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Interactions between meat ants (*Iridomyrmex spadius*) and bellyache bush (*Jatropha gossypiifolia*)

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Abstract. Understanding the dispersal of weed species is important for the development of effective control strategies. In this study, a series of experiments was conducted to clarify the role that meat ants (*Iridomyrmex spadius*) play in dispersing bellyache bush (*Jatropha gossypiifolia*), an exotic shrub currently invading the rangelands of northern Australia. The nutrient composition of food [lipids (fatty acids), fat and soluble carbohydrates] provided by bellyache bush seed components [caruncle, exotegmen and seed (without caruncle and exotegmen)] was identified. Seed components were rich in lipids, particularly palmitic, oleic, stearic, linoleic and eicosenic acids. Oleic and palmitic were most abundant in the caruncle (30% each), linoleic in the seed (61%) and palmitic in the exotegmen (36%). Over all seed components, fat concentration was relatively high (6.3%) compared with soluble carbohydrates (2.3%). The impact of feeding was then determined by comparing germination and viability of intact, non-caruncůlate (caruncle manually removed) and ant-discarded bellyache bush seeds. Feeding by meat ants significantly increased seed germinability, whilst having no adverse affects on viability. The quantity of seeds dispersed and the seasonal pattern of dispersal was recorded by collecting seed from the middens of randomly selected meat ant nests on a monthly basis. On average, 12 330 ± 603 seeds were retrieved from the middens of individual meat ant nests over 12 months, with highest numbers recorded between February and June (>1200 seeds/ant nest). The effect of this dispersal was determined through comparisons of plant densities within core infestations of bellyache bush, meat ant nest middens and pastures located directly adjacent to core infestations and that were being invaded primarily through localised ballistic dispersal. The density of bellyache bush plants growing from the seed reserves within middens averaged 79 plants/m^2, just 18% less than that within core infestations. Seedling survival (1 year) and growth within core infestation and meat ant sites was also quantified. The middens of meat ant nests provided an environment conducive to higher seedling survival and faster growth rates than occurred within core infestations. Mutualistic interaction between bellyache bush and meat ants is likely to build local ‘infestation pressure’ that may be conducive to range extension in years of exceptionally wet seasons. Management of seed dispersal by meat ants may reduce that risk.

Introduction

With increasing concern over the sustainability of pasture production, many pastoralists are becoming interested in alien invasions threatening more pasture habitats, particularly those located in riparian and subriparian zones of North Queensland. Alien invasions, particularly weed invasions are one of the most serious threats to primary production and biodiversity in Australia. They reduce agronomic and animal productivity, displace native plant species and contribute significantly to land degradation (Vitelli 2000). Alien species need to be managed so that the unwanted species decline or are eliminated. Salisbury (1961) emphasised characteristics of seeds, and seed production and transport, as important features determining the ability of aliens to spread. Understanding how an alien species is dispersed may lead to management practices that will reduce the risk of spread.

Bellyache bush (*Jatropha gossypiifolia*) is a serious invader of riparian and subriparian habitats of North Queensland (Bebawi and Campbell 2002). The plant is unpalatable to livestock, competes with and displaces native vegetation, obscures fence lines, interferes with mustering, degrades productive pastoral lands and threatens the sustainable utilisation of several pastoral enterprises (Ashley 1995; Miller and Pitt 1990).

Variations within morphology, phenology and physiology of bellyache bush exist within Australia. In Queensland, 3 biotypes exist (F. Bebawi pers. comm.). These include 2 from North Queensland (Queensland bronze leaf and Queensland green leaf) and one from Far North Queensland

 10.1071/EA03194 0816-1089/04/121157

(Queensland purple leaf). In the Northern Territory, 2 distinct biotypes exist (F. Bebawi pers. comm.). These include Katherine green leaf and Darwin purple leaf biotype. Pitt and Miller (1991) reported that the leaves of some bellyache bush plants in the Northern Territory have a purple colouration, while others are glossy green. Detailed studies of the taxonomic and ecological features that distinguish these biotypes need further investigation.

Most parts of the plant, including seeds, are toxic (Parsons and Cuthbertson 2001). Bellyache bush produces 3 seeds/capsule and up to 12000 seeds/plant.year (Bebawi and Campbell 2002). Dispersal of these seeds at a local level is diplochorous (2-step dispersal mechanism), combining ballistic seed ejection (ballistichory) with subsequent ant dispersal (myrmecochory, Fig. 1*a*) (Bebawi and Campbell 2002). Floodwater is considered important at a catchment scale and humans are recognised as the main dispersers of bellyache bush at a national and global scale (Csurhes 1999).

Ballistic dispersal of ripe seeds occurs in a random horizontal pattern, with the distance of spread positively correlated to the height from which seeds are propelled, assuming there are no obstructions in the way. Mean distances for ballistic dispersal ranges from 2.8 m for capsules located less than 50 cm aboveground to 7.2 m for capsules located 3 m aboveground with a maximum recorded distance of about 13 m (Bebawi and Campbell 2002).

Once on the ground, bellyache bush seeds are susceptible to dispersal by ants. Ants generally disperse seeds for structural (building materials) or food reasons (Smith 1971). Seeds of many plants are dispersed for food reasons because of attached food bodies called elaiosomes (caruncles, arils) that are rich in lipids (O'Dowd and Gill 1986). Ants drag

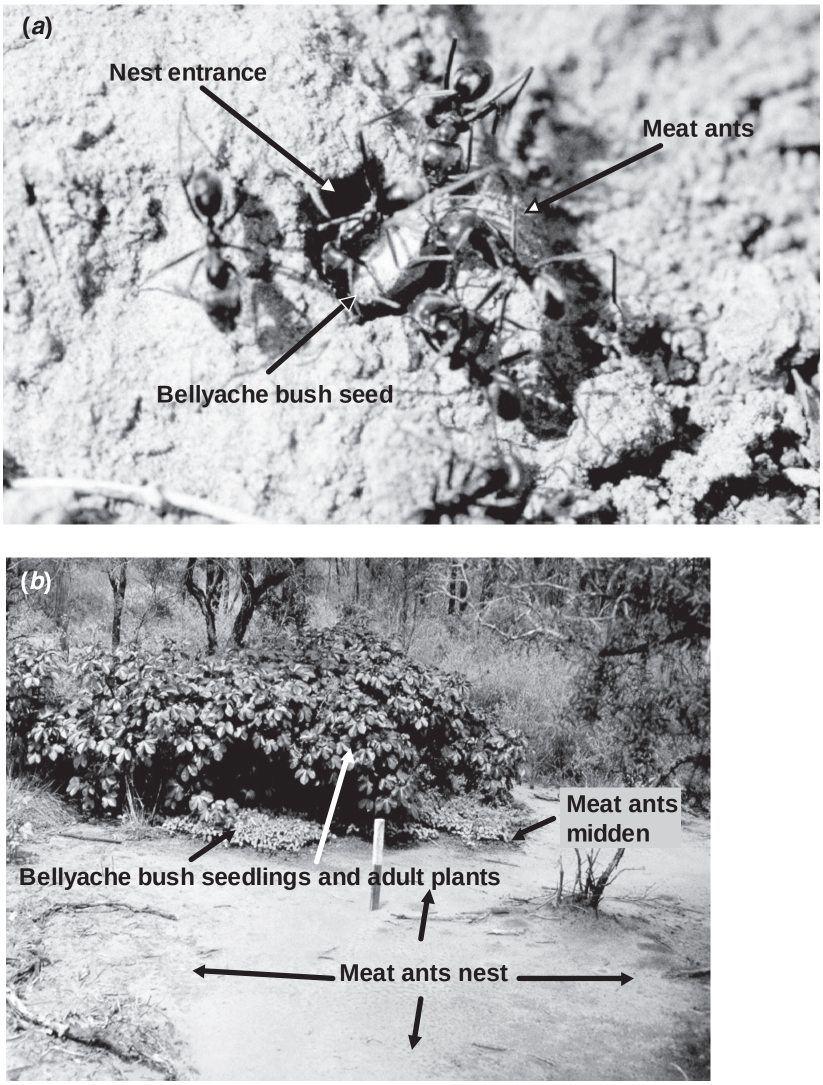

Figure 1. (*a*) Meat ants (*Iridomyrmex spadius*) dispersing bellyache bush seeds. (*b*) Meat ants (*Iridomyrmex spadius*) nest showing midden site and clumped seedling and mature plants populations.

seeds bearing elaiosomes to their nests to feed the elaiosome to larvae and discard the remaining seed in their refuse piles or middens (Beattie 1985).

Seed dispersal may provide the plant with escape from predation (Kjellsson 1985*a*), escape from competition (Kjellsson 1985*b*), enhanced germination (Culver and Beattie 1980; Horvitz 1981), nutrient-rich germination sites (Beattie and Culver 1983; Hanzawa *et al*. 1988), or enhanced growth and survival (Levey and Byrne 1993). However, not all ant–plant interactions are beneficial. For example, fire ants (*Solenopsis invicta* Buren) destroyed 86% of *Viola rotundifolia* Michx. seeds fed to them (Zettler *et al*. 2001).

Australia is the world's main centre for ant-dispersed plants (Berg 1975). Understanding the ecology of ant–plant interactions is necessary for long-term management of myrmecochorous weeds, such as bellyache bush. The purpose of this study was to assess outcomes of interactions between meat ants and bellyache bush in terms of seed dispersal, seed germination and viability, seedling survival and population density of bellyache bush.

Materials and methods

Field study site

The 4 ha field site was located 15 km northwest of Charters Towers (20°01´S, 146°01´E), Queensland, along Southern Cross Creek, which is a tributary of the Burdekin River. The soil was a brown texture contrast soil. Vegetation at the site is open woodland with a canopy dominated by *Eucalyptus* spp., a mid-storey dominated by bellyache bush and false sandalwood (*Eremophila mitchellii* Benth.), and an understorey dominated by buffel grass (*Cenchrus ciliaris* L.). Average rainfall is 658 mm/year (Bureau of Meteorology 1988). Daily temperature range in summer (November–April) is between 27 and 37°C, and in winter (June–August) between 15 and 18°C (Bureau of Meteorology 1988).

A feature of this site is the presence of large numbers of meat ant (*Iridomyrmex spadius* Schattuck) nests which are predominantly circular in shape, averaging 4 m^2 and devoid of any vegetation other than dense clumps of bellyache bush seedlings, juvenile and adult plants growing at their periphery (Fig. 1*b*). The number of meat ant nests on the experimental site averaged 27.9 ± 3.2 nests/ha. There were 50.0 ± 1.3 entrances/m^2 of nest mound and entrances were 6.9 ± 0.2 mm in diameter (n = 50), respectively. Colony size ranges from a few hundred to over 300 000 workers (Shattuck 2000). Colonies of meat ants are often spread over wide areas with many individual nests connected by well-defined paths, creating 'super nests' that can stretch up to a distance of 650 m (Shattuck 2000).

In this study, areas characterised by dense clumps or dense belts of bellyache bush with no pasture grasses growing beneath their canopies are referred to as 'core infestation' sites. Areas of pasture that were directly adjacent (within 10 m) to core infestations and being invaded by bellyache bush primarily through localised ballistic dispersal were referred to as 'grass-dominant' sites.

Bellyache bush seeds

Bellyache bush seed is endospermic, caruncluate, ovoid with flat dorsal and wedged ventral sides (Fig. 2*a* and *b*). Caruncle and exotegmen material was either removed or scraped with a sharp scalpel from 300 seeds selected from a freshly collected seed pool. The seed material was placed in separate 5 cm diameter by 5 cm height cylindrical glass jars. Three samples (20 g each) of seed components including caruncles, exotegmens (outer integument), and seeds without caruncles were analysed for fatty acids, fat and soluble carbohydrates content, at the Agritech Analytical Laboratories, Toowoomba, Queensland, using the methods of analysis developed by the Association of Official Analytical Chemists (1995). Seed caruncle and exotegmen were selected for chemical analysis because they form part of the meat ant diet (Bebawi and Campbell 2002). They are components of the 'reward system' that drives the interaction between these 2 organisms. The reward system in this study is based on myrmecochory, which is simply defined as 'the provision of food by one organism in return for transport by the other' (Bebawi and Campbell 2002).

Bellyache bush seeds used in this study were of 3 types: intact (caruncluate), non-caruncluate (intact seeds whose caruncles were manually removed using forceps) and ant-discarded seeds [seeds whose caruncles and exotegmen were eaten by meat ants and ultimately discarded on their middens with other nest waste as described by Bebawi and Campbell (2002)]. Intact seeds were collected from mature capsules about 4 weeks after capsules were harvested from parent plants. Capsules were placed in jackets of

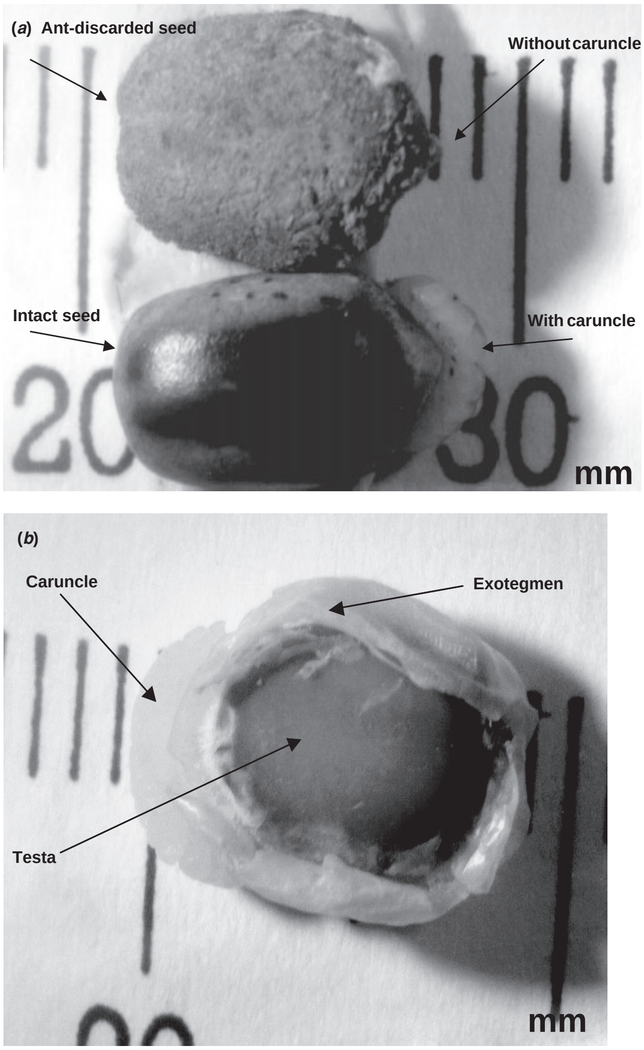

Figure 2. (*a*) Bellyache bush seeds that are meat ant-discarded (caruncle and exotegmen absent), and intact (caruncle and exotegmen present). (*b*) Immature bellyache bush seed showing seed testa, exotegmen layer and lobed caruncle.

aluminium mosquito gauze in an open-air environment to dry and release their seed. Attributes of intact and ant-discarded bellyache bush seeds are shown in Table 1.

Seed germination, germination rate and viability

An experiment was undertaken to determine whether the foraging activity of meat ants on appendages of bellyache bush seeds has any effect on subsequent germination and viability. Six seed lots (20 randomly selected seeds) each of intact, non-caruncular and ant-discarded seeds were sown 0.5 cm deep into PVC end caps (11 cm diameter, 2.5 cm height) filled with 300 g (dry weight) of fine river sand. The caps were perforated at the base to allow for water drainage. The soil was watered to approximate field capacity by adding water on 2 successive days until it drained freely for 2 days through the perforated base of the cap. The caps were then placed in a controlled-environment glasshouse set at a 12/12 h temperature of 30 ± 1/20 ± 1°C. Within the glasshouse the caps were arranged in a randomised complete block design to account for possible lighting differences. The caps were re-watered daily to prevent the soil from drying out.

Seedling emergents were counted, and removed daily. Germination was considered to have ceased when no seedlings emerged for 7 consecutive days. The soil was then washed through a 3 mm copper mesh sieve to retrieve non-germinated seeds. Seed viability was tested using the tetrazolium method (Moore 1985). This involved placing seeds for 5 days in Petri dishes filled with 10 mL of 1% triphenyl tetrazolium chloride. Seeds that were pink when cut longitudinally with a sharp scalpel were considered to be viable.

Cumulative germination and viability percentages were calculated on the basis of total seed numbers. Viable seeds were defined as those that germinated following exposure to favourable environmental conditions plus any ungerminated seeds identified as viable following tetrazolium testing. The germination rate index was calculated as the time taken to reach 50% of maximum germination for individual seed lots (Gramshaw 1972).

For germination, germination rate and viability, statistical analysis using analysis of variance was performed on arcsine-transformed data that were later back-transformed. Fisher's protected l.s.d. test was used to identify differences between treatments.

Myrmecochorous seed dispersal

To determine the quantity of seed dispersed by meat ants and the seasonal pattern of dispersal, 6 meat ant nests were randomly selected from within the field site and monitored for a year beginning in January 2000. Initially, old middens were cleared from nests. Fresh middens were then collected at monthly intervals. Any bellyache bush seeds located within middens were retrieved, by sieving all collected material through a 3 mm diameter copper sieve. Paired *t*-tests (Steel and Torrie 1980) were used to analyse differences in monthly recordings of seed dispersal.

Population density and soil nutrients

To determine the relationship between meat ants and population density of bellyache bush, densities of seedlings and mature plants within grass-dominant areas, meat ant nest middens and core infestations were compared. In June 2000, 18 transects (40 m long) that contained the 3 designated habitats were established within the field site. Along each transect, 1 quadrat (1 m^2) was then randomly located within each of the grass-dominant, core infestation and meat ant nest areas. All bellyache bush plants located within quadrats were counted and their height and basal diameter recorded. Meat ant nests were located 1–2 m away from infested areas for bellyache bush populations impacted by meat ants.

Three soil samples (0–5 cm depth) each about 100 g were also randomly removed using a garden trowel from each quadrat and bulked together in snap lock resealable plastic bags. Soil subsamples were analysed at the Analytical Services, Natural Resources and Mines Laboratories, Indooroopilly, Queensland, for total nitrogen (N), phosphorus (P) and potassium (K). Paired *t*-test analysis (Steel and Torrie 1980) was used to compare treatments.

Early (1 year) seedling survival, height and basal diameter

Twelve blocks (10 × 20 m) containing both core infestation and meat ant nests were used to compare differences in seedling survival and subsequent growth. For each block, permanent subplots (20 × 20 cm) containing an average density of 781.3 ± 97.5 seedlings/m^2 were randomly established within a core infestation site and on the middens of 12 meat ant nests.

Seedling survival was then monitored monthly for a year. Seedling counts commenced in November 2000 after the first rains fell in

Table 1. Morphological characteristics of intact and ant-discarded seeds of the bronze-leafed biotype of bellyache bush plants

A computerised Digital Image Analysis System (DIAS) was used to determine length and width of 200 intact and ant-discarded bellyache bush seeds

Dry mass of seeds and caruncles was determined after drying 6 lots of 50 carunculate, non-carunculate and ant-discarded seeds at 80°C for 5 days

Variables	Bellyache bush seeds	
	Intact	Ant-discarded
Shape	Oblong with caruncle	Oblong without caruncle
Length (mm)	6.98 ± 0.04	7.06 ± 0.04
Breadth (mm)	4.20 ± 0.04	4.66 ± 0.04
Fresh weight (mg)	49.5 ± 1.3	58.4 ± 2.3
Moisture content (%)	2.26 ± 0.02	1.05 ± 0.04
Caruncle shape	Bilobed	—
Caruncle fresh weight (mg)	6.0 ± 0.7	—
Caruncle colour	Pale	—
Seed colour	Greyish-brown with 2 dark brown lines on dorsal side, black, reddish-brown or grey	Greyish-brown, grey or black
Seed coat texture	Smooth and shiny, sealed with an outer plastic-like starchy layer (exotegmen)	Rough with corrugated surface without an outer plastic-like starchy layer (exotegmen)

October 2000. Seedling height and basal diameter were determined later when seedlings (n = 50) were 8 months old using a similar methodology to that described in the population density study.

Paired t-test analysis (Steel and Torrie 1980) was used to analyse differences between meat-ant's nests and core infestation treatments on seedling survival, basal diameter and height data.

Results

Bellyache bush seeds

Detectable amounts of 5 fatty acids including palmitic, stearic, oleic, linoleic and eicosenic were identified in bellyache bush seeds (Table 2). Variations in amounts and composition of fatty acids were detected between seed components. In the caruncle, palmitic and oleic acid were the most abundant fatty acids. Palmitic acid was also most abundant in the exotegmen while linoleic was most abundant in the seed. The highest concentration of stearic (15.4%) and oleic (29.8%) acid was detected in the caruncle, whereas the exotegmen contained the highest concentration of palmitic (36%) and eicosenic (34.5%) acid. The seed (without caruncle and exotegmen) contained the highest concentration of linoleic (61.1%) acid. Both stearic and oleic acids were not detectable in substantial amounts in the exotegmen. The highest concentration of fat (3.6%) was found in the caruncle (Table 2). About equal amounts of soluble carbohydrates were detected in the caruncle, exotegmen and seed but these were, on average, very low (0.8%) compared with those of fatty acids (23%) (Table 2).

Seed germination, germination rate and viability

Ant-discarded seeds were highly germinable, with 98% of viable seeds germinating following the receipt of favourable moisture and environmental conditions (Fig. 1). In contrast, only 10% of viable intact seeds germinated. The physical removal of caruncles (non-caruncalate treatment) promoted a significant increase in germinability (71%) but not to the same extent as that of ant-discarded seeds. The rate of germination was not significantly (P>0.05) different between the 3 seed types, with germination commencing 5 days after the imposition of favourable environmental conditions and maximum cumulative germination was reached on average between days 11 and 12. Total viability of ant-discarded seed was on average 10% greater than that of both intact and non-caruncalate seed, which were similar to one another (Fig. 1).

Table 2. Percentages (%) of fatty acids (palmitic, stearic, oleic, linoleic and eicosenic), fat and soluble carbohydrate present in 3 components of bellyache bush seed including caruncle, exotegmen and seed that had caruncle and exotegmen removed

Variables	Caruncle	Exotegmen	Seed
Palmitic acid	29.7	36.0	10.2
Stearic acid	15.4	—	5.2
Oleic acid	29.8	—	15.7
Linoleic acid	8.5	29.5	61.1
Eicosenic acid	16.7	34.5	7.7
Fat	3.6	0.4	2.3
Soluble carbohydrates	0.6	0.9	0.8

Myrmecochorous seed dispersal

On average, 12 330 ± 603 (s.e.) seeds were retrieved from the middens of individual meat ant nests over the 12 months of the study. With the density of meat ant nests at the field site averaging 28 per hectare, this equates to 334 000 seeds/ha being dispersed away from their initial point of contact with the ground following ballistic dispersal.

While some seeds were retrieved from middens at each of the monthly recordings (Fig. 2), significant (P<0.05) differences in the number of seeds discarded onto middens were detected between months. High numbers (>1200 seeds/ant nest) of seeds were recorded between February and June. Thereafter monthly seed numbers declined to average less than 60 seeds/nest from August to November.

Population density and soil nutrients

Significant (P<0.05) differences in the density of bellyache bush plants were detected between grass-dominant, core infestation and meat ant nest sites (Fig. 3). Maximum density of bellyache bush plants (96 plants/m^2) occurred within core infestations. Nevertheless, the dispersal ability of meat ants resulted in meat ant nest sites averaging only 18% fewer plants than those within the core infestations. In comparison, grass-dominant areas located adjacent to core infestations had a population of 16 plants/m^2. In all areas, seedlings were the most numerous growth stage present (93% of the population).

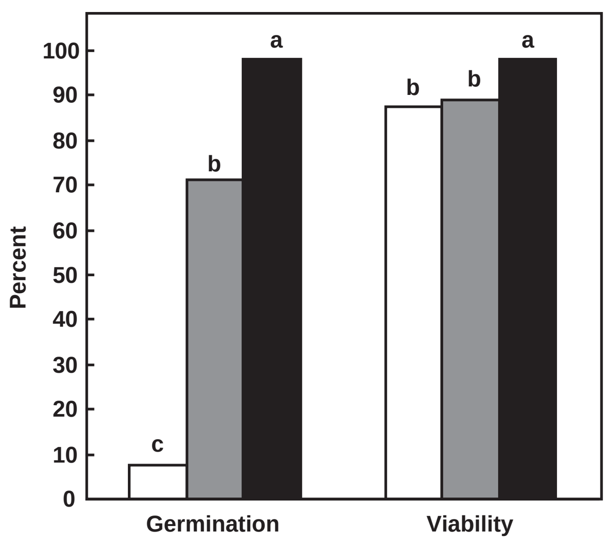

Figure 3. Germination and viability of intact (open bars), non-caruncalate (shaded bars) and meat ant discarded (solid bars) bellyache bush seeds. Within seed variables, bars with the same letter are not significantly different (P>0.05).

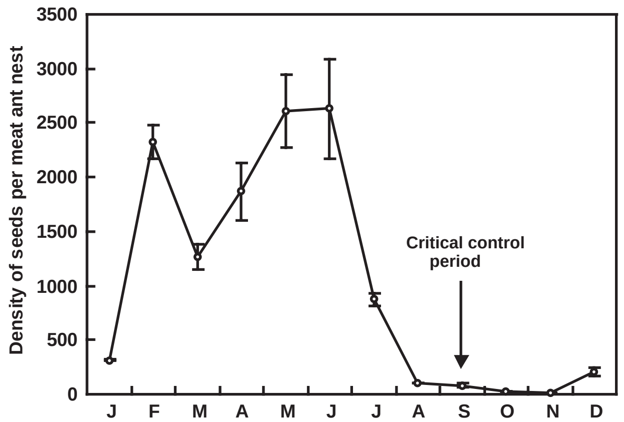

Figure 4. The average number of bellyache bush seeds retrieved monthly from the middens of meat ant nests. Vertical bars indicate ± s.e.

Maximum concentrations of total soil N, P and K were detected on meat ant nests (Fig. 4). Total N, P and K on meat ant nest sites were 35-, 9- and 1.5-fold greater compared with grass-dominant sites and 4-, 4- and 1.2-fold greater compared with core infestation sites. Percent ranking of nutrients on meat ant sites was N>K>P compared with K>N>P on both core infestation and grass-dominant sites.

Early (1 year) seedling survival, height and basal diameter

Even though some 400 mm of rainfall was received at the field site for 2 months following seedling emergence (November–December), a linear decline in seedling survival occurred over the 12 months that monitoring was undertaken, irrespective of whether plants were growing within core infestation or meat ant nest sites (Fig. 5). After 12 months, seedling survival averaged 8.5 and 0.5% within meat ant nest sites and core infestations, respectively.

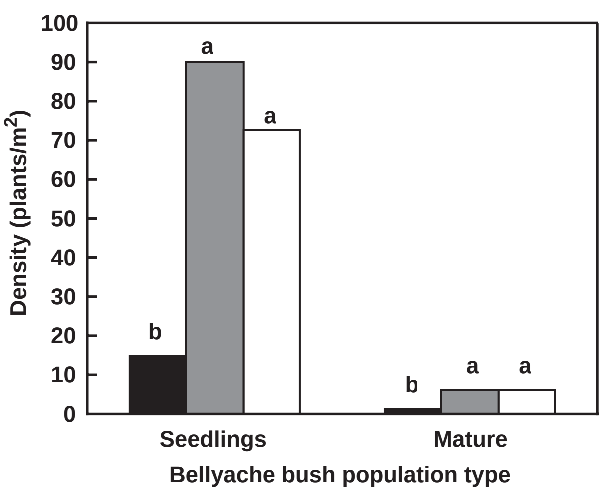

Figure 5. Density of bellyache bush populations (seedlings, mature plants and seedlings + mature plants) within grass-dominant (solid bars), core infestation (shaded bars) and meat ant nest (open bars) sites at Southern Cross Creek. For population types bars with the same letter are not significantly different (P>0.05).

Seedlings growing on meat ant nest sites were significantly larger than those within core infestations. After 8 weeks, the basal area of seedlings averaged 0.35 and 0.18 cm for meat ant nest and core infestation sites, respectively. Similarly, seedlings growing on meat ant nests were 41% taller (11.9 cm high) than those within core infestations (8.2 cm high).

Discussion

This study has helped clarify the key role that meat ants play in dispersal of bellyache bush seeds and expansion of infestations. More than 12 000 seeds were discarded in the middens of individual ant nests over 12 months and subsequent plant densities averaged 79 plants/m^2. With findings from previous studies indicating that meat ants can move bellyache bush seeds to ant nests located up to 40 m away from where they have been collected (Bebawi and Campbell 2002), it can be argued that the rate of localised invasion may be markedly increased in areas where meat ants are present. One of the unique attributes of this mode of dispersal is that seeds can also be moved into previously clean upstream habitats, which would generally not occur, except for perhaps some localised ballistic dispersal, as seeds are too heavy for wind dispersal.

This study has also shown a high concentration of fatty acids present in the external structures of the seed, namely the caruncle and exotegmen. The abundance of oleic acid (29.8%) found in the caruncle of bellyache bush is consistent with findings for seeds of some other ant dispersed plants (Brew *et al*. 1989; Kusmenoglu *et al*. 1989; Lanza *et al*. 1992; Soukup and Holman 1987; Skidmore and Heithaus 1988). If nutrient requirement is the reward that drives meat ants to collect bellyache bush seeds, then energy efficiency becomes a factor in this interaction. Meat ants selectively chose large bellyache bush seeds that contained bigger than average caruncles and a greater surface area of exotegmen. In seed removal assays performed in the field, Davidson and Morton (1981) also found that meat ants (*Iridomyrmex* sp.) dispersed heavier seeds (*Sclerolaena diacantha* Benth.) compared with other ants such as *Melophorus* spp.

Not only were discarded bellyache bush seeds generally bigger than the average, the percentage viability was also higher. Almost all discarded seeds were viable (98%) and readily germinable (100%). In comparison, viability of intact seeds was on average 10% lower than that of ant-discarded seeds, and only 8% of fresh viable seeds were capable of germinating. Culver and Beattie (1978) reported a similar stimulatory effect on viola seeds that had been bitten by *Aphenogaster* spp. ants. The literature reports a plethora of examples where the outer protective layer of seeds of many plant species needs to be scarified or ruptured before germination can occur (Baskin and Baskin 1997; Bewley and Black 1994; Lush *et al*. 1984; Mayer and Poljakoff-Mayber 1989). In this study the physical removal of caruncles of bellyache bush seeds to imitate the activity of meat ants did stimulate germination of seeds but not to the same extent as ant-discarded seeds. This finding tends to suggest that additional scarification through feeding on other external structures such as exotegmen may also be an important factor in promoting germinability of viable seeds.

The resultant effect of large numbers of highly germinable seeds being discarded in the middens of meat ant nests is the establishment of a population almost as dense as that found within core infestations. Meat ant nests appear also to provide an environment conducive to higher seedling survival and faster growth rates than that within core infestations. This may be partly attributable to meat ants nests having higher concentrations of total soil N, P and K compared with those within core infestation sites. Similar results have been reported for the myrmecochorous sedge *Carex pedunculata* Muhl. (Handel 1976) and for the ruderal thistle *Silybum marianum* (L.) Gaertner (Danin and Yom-Tov 1990). Dominance of *S. marianum* in patches of grassland was attributed to harvester ants (*Messor semirufus* Andre) dispersing seeds into nutrient-enriched refuse zones, which had high concentrations of N, P and K compared with control sites (Danin and Yom-Tov 1990).

Increased N availability is known to favour invasion by non-native plants into natural grasslands (Burke and Grime 1996; Alpert and Maron 2000). Placement of seeds in ant nests is also thought to be especially important on nutrient-poor soils (Andersen 1988; Czerwinski *et al*. 1971; Westoby *et al*. 1982), particularly in the Australian arid zone (Davidson and Morton 1981).

The management implications of meat ant dispersal of bellyache bush are substantial. Not only is the invading front able to move more rapidly through the establishment of new foci from which expansion can occur, but these new outbreaks are growing in a nutrient rich environment and would generally be protected from fire due to the lack of flammable vegetation.

Consideration needs to be given to whether it is feasible to control these outbreaks so as to slow down the rate of spread. This however, may need to be an ongoing process as the ants will continue to utilise bellyache bush seeds and discard them in their middens, thereby regularly replenishing the seed bank.

It can be concluded from this study that where both meat ants and bellyache bush plants are present in the same location, myrmecochory appears to be playing a major role in the rate at which localised infestations are expanding. This finding emphasises the importance of controlling small isolated infestations as soon as possible, before dispersal vectors such as the meat ant contribute to the formation of large infestations that are more difficult and costly to control. Meat ants were, however, only 1 of a number of ant species observed within the study site and it is plausible that other species could also contribute to dispersal, and warrant further investigation.

Acknowledgments

Special thanks are extended to The Queensland Department of Natural Resources and Mines for providing financial support, and to Dave and Pauline Chapman (Almora Station) and Charlie Truscott (Lynmore Station) for allowing us to use their property for research purposes. We also thank D. Panetta, A. Grice and A. Lindsay for reviewing the manuscript. The technical assistance of M. Madigan, R. Stevenson, C. Dennis and K. Risdale is also acknowledged.

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Received 19 September 2003, accepted 10 March 2004