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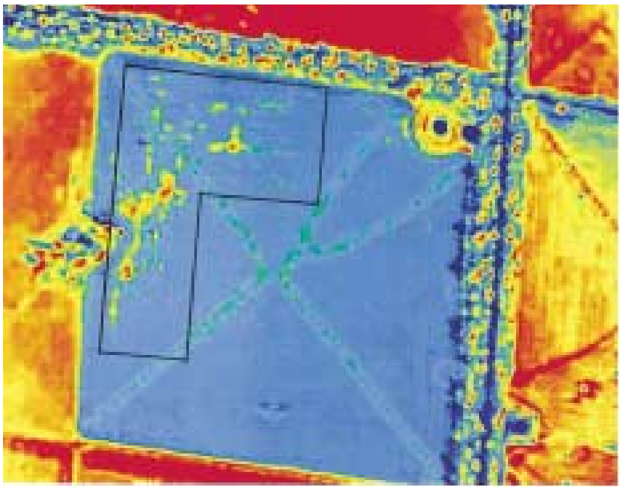

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Effects of fire on germination and viability of bellyache bush (*Jatropha gossypiifolia*) seeds

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Abstract. If treatments imposed to control exotic plants also have a deleterious impact on their residual seed bank, the duration and extent of follow-up control may be reduced. Fire is one such technique that has this ability, particularly if seeds are located on or close to the soil surface. Three studies were undertaken in a riparian habitat in the dry tropics of northern Queensland to quantify the effects of spring burning on the seed bank of the exotic weed bellyache bush (*Jatropha gossypiifolia*). The first determined the distribution of seeds within the vertical profile of the trial site. The other 2 studies were experiments that quantified the effects of fire on germination and viability of both dispersed bellyache bush seeds and seeds held in mature capsules. Dispersed seeds of 2 types (intact and ant-discarded) were placed at the following 6 positions in the vertical profile of bellyache bush infestations: 0.5, 1, 2 and 4 cm depth below ground, on bare ground, and below fuel. Seeds held in capsules were located at random on the crown of bellyache bush plants. For both experiments, comparisons of burnt plots were made with unburnt controls. Fire was imposed in spring (September); the season in which burning for weed control in northern Queensland generally occurs. While maximum fire temperatures averaged 590 ± 46°C, the temperatures that seeds or capsules were exposed to depended on their location within the vertical profile, with temperatures decreasing in the following order: below fuel > crown of bellyache bush > 1 cm > 0.5 cm > bare ground > 2 cm > 4 cm below ground. There were negative correlations between seed germination and peak fire temperature and between viability and peak fire temperature. Seed viability was nil for seed under fuel but >80% for seeds placed on bare ground or ≥2 cm below ground. Fire reduced germination and viability of seeds held in capsules by 31 and 35%, respectively, when compared with unburnt seeds. While ant-discarded seeds generally had a higher germinability than intact seeds, they were more susceptible to fire. This may be attributed to loss of the external protective barrier of the seed coat (exotegmen) caused by the feeding of ants. Bellyache bush seeds were recorded across all soil depths, reaching a peak of 3.8 million seeds per hectare at 1–5 cm soil depth. These results suggest that while bellyache bush seeds are susceptible to fire, many are buried beyond the reach of lethal temperatures. Therefore, viable seeds will be available for post-fire recruitment and other measures, such as chemical control, may need to be employed in conjunction with burning.

Introduction

Bellyache bush (*Jatropha gossypiifolia*) is not only an invasive woody weed of the dry tropics of northern Australia (Parsons and Cuthbertson 2001) but it is also a myrmecochorous weed (Bebawi and Campbell 2002*a*). Myrmecochorous plants are plants whose seeds are dispersed by ants (Beattie 1985). Ants can move seeds considerable distances from parent plants (Bebawi and Campbell 2001) and are also capable of burying seeds below the ground surface (Berg 1975; Slingsby and Bond 1981). Bellyache bush seeds have a caruncle, which is a source of food for ants (Dehgan and Webster 1979). The effects of ants on a bellyache bush seed whose caruncle and exotegmen (outer layer of the seed coat) were consumed for food are shown in Figure 1.

Bellyache bush predominantly infests riparian habitats (Bebawi and Campbell 2002*a*) but can also spread into open pastures and rocky areas in regions where rainfall ranges between 200 and 1500 mm per year (Bebawi *et al.* 2001). The worst infestations in Queensland are currently found along the banks of the Burdekin River and its tributaries (Csurhes 1999). Dense infestations of bellyache bush are known to prevent the growth of pasture grasses and reduce profitability of cattle enterprises (Miller 1982; Csurhes 1999). Bellyache bush is also unpalatable to livestock, competes with and displaces native vegetation, obscures fence lines and interferes with mustering (Miller and Pitt 1990). Most parts of the plant, including seeds, are toxic (Parsons and Cuthbertson 2001). Reproductive plants can produce between 2000 and 12 000 seeds per plant per year in northern Queensland (Bebawi and Campbell 2002*a*). They also have the potential to flower and set seed throughout the year if soil moisture is sufficient. This is often the case for

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plants growing along the edges of natural watercourses or artificial water storages, such as dams (F. F. Bebawi and W. D. Vogler pers. obs.).

If a treatment could be imposed to reduce the size of the available seed bank of bellyache bush before germination commences, recruitment over the ensuing season might be reduced. Ideally, a treatment that kills both plants and seeds would give land managers a greater likelihood of controlling bellyache bush. Two chemicals, metsulfuron-methyl (sold as 'Brushoff') and fluroxypyr (sold as 'Starane'), applied as foliar sprays, are registered for use in Queensland in controlling bellyache bush (Csurhes 1999). However, herbicides are expensive, as well as logistically difficult and costly to apply in remote locations (Carter and Signor 2000; Schroder and Howard 2000). Furthermore, observations following chemical control suggest that large-scale recruitment of bellyache bush will occur over the ensuing wet season (J. S. Vitelli unpublished data).

Fire is relatively cheap and has been shown to have an impact on both soil-stored and canopy-stored seeds of some woody species (Shaw 1957; Floyd 1966; Whelan 1995; Bebawi and Campbell 2000; Downey 2000). There is a need to know how bellyache bush seeds respond to fire and to incorporate this knowledge into fire-management strategies, particularly as preliminary research suggests that both seedlings and mature plants may be susceptible to fire (Bebawi and Campbell 2002*b*).

This paper reports the results of 3 studies designed to quantify the effects of spring burning on the seed bank of bellyache bush. The first investigates the distribution of seeds within the vertical profile of an infestation. The other 2 studies were experiments designed to determine the effects of fire on germination and viability of both dispersed bellyache bush seeds and seeds held in mature capsules.

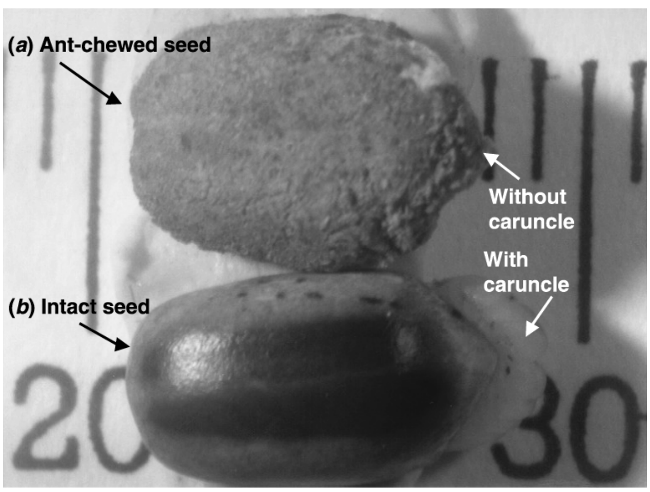

Figure 1. Dispersed bellyache bush seeds: (*a*) ant-discarded without caruncle and (*b*) intact with caruncle. Graduated scale is in millimetres.

Seeds held in mature capsules were selected as a treatment for 2 reasons. First, seed production occurs nearly all-year-round and not all capsules mature at the same time (F. F. Bebawi unpublished data). Second, burning is likely to occur at a time when some seeds are still in capsules. Two types of dispersed seeds were tested, intact seeds and those that had been discarded by ants (referred to as ant-discarded seeds). Both types were tested because they were structurally different. Ant-discarded seeds differed from intact seeds in that the caruncle was removed and the external layer of the seed coat (exotegmen) frequently chewed (scarified) by ants (Fig. 1). The influence of seed position within the fire site on germination and viability was also examined for dispersed seeds.

Materials and methods

Site description

The experiments reported in this paper form 1 component of a larger study investigating the impacts of fire on populations of bellyache bush growing in a riparian habitat at Sandy Creek near Charters Towers (20°05′S, 146°0′E). Bellyache bush density within the 1 km^2 field site averaged 10 750 plants per hectare. This is considered a 'medium infestation' according to Bebawi and Campbell (unpublished data: light infestation up to 1000 plants, medium infestation between 1001 and 10000 plants, and high infestation over 10000 plants per hectare).

The soil at Sandy Creek has a sandy A horizon of varying thickness over a B horizon ranging from sandy loam to sandy clay. The herbaceous vegetation is dominated by buffel grass (*Cenchrus ciliaris*), mossman river grass (*C. echinatus*), couch (*Cynodon dactylon*), parthenium weed (*Parthenium hysterophorus*), feathertop Rhodes grass (*Chloris virgata*) and liverseed grass (*Urochloa mozambicensis*). The shrub stratum is dominated by bellyache bush, castor oil plant (*Ricinus communis*), lantana (*Lantana camara*), rubber vine (*Cryptostegia grandiflora*), chinee apple (*Ziziphus mauritiana*), mimosa bush (*Acacia farnesiana*) while a mixture of bloodwood (*Eucalyptus erythrophloia*), narrow-leaved iron bark (*E. crebra*), river tea tree (*Melaleuca linariifolia*), white wood (*Atalaya hemiglauca*) and river oak (*Casuarina cunninghamiana*) dominate the tree stratum.

Seed density

Twenty soil cores beneath the canopy of bellyache clumps were taken at random with a 20 cm diameter auger at each of 4 depths (litter, 1–5 cm, 5–10 cm, and 10–15 cm) to determine seed density distribution within the trial site before the fire. Soil cores were sieved on site through a 3 mm diameter aluminium sieve to retrieve bellyache bush seeds. Retrieved seeds were placed in 11 by 6 cm 'Tudor' moist seal envelopes and transported to the laboratory where they were counted and their number recorded regardless of whether they were intact or ant-affected.

Effects of fire on seeds in capsule

At the field site, 13 mature bellyache bush plants were randomly selected from within both the burnt (1 km^2 area) and surrounding unburnt areas (within 50 m radius of burnt area). At the time, bellyache bush plants were fully foliated, flowering and bearing capsules of different maturity stages.

On selected plants, 4 mature capsules (woody in texture and green in colour) were each encapsulated in perforated aluminium mosquito gauze cubicles (4 by 4 by 0.5 cm). Cubicles ensured that seed retrieval was possible after burning, while still allowing free movement of heat. The location of each cubicle was marked with a uniquely numbered metal tag to facilitate cubical retrieval after the fire. The average number of seeds per capsule, estimated from 200 randomly collected capsules, was 2.90 ± 0.02 (Table 1).

Cubicles containing burned and unburned capsules were retrieved immediately after the fire and transferred to a drying oven (28 ± 1°C) to facilitate capsule dehiscence. After 4 weeks, all seeds were removed from cubicles ready for germination and viability tests.

Since germination requirements of bellyache bush under controlled conditions are not yet known, seedling emergence from seeds sown in garden soil (supplied by a registered landscaping contractor) was used as an indicator of germination. Following treatment, seeds were removed from cubicles and sown 1 cm deep in plastic pots (20 cm diameter). Seed burial has been reported to promote maximum germination for a number of weed species (Barker *et al.* 1996; van Klinken and Campbell 2001). All pots were placed in the open air and irrigated to field capacity. This was achieved by adding water until it drained off through the perforated base of the pot. The pots were re-watered daily to prevent the soil from drying out. Germinated seeds were allowed to emerge as seedlings, counted and removed daily. Germination was considered to have ceased when no seedlings emerged for 3 consecutive days. Ungerminated seeds were then retrieved by washing the soil through a 3 mm diameter copper mesh sieve and their viability tested by the tetrazolium method (Moore 1985). This involved placing seeds in petri dishes filled with 10 mL of 1% tetrazolium chloride. Seeds that were pink when cut longitudinally with a sharp scalpel were considered to be viable.

Effects of fire on dispersed seeds

A 2-factor experiment replicated 6 times in a randomised complete block design was undertaken to evaluate the effects of fire on dispersed bellyache bush seeds. Factor 1 comprised 2 seed types (intact and ant-discarded) and factor 2 comprised 7 seed-placement positions within the vertical profile [unburned, below fuel, on bare ground, buried 0.5 cm below ground (0.5 cm), buried 1 cm below ground (1 cm), buried 2 cm below ground (2 cm), and buried 4 cm below ground (4 cm)]. Below-fuel treatment refers to a position where seed lots were placed on the ground underneath plant material. In contrast, bare ground treatment refers to ground surface placement of cubicles containing seeds on an area of 50 by 50 cm, with all plant material completely removed.

Experimental units comprised 20 bellyache bush seeds enclosed in cubicles (4 by 4 by 0.5 cm) of aluminium mosquito gauze.

Blocks (1 m^2) were established at equal spacings along a 20 m transect that ran parallel to sandy creek and in close proximity to the buried data loggers. Within blocks, 1 cubicle each of intact and ant-discarded seeds was randomly placed or buried at the 7 designated locations within the vertical profile on the day before burning. The unburnt seed lots (controls) were placed on the ground surface, but retrieved just before burning. Fuel was put back in place on the surface in areas that were dug to bury seeds and the location of each cubicle was marked with a uniquely numbered metal tag to facilitate retrieval after fire. Seed characteristics are summarised in Table 1.

In this study, intact seeds were collected from mature capsules about 4 weeks after harvest. Capsules were placed in jackets of aluminium mosquito gauze in open air in order to dry and release their seed. This was necessary because bellyache bush capsules release their seeds explosively.

Ant-discarded seeds were collected from meat ant (*Iridomyrmex spadius* Shattuck) middens (refuse piles) (Bebawi and Campbell 2002*a*), 4 weeks after cleaning up the middens from previously discarded seeds to ensure that they were of similar age to that of intact seeds. Preliminary observations with retrieval of colour-paint intact seeds fed to meat ants showed that up to 75% of seeds were discarded on middens within 4 weeks. All ant-discarded seeds were without caruncles and their exotegmen abraded (Fig. 1). The exotegmen abrasion could not have been a result of burial but of a chewing process by powerful ant mandibles. Longitudinal scars on the seed coat and the overall removal of the exotegmen indicated that a biotic agent had been at work (Fig. 1). The authors have also observed meat ants chewing the exotegmen before dispersing the seeds to their nest.

Cubicles containing burned and unburned seeds were retrieved immediately after the fire and transferred to the laboratory where seeds were removed from cubicles. Seed germination and viability procedures were similar to those described for seeds held in capsules.

Fire behaviour

The fuel load and soil moisture content at the site were estimated on the day of burning. Soil moisture content was determined gravimetrically from 36 randomly selected soil samples (0–5 cm depth) and fuel load was estimated by removing all above-ground plant material from 48 randomly placed 0.5 by 0.5 m quadrats. Both the soil moisture and fuel load samples were stored in waterproof plastic bags and transferred to the laboratory where their fresh weight was determined. The samples were then oven-dried (80 and 105°C for 48 h for the fuel load and soil moisture samples, respectively), their dry weight recorded and gravimetric soil moisture and fuel moisture contents calculated.

Ambient temperature, relative humidity, and wind speed and direction were measured on the day of burning, immediately before ignition of the site. Temperature of fire was measured by placing 2 type K steel-encased thermocouples 5 m apart at each of the positions within the vertical profile where dispersed seeds or seeds held in capsules were placed [unburnt (control), on crown of bellyache bush (crown), below fuel, on bare ground, buried 0.5 cm below ground (0.5 cm), buried 1 cm below ground (1 cm), buried 2 cm below ground (2 cm), and buried 4 cm below ground (4 cm)]. The data collected from the thermocouples were stored in data loggers (Data Electronics Pty Ltd) buried underground during the fire. Duration of maximum temperature was the length of time within 5% of the maximum that was recorded. Burning was undertaken close to the middle of the day in order to maximise uniformity in fire behaviour over the site. Drip torches were used to ignite fuel to promote a continuous fire line, with all fuel burnt as head fires following an initial back-burn phase on the north eastern corner of the site.

Data analyses

Paired *t*-tests (Steel and Torrie 1980) were used to (i) test for significant differences in seed density between soil depths, and (ii) to

Table 1. Seed and capsule characteristics of bellyache bush

Characteristic	
Seed	
Fresh weight of intact seed (g)	0.05 ± 0.01
Fresh weight of ant-discarded seed[A] (g)	0.06 ± 0.02
Moisture content of intact seed (%)	2.26 ± 0.06
Moisture content of ant-discarded seed (%)	1.05 ± 0.18
Length of intact seed (mm)	6.98 ± 0.38
Breadth of intact seed (mm)	4.2 ± 0.35
Caruncle : seed weight ratio	1 : 8
Mature capsule	
Fresh weight (g)	1.17 ± 0.12
Moisture content (%)	4.53 ± 0.21
Length (mm)	12.9 ± 0.68
Breadth (mm)	12.4 ± 0.65
Mean number of seeds per capsule (n = 200)	2.90 ± 0.02

[A]Seeds were heavier than intact seeds.

Table 2. Site conditions during a late dry-season fire at Sandy Creek

Parameter	
Fuel load (t/ha)	9.5 ± 3.5
Fuel moisture (%)	16.9 ± 5.0
Soil moisture (%)	1.3 ± 0.5
Weather	Clear
Air temperature (°C)	35.2 ± 2.0
Relative humidity (%)	19.7 ± 2.1
Wind speed (km/h)	6.1 ± 1.9
Wind direction	South-east

determine whether fire significantly affected seeds held in capsules. Analysis of variance was performed to test whether seed type and seed location of dispersed seeds at the time of burning had any significant individual or interactive effects on seed germination and viability. Where the *F*-test was significant ($P<0.05$), the mean differences were determined using Fisher's protected least significant difference (l.s.d.) test. All statistical analysis concerning seed germination and viability was undertaken on arcsine-transformed data, which was later back-transformed for display.

The germination-rate index was calculated by dividing the number of germinated seeds obtained at each daily counting by the number of days seeds had been in pots. The values obtained at each count were then summed at the end of the germination test to obtain the germination-rate index (Maguire 1962). Regression analysis was used to relate seed germination and viability following fire to placement position, fire temperature and duration, and to relate seed density to soil depth.

Results

Fire temperature and duration

The presence of a large dry fuel load combined with hot temperatures, low humidity and light wind (Table 2) resulted in a high-intensity fire. Temperatures recorded during burning varied within the vertical profile of the infestations, ranging from as low as 36 ± 1.4°C to as high as 590 ± 46°C (Table 3). Temperatures below ground reached a maximum of 93 ± 0.8°C at 0.5 cm, decreasing thereafter with increasing depth. Above ground, temperatures peaked at 590 ± 46°C on the surface, decreasing thereafter as the height above ground increased. In contrast, temperatures within bare patches where fuel was not present reached a maximum of only 62 ± 0.4°C on the ground surface. A negative correlation was detected between peak fire temperature and duration ($r = -0.60$). Some of the dispersed seeds exposed to fire were carbonised whereas most capsules were scorched by fire.

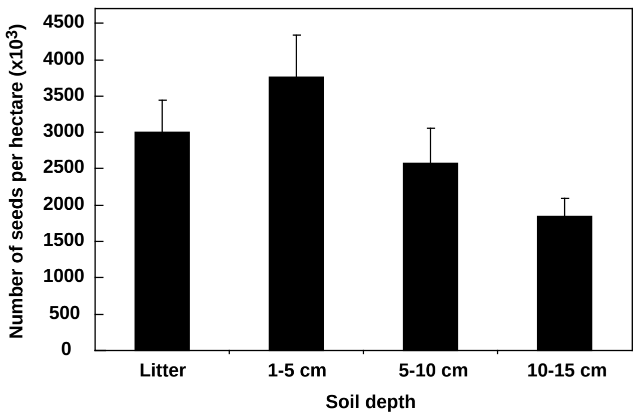

Figure 2. Mean density distribution of dispersed bellyache bush seeds within the vertical profile of the soil at Sandy Creek. Vertical bars indicate the s.e. of the mean.

Seed density

The density of seeds significantly (*P<0.05*) varied within the vertical profile of the site (Fig. 2). A negative correlation occurred between seed density and soil depth ($r = -0.88$), with most seeds (3.8 million seeds/ha) located between 1–5 cm depth (Fig. 2).

Ants affected most seeds that were retrieved from the 4 soil depths within the trial site. Absence of caruncle and rough seed-coat surface were visible indicators of ant interaction with bellyache bush seeds.

Effects of fire on seeds in capsules

Germination and viability of bellyache bush seeds held in mature capsules were significantly ($P<0.01$) affected by fire (Fig. 3). Germination decreased from 40 to 9%, whereas viability decreased from 82 to 47%, respectively (Fig. 3). The rate of germination, however, was not significantly different, with germination commencing 5 days after sowing and continuing on for 11 days. Maximum germination occurred 6 days after sowing.

Table 3. Mean maximum fire temperature and duration (the length of time within 5% of the maximum temperature that was recorded) at different seed placement positions and at the crown of bellyache bush plants where seeds held in capsules were exposed to fire at Sandy Creek

Crown, seeds held in capsules on the crown of bellyache bush plants; BF, seeds placed below fuel; BG, seeds placed on bare ground; 0.5 cm, seeds buried at 0.5 cm depth; 1 cm, seeds buried at 1 cm depth; 2 cm, seeds buried at 2 cm depth; 4 cm, seeds buried at 4 cm depth

Variable	Seed held in capsule	Intact and ant-discarded seed					
	Crown	BF	BG	0.5 cm	1 cm	2 cm	4 cm
Fire temperature (°C)	262 ± 48	590 ± 46	62 ± 0.4	93 ± 0.8	70 ± 17	49 ± 0.8	36 ± 1.4
Duration (s)	9 ± 3	52 ± 34	225 ± 0	101 ± 1	615 ± 327	538 ± 43	877 ± 82

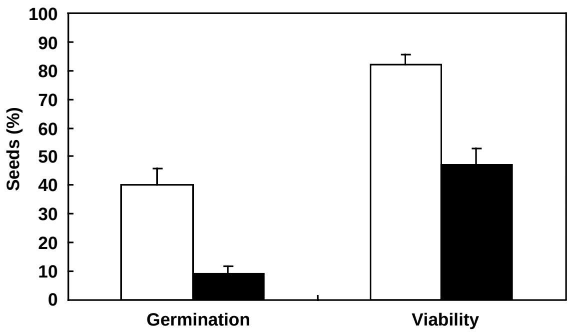

Figure 3. Mean percentage germination and viability of seeds held in unburnt (open bars) and burnt (closed bars) mature capsules of bellyache bush. Vertical bars indicate the s.e. of the mean.

Effects of fire on dispersed seeds

There were highly significant (*P*<0.01) interactions between seed type and placement position on germination and viability of dispersed bellyache bush seeds (Fig. 4). Under control conditions, both intact and ant-discarded seeds exhibited very high viability (≥98%). Germinability averaged 48 and 100% for intact and ant-discarded seeds, respectively.

Seeds located above ground were generally highly susceptible to fire irrespective of seed type, with 100% mortality occurring if seeds were located below fuel (Fig. 4). The only exception were those seeds that avoided being directly exposed by being located on bare ground. For these, germination and viability were not significantly different from the unburned treatment. One hundred percent mortality occurred if seeds were located below fuel.

Seed mortality below ground was significantly less than that recorded above ground and only occurred up to a depth of 2 cm (Fig. 4). At 1 cm depth, 77% of ant-discarded and 69% of intact seeds remained viable. At 0.5 cm, however, 40 and 74% of intact and ant-discarded seeds were killed, respectively.

Seed germination and viability were negatively correlated (*r* = – 0.80 and – 0.88, respectively) with fire temperature. Ants enhanced germination at all fire temperatures but germination declined with increased heat for both intact- and ant-discarded seeds. The germination pattern of dispersed seeds was similar to that manifested by seeds held in mature capsules, except that peak germination occurred 12 days later in burnt ant-discarded seeds than in burnt intact-discarded seeds (Fig. 5).

Discussion

Fire can kill bellyache bush seeds, irrespective of whether they still remain held in capsules or have matured and been released. The determining factor is whether they are located at positions within the vertical profile that receive high enough temperatures for sufficient duration to cause mortality.

During this study, maximum temperature within the vertical profile decreased in the following order: below fuel > bellyache bush crown > 1 cm depth > 0.5 cm > bare ground > 2 cm depth > 4 cm depth. It is not surprising, therefore, that the greatest impact was on seeds located below the fuel: the location where temperatures were generally highest. Similarly, Bebawi and Campbell (2000) found that rubber-vine seeds were most affected if located on top of or below the fuel.

The high above-ground temperatures recorded in this study are typical of grass fires with fuel loads >3.5 t/ha, which are used to control other woody weeds such as rubber vine (*Cryptostegia grandiflora*) in the dry tropics of northern Queensland (Bebawi *et al.* 2000; Bebawi and Campbell 2000).

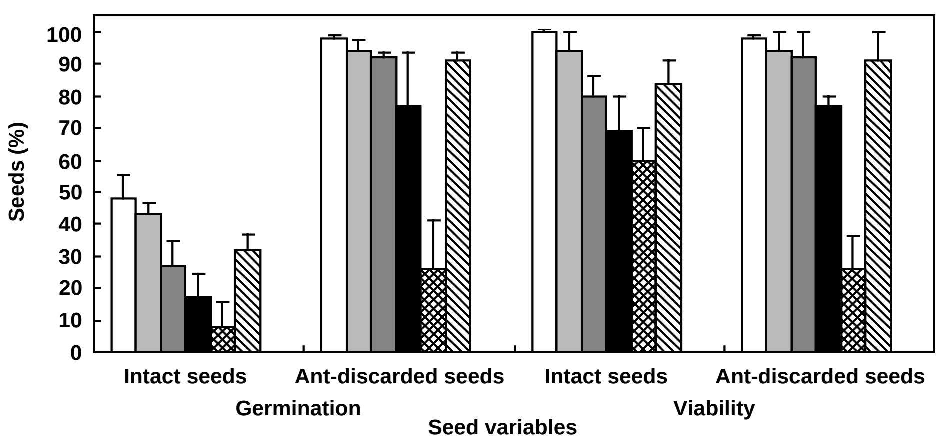

Figure 4. Mean percentage germination and viability of dispersed bellyache bush seeds located at a range of positions within the vertical profile of an infestation at Sandy Creek. Open bars, unburnt; lightly shaded bars, 4 cm depth; heavily shaded bars, 2 cm depth; closed bars, 1 cm depth; cross-hatched bars, bare ground; striped bars, below fuel. Vertical bars indicate the s.e. of the mean.

The efficacy of fire in killing bellyache bush seeds decreased as the depth of burial increased. Once seeds were buried at a depth of 2 cm or greater, they appeared to be protected from lethal temperatures. Similar results have been obtained for a range of other plant species (Zacharias *et al.* 1988; Whelan 1995; Bebawi and Campbell 2000).

While this study has shown that seeds located in certain positions within the vertical profile are susceptible to fires, the overall impact on the size of bellyache bush seed banks has not been quantified. This will largely depend on how much of the area containing bellyache bush is actually burnt and how much of the seed bank is located in positions that receive lethal temperatures. In this study, 73% of the estimated 14.5 million seeds/ha were buried at depths more than 1 cm below ground. As such, most of these would escape exposure to lethal temperatures. However, the location of seeds within the vertical profile of an infestation at the time of burning could vary markedly, depending on several factors, which include the season in which burns are undertaken, soil type and the effect of myrmecochory. Seed density of bellyache bush recorded in this study is not considered high when compared with the large reserves (pools) of weed seeds accumulating in arable soils. Work reviewed by Kropac (1966) and Roberts (1981) shows that the number of seeds per m^2 in the upper 15–25 cm of soil in cultivated fields may be as high as 70 000–90 000.

In northern Queensland, meat ants store bellyache bush seeds underground up to 40 cm depth. Once they have eaten the caruncle, they then discard the seeds on refuse piles (middens) in the vicinity of their nest (Bebawi and Campbell 2002*a*). These discarded seeds are much more germinable at this stage than at their previously intact state. In the current study, 100% of ant-discarded seeds were germinable without heating, compared with only 48% for intact seeds, implying a seed-coat enforced dormancy. Literature on other ant-dispersed species (*Viola* spp. and *Calathea microcephala*) report either no change in germination after seed handling by ants (Culver and Beattie 1978) or increased germination (Horvitz 1981). In contrast, removal of the elaiosomes and/or caruncles (ant-attractant food bodies) of *Leucospermum conocardpodendron* by the Argentine ant (*Iridomyrmex humilis*) resulted in complete failure of seedling emergence after fire (Slingsby and Bond 1985). These discarded seeds do, however, appear more vulnerable to the effects of high temperatures than intact seeds. This difference was most apparent in seed samples located at 0.5 cm below ground. At 0.5 cm depth, temperatures peaked at only 88°C, with the duration of high temperatures lasting for 288 s. While this exposure was sufficient to kill 73% of ant-discarded seeds, mortality of intact seeds reached just 40%. Perhaps the removal of the caruncle creates an entry point for the excessive temperatures to penetrate the living tissues of the seeds, or possibly these seeds absorbe moisture and this makes them more vulnerable to high temperatures.

It can be concluded that fire has the ability to kill some bellyache bush seeds, irrespective of whether they are

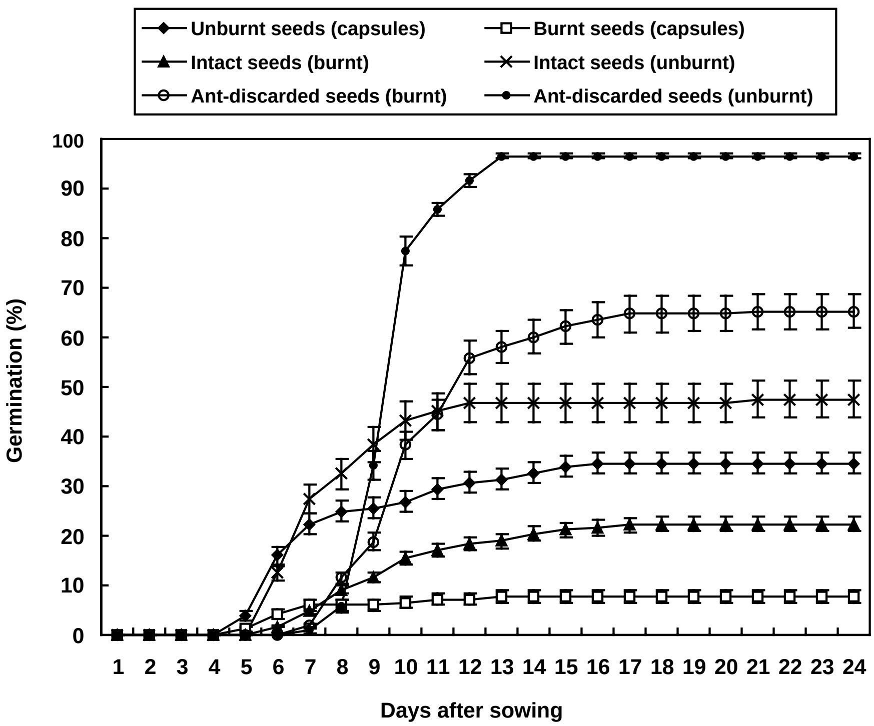

Figure 5. Germination pattern of dispersed seeds (intact and ant-discarded seed) and those held in capsules. Vertical bars indicate the s.e. of the mean.

dispersed or held in capsules. The proportion killed may vary depending on whether the seeds have been damaged by ants and their location in the vertical profile of the burned site. Seeds held in mature capsules are somewhat protected compared with dispersed seeds but greatest protection is afforded by an insulating layer of soil. Seeds at a distance from the fire (on bare ground) are also afforded some protection. Fire may prove a useful tool in controlling bellyache bush in riparian and subriparian habitats of the dry tropics, where sufficient fuel is found under the canopy of bellyache bush plants to carry a fire. Nevertheless, seed burial and dispersion to locations without fuel are likely to necessitate an integrated approach that combines fire with other control options such as chemical control.

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