecosystem function (see http://www.terc.csiro.au/burningforbiodiversity). The site is covered with tropical savanna woodland dominated by *Eucalyptus tetrodonta* and *E. miniata*. Other important woody species include *Acacia* spp., *Calytrix exstipulata*, *Exocarpus latifolius* and *Petalostigma pubescens*. The grass layer is dominated by perennial species of *Eriachne* and *Eragrostis*.

Prescribed burning commenced on the experimental plots on 21 and 22 June 2005 (early dry-season fires), and fieldwork took place for approximately 3 weeks before and 3 weeks after these fires. The majority of ground-layer cover on the plots was consumed in the fires with measured fire intensities at the three burnt plots being 145, 150 and 2,100 kW/m/s, respectively (R. J. Williams, unpublished data; methods follow Williams et al. 1998). These intensities are relatively low, and contrast with an average of about 8,000 kW/m/s for fires occurring late in the dry season (Williams et al. 1998). We refer to pre- and post-fire for both burnt and unburnt plots, so that the term "post-fire" refers to the sampling period, and does not imply that a site was actually burnt.

Fieldwork

Sampling took place on three burnt and three unburnt plots, following the protocol used by Andersen and Morrison (1998). Two 6 × 6 grids of seed depots, with 2-m spacing between depots and 80-m separation of grids, were established at each plot. The location of each seed was marked with a wooden stake and flagging tape. Seed removal from each grid was examined for two 2-h periods (once in the morning from 0830 to 1030 hours, and once in the afternoon from 1500 to 1700 hours), both in the 3 weeks immediately before and 3 weeks immediately after burning. These hours corresponded with the periods of highest ant activity because it was neither too hot nor too cool.

Myrmecochory involves a very generalised relationship between ants and seeds (Beattie 1983), so

that local patterns of distance dispersal are to a large extent determined by the composition of the local ant community, rather than being specific for a given seed species (Westoby et al. 1982, see also Andersen 1988a). Seeds of *Acacia holosericea*, a shrub that is widely distributed throughout northern Australia and naturally occurs at the TWP, were used for the study (see Brock 1988; Flora of Australia 2001). Seeds of *A. holosericea* are average-size for a myrmecochore (approximately 2 mm in length; see Andersen and Morrison 1998), and dark brown in colour with bright yellow-orange arils. The field experiment, both pre- and post-fire, coincided with the natural seed fall of this species. Indeed the majority of myrmechochores in the region (predominantly species of *Acacia*) fruit during the dry season (June–October; Brock 1988; Brennan 1996), which coincides with the fire season. *A. holosericea* is an obligate seeder whose establishment is favoured by disturbance.

For each sampling session at each grid, ant species taking the seeds were recorded if observed, as well as whether seeds were dropped (abandoned) or taken to a nest. Such nests were mapped, and the removal distance (displacement) measured for seeds both taken to nests and abandoned. Where seeds were taken but not observed, the seeds were replaced, but as with Andersen and Morrison (1998), the replacement seed was not counted when analysing rates of removal. This gives a maximum of one removal per depot per 2-h session.

Ant specimens were identified to species where possible, and otherwise assigned code numbers following those used in previous studies in the Darwin area. Voucher specimens are held at the CSIRO Tropical Ecosystems Research Centre, Darwin.

Analysis

Difference in the number of seed removals pre- and post-fire was assessed using a Wilcoxon matched-pair test performed at the grid level ($n = 6$). Given the patchy distribution of species and variation between sites, a paired test, with grids paired for total number of removals pre- and post-fire, was used to reduce background variation. The test was conducted for both burnt and unburnt plots. Paired *t*-tests at the grid level ($n = 6$) were also used to determine whether there was any difference in the number of colonies removing seeds in the post-fire period. All parametric tests (*t*-tests) were only undertaken where data fulfilled assumptions of normality.

Paired *t*-tests were used to establish whether dispersal distance changed significantly following fire. The mean dispersal distance per grid pre- and post-fire was used for both burnt and unburnt plots ($n = 6$). The use of mean dispersal distance per grid avoided the potential problem of non-independence of individual removals. Frequency distributions of dispersal distances were constructed for pre- and post-fire in both burnt and unburnt sites, and compared using Kolmogorov–Smirnov two-sample tests.

Changes in dispersal distance were also investigated for individual ant species. Due to the patchy nature of ant distribution and number of records for each species, analysis was limited to six species with sufficient removal observations to permit statistical analysis: *Iridomyrmex* sp. 21, *I. reburrus*, *I. pallidus*, *Iridomyrmex* sp. 1, *Rhytidoponera aurata*, and *R. borealis*. For each of these species, the non-parametric Mann–Whitney *U*-test was used to compare dispersal distance pre-and post-fire on burnt and unburnt plots where the species was present.

Results

Overall there was uneven and patchy removal of seeds from grids. Some grids had very little activity (only 5% seeds were taken, and in a few sessions no seeds were removed at all), while others had much greater activity with almost all (up to 94%) seeds removed. The total number of observed seed removals was 151 pre-fire, and 140 post-fire (Table 1), which represents 38.4 and 47.6% of all removals, respectively. Only 7% (21) of observed seed removals were abandoned and did not reach nests.

Composition of ant species removing seeds

A total of 17 species from nine genera was observed removing seeds (Table 1), with 15 species on unburnt plots and 11 on burnt plots. *R. aurata* (79 removals), *Iridomyrmex* sp. 21 (*gracilis* group) (48 removals), and *Iridomyrmex reburrus* (46 removals) were responsible for most (nearly 60%) of the removals.

Following experimental burning, eight species were no longer recorded on unburnt plots and one on burnt plots, while four new species were recorded removing seeds on burnt plots, and none on unburnt plots. Most notable was the appearance (four observed removals) of *I. reburrus* after burning on one plot, which had a nest on the edge of the plot (about 15 m away), but did not appear at seed depots until after the fire.

Table 1 Seed removal pre- and post-fire

Ant species	Pre-fire				Post-fire			
	Number of observed removals	Distance removed (cm)			Number of observed removals	Distance removed (cm)		
		Mean	SE	Maximum		Mean	SE	Maximum
Unburnt plots								
Ponerinae								
Brachyponera lutea	1	2	–	2				
Odontomachus sp. nr. *turneri*	10	111	39.4	424	1	51	–	51
Rhytidoponera aurata	6	444.7	53.6	595	31	349.7	41.8	870
Rhytidoponera (*borealis* complex)	1	110	–	110				
Rhytidoponera reticulata	2	25	125.0	375	1	100	–	100
Formicinae								
Paratrechina sp. 4 (*vaga* group)	3	20	15.0	50	1	5	–	5
Dolichoderinae								
Iridomyrmex sp. 1 (*anceps* group)	4	113.3	29.9	160	3	128.33	53.6	235
Iridomyrmex pallidus	19	70.8	8.2	150	8	58.75	11.6	110
Iridomyrmex reburrus	21	651.7	65.4	1,306	21	724.7	71.9	1,285
Myrmicinae								
Monomorium donisthorpei	1	4	–	4				
Monomorium sp.7 (group A)	1	27	–	27				
Pheidole sp. 11 (group K)	1	132	–	132				
Pheidole sp. 13 (*ampla* group)	1	12	–	12				
Pheidole sp. 8 (group F)	1	4	–	4				
Tetramorium lanuginosum	1	5	–	5				
Total	73	275.6		1,306	66	410.2		1,285
Burnt plots								
Ponerinae								
Brachyponera lutea					1	5	–	5
Odontomachus sp. nr. *turneri*	3	62.7	16.7	85				
Rhytidoponera aurata	26	284.2	33.1	755	16	319.9	64.5	810
Rhytidoponera (*borealis* complex)	15	148.7	19.1	302	12	108.6	20.1	263
Rhytidoponera reticulata	1	10	–	10	1	215	–	215
Formicinae								
Melophorus Kak. sp.10 (group D)					1	247	–	247
Dolichoderinae								
Iridomyrmex sp. 1 (*anceps* group)	8	108.8	39.7	340	2	222	111.0	333
Iridomyrmex pallidus	11	70.1	14.5	130	2	20.5	18.5	39
Iridomyrmex sp. 21 (*gracilis* group)	14	205	48.6	605	34	403.82	47.5	1,263
Iridomyrmex reburrus					4	1,434.8	156.2	1,870
Myrmicinae								
Monomorium donisthorpei					1	5	–	5
Total	78	183.7		755	74	362.8		1,870

Rates of seed removal

Rates of removal before burning were similar on burnt (44.4%) and unburnt (46.5%) plots. After burning, this rate was maintained on burnt plots (40.7% removal) but dropped to 27.3% on unburnt plots (Table 1). The drop in removal activity on unburnt plots post-fire was somewhat more pronounced in the morning (44.5, cf 36.6% in the afternoon). Wilcoxon matched-pair tests revealed a significant reduction in the number of removals per grid
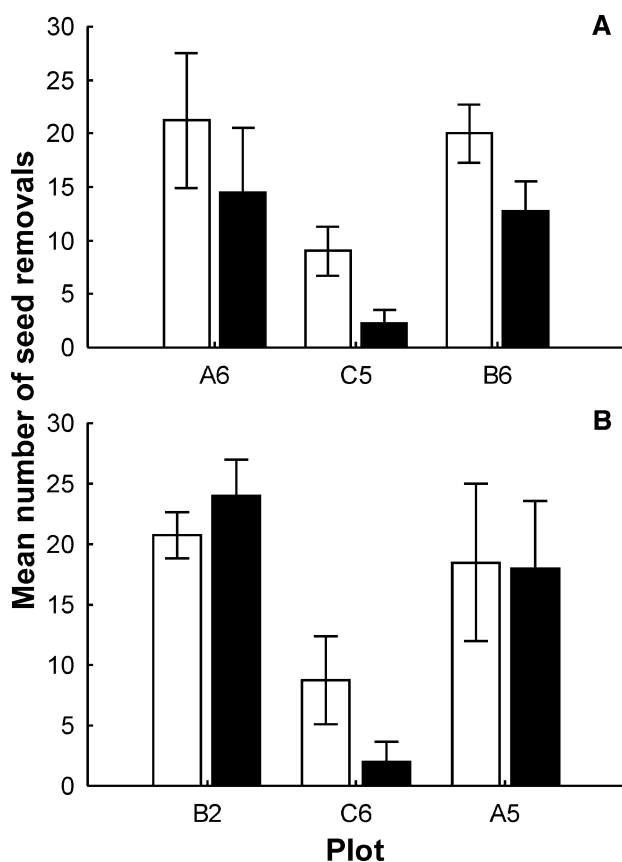
Fig. 1 Mean (±SE) rate of seed removal pre-fire (*unfilled* bars) and post-fire (*black filled* bars) for **a** unburnt and **b** burnt plots

Fig. 2 Overall seed dispersal curve for all ant species and all plot types ($n = 292$)

pre- and post-fire on unburnt plots ($Z = 2.20$, $P = 0.03$; Fig. 1a), but no difference on burnt plots ($Z = 0.734$, $P = 0.46$; Fig. 1b). The marked reduction in rates of removal occurred consistently across unburnt plots (Fig. 1a), and also on one of the burnt plots (plot C6, Fig. 1b).

There were also significantly fewer ant colonies collecting seeds in the post-fire period on unburnt plots (paired *t*-test, $t = 2.95$, $P = 0.03$, mean number of colonies/grid = 6.5 and 4.0 for pre- and post-fire periods, respectively), but no significant difference on burnt plots (paired *t*-test, $t = 0.98$, $P = 0.37$).

Dispersal distance

The overall dispersal-distance curve shows a mean distance of 3.04 m (SE = 0.18), with a high frequency (44% all observations) of recorded distances being less than 1.50 m (Fig. 2). The highest mean dispersal distance was for *I. reburrus* (7.41 m), which also had the highest maximum dispersal distance (18.7 m). The shape of the dispersal curve also varied markedly with
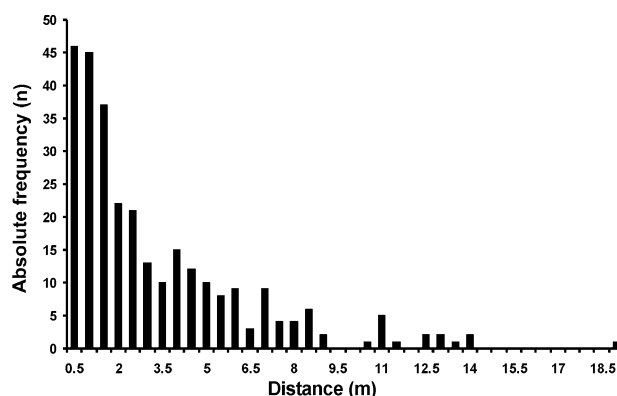
ant species (Fig. 3), with negative skew for *Iridomyrmex* sp. 21, and a normal distribution for *I. reburrus*.

There was no significant difference in mean dispersal distance between the pre- and post-fire periods on unburnt plots (paired *t*-test, $t = -0.961$, $P = 0.38$), but mean dispersal distance more than doubled (137% increase) on burnt plots (3.8 cf. 1.6 m; paired *t*-test, $t = -2.83$, $P = 0.037$, Table 1). A very marked increase in mean dispersal distance occurred at all burnt plots: 94.7% at A5, 76.7% at B2, and 326.8% at C6.

On unburnt plots there was a slightly more even frequency distribution post-fire compared with pre-fire (Kolmogorov–Smirnov-test; $D = 0.254$, $P = 0.01$; Fig. 4a). However, on burnt plots the shape of the dispersal curve changed markedly following fire ($D = 0.287$, $P = 0.005$), with lower frequencies of short dispersal distances, and a far more pronounced tail of longer distances (Fig. 4b); pre-fire the maximum distance was 7.55 m while post-fire this more than doubled to 18.7 m, and there were ten removals greater than 7.55 m.

When analysed at the species level, the only significant difference between pre- and post-fire dispersal distance was for *Iridomyrmex* sp. 21 on burnt plots (Mann–Whitney *U*-test, $U = 118.5$, $P = 0.007$); its mean dispersal distance nearly doubled from 2.05 m pre-fire to 4.04 m post-fire (Table 1). It did not occur at all on unburnt plots, nor on the burnt plot C6 (where, in contrast to other burnt plots, rates of removal declined post-fire; see above).

Discussion

Rates of seed removal varied markedly between grids, reflecting variation in the distribution of seed-removing ants (see Andersen 1982). For example, *Iridomyrmex*
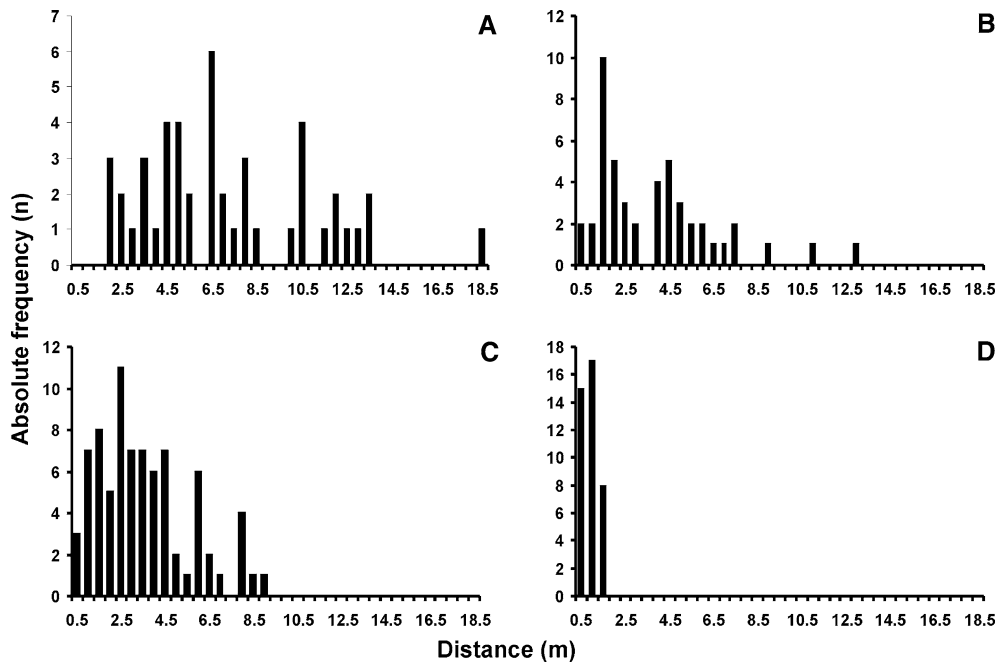
Fig. 3 Myrmecochorous dispersal curves for **a** *Iridomyrmex reburrus* (7.41 m, SE 0.56), **b** *Iridomyrmex* sp. 21 (mean = 3.46, SE 0.39), **c** *Rhytidoponera aurata* (mean = 3.29 m, SE 0.24) and **d** *Iridomyrmex pallidus* (mean 0.66, SE 0.06). All data (sites and time periods) combined
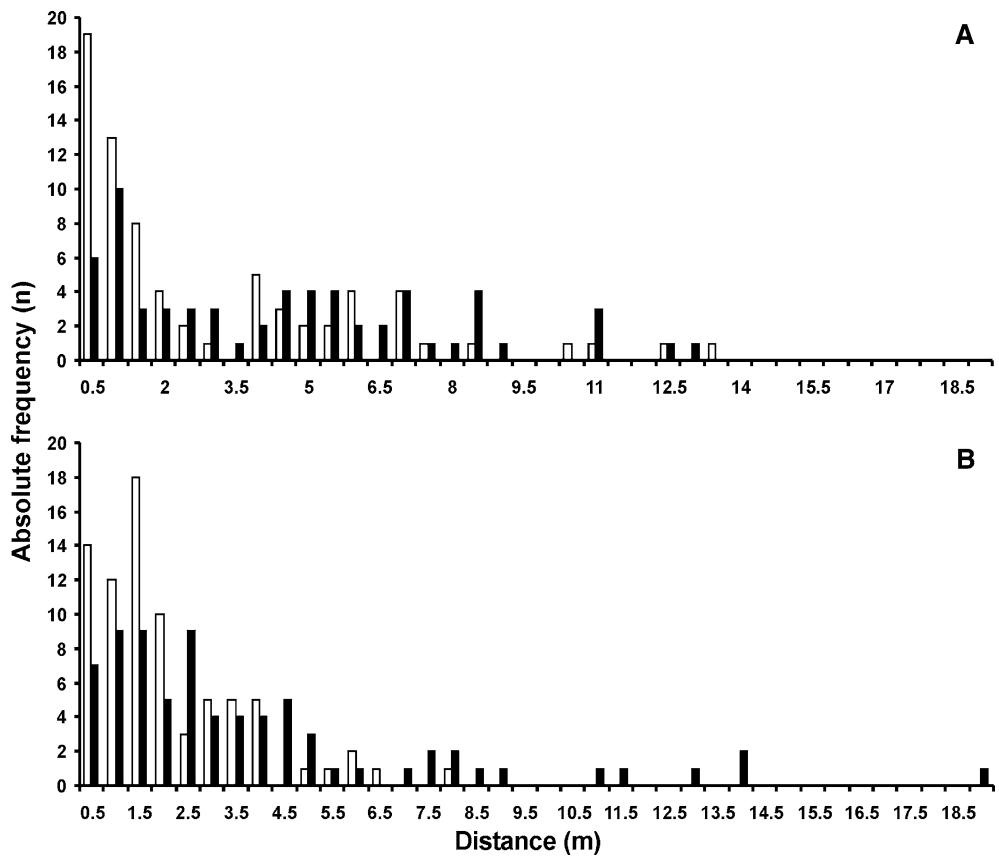

Fig. 4 Ant seed dispersal curves pre-fire (*unfilled* bars) and post-fire (*black filled* bars) for **a** unburnt and **b** burnt plots

sp. 21 was one of the most commonly recorded seed-removing species overall, but its distribution was highly patchy, occurring on only three grids across two plots. Notwithstanding this variation, seed removal rates were high overall (average of 42.6% seeds removed over the 2-h periods) compared with similar studies; for example, Andersen and Morrison (1998) reported only 29% of seeds were removed over a similar time period at savanna sites in nearby Kakadu National Park.

The ants observed removing seeds were primarily species of *Rhytidoponera* and *Iridomyrmex*, which was also the case in nearby Kakadu National Park (Andersen and Morrison 1998). They are arguably the two most important seed-dispersing ant genera throughout Australia (Berg 1975; Davidson and Morton 1981; Westoby et al. 1982; Andersen 1988a).

The variation in dispersal curves generated by the different ant species can be related to ant body size (Andersen 1988a; Bestelmeyer and Wiens 2003; Ness et al. 2004). Large-bodied ants typically have large foraging ranges, with the micro-landscape presenting much less of an obstacle to movement than it does to smaller species (see Kaspari and Weiser 1999). *I. reburrus* is a large ant (total length 8 mm), and like other meat ants is capable of dispersing seeds very long distances. The record at this study site is a relatively modest 23 m (C. L. Parr, personal observation), but distances up to 180 m have been reported for *I. viridiaeneus* in the Australian arid zone (Davidson and Morton 1981; Whitney 2002).

The mean dispersal distance recorded in the study (3.04 m) is greater than that (2.61 m) reported in a similar habitat by Andersen and Morrison (1998), and nearly twice the southern hemisphere average (1.52 m) reported by Gómez and Espadaler (1998). This can be attributed to a greater representation of large-bodied species as seed-removers in the present study, with relatively few removals by small ants such as species of *Pheidole* and *Monomorium*.

Fire and seed removal

In the post-fire sampling period, there was a decline in the number of seed removals and number of colonies removing seeds on unburnt plots. This indicates lower ant activity during this period, independent of burning. The fact that the decline was most pronounced in the mornings suggests that the lower overnight temperatures coinciding with the start of the dry season might have been a factor. In this context, the finding that both the number of removals and the number of colonies removing seeds was maintained at a high level at burnt plots suggests that fire promoted ant activity. Ant activity might have been enhanced by the simplified micro-habitat on the ground following burning, allowing for greater foraging efficiency and possibly producing warmer conditions at the soil surface. Alternatively, ant forager abundance may have increased immediately following fire, as has been documented elsewhere (Andersen 1988b; York 1999; Sanders and Gordon 2002). Notably, the reduction in removal rates at unburnt plots also occurred at one of the burnt plots (C6; see below).

The shape of the dispersal curve changed from the pre-fire to the post-fire period on unburnt plots, and, as for rates of removal, this describes changes in ant activity independent of fire. Such changes were, however, far more marked on burnt plots, where there was a significant increase in mean dispersal distance (more than twofold), and there were many records of distance dispersal greater than the pre-fire maximum. These changes were due primarily to longer foraging ranges of species of *Iridomyrmex*. In particular, fire triggered foraging by the meat ant *I. reburrus* into one newly burnt plot. Indeed, not only were seeds being dispersed further, but they were being moved between habitat types (burnt to unburnt). *Iridomyrmex* sp. 21 was also able to take advantage of the post-fire conditions on burnt sites, doubling its mean dispersal distance. It was visibly more active following fire, creating "highways" on the newly bare earth, and its rate of seed removal was more than double that prior to burning. The important contribution made by *Iridomyrmex* sp. 21 to changes post-fire is illustrated by the fact that activity was maintained post-fire on plots where it was present (A5, B2, see Fig. 1), but, as at unburnt plots, declined where this species was absent (C6). In contrast, many nests of *R. aurata* became inactive on burnt plots after fire (only one out of eight remained active), with new nest building observed sometimes only a few centimetres from the old nest.

The most likely explanation for the increased foraging distances following fire is simplification of the ant foraging landscape. Ant foraging speed and efficiency is positively related to the amount of bare ground (Fewell 1988), and other studies have shown increased seed-removal rates and dispersal distances with increased bare ground (Crist and Wiens 1994; Usnick 2000). With enhanced ease of movement and faster foraging post-fire, energetic costs of movement decline (Nielsen 2001), so ants are able to cover greater distances when foraging; this translates to increased distance of seed dispersal. Species of *Iridomyrmex* would be expected to show a particularly strong response to post-fire conditions because they are highly active, behaviourally dominant ants that strongly favour open

habitats (Andersen 2003). In contrast, species of *Rhytidoponera* are behaviourally subordinate ants whose activity is strongly influenced by dominant species, and it is possible that reduced activity in *R. aurata* following fire was in response to increased interference from *Iridomyrmex*. Indeed, *R. aurata* activity declined only on plots where *Iridomyrmex* sp. 21 was present (plots A5, B2, Fig. 1). Where *Iridomyrmex* sp. 21 did not occur (plot C6), *R. aurata* removals actually increased after fire, and mean dispersal distance increased from 1.80 to 5.51 cm; this explains why dispersal distance increased markedly following fire at all burnt plots.

A reduction in food availability can also increase foraging ranges in ants (Sanders and Gordon 2002; McGlynn et al. 2003). However, the pre-fire foraging territory of *I. reburrus* was not burnt (it was only recorded foraging on burnt plots after burning), so that reduced food availability following fire can be discounted as a factor contributing to increased foraging range in this case.

Conclusion

Two questions need to be addressed when evaluating the significance of our findings. First, we have demonstrated enhanced seed-removal rates and distance dispersal by ants immediately following fire, but how persistent is this effect? Enhanced seed removal presumably persists as long as the simplified foraging conditions are maintained, which would be up to the re-development of the grass layer in the following wet season, around December. For fires such as ours early in the dry season, this is a period of at least 5 months. Given that about half of the regional savanna landscape is burnt each year (Andersen et al. 2003), this means that in any year about half of the area potentially has enhanced seed removal for up to half the time. This time would obviously be shorter for sites burnt late in the dry season. However, because fire intensity is higher and therefore simplification of the ground layer is more pronounced at this time of the year (Williams et al. 2003), the level of enhancement of seed removal could be expected to be greater.

Second, what is the significance of enhanced seed-removal rates and distance dispersal for seedling establishment? The benefits to plants in having their seeds dispersed by ants in northern Australia are too imprecisely known to answer this conclusively. However, if the benefit is reduced predation by rodents, then an enhanced removal rate represents a direct benefit. Similarly, the broader range of dispersal distances would appear to benefit plants from a distance-dispersal perspective, through an influence on the proximity of seeds to their parent plants (Westoby et al. 1982; Bond and Stock 1989) and thereby local densities of intra- and interspecific neighbours (Christian and Stanton 2004), as well as through the location of favourable microsites in the context of small-scale patchiness in nutrients and moisture availability (Antonovics et al. 1987).

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