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Determining the factors affecting seed germination in *Livistona* australis (Arecaceae) for the recovery of fragmented populations

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Abstract. Understanding seed germination and seedling recruitment is important for managing long-lived plant species, particularly palms that are transplanted from the wild and where regeneration is suppressed by seed predators and exotic herbivores. Seed viability, the timing of germination, and the factors influencing germination were investigated for the cabbage tree palm, *Livistona australis* (R.Br.) Mart. Greenhouse studies were combined with *in situ* experiments conducted on the Australian mainland and on a nearby mammal-free island. Under greenhouse conditions, >90% of seed germinated within 4 months. In the field, burial rather than surface sowing of seed increased germination success. Seed without mesocarp and in sunlight had increased germination when compared with fruits in shade on the island, whereas neither presence/absence of mesocarp or light levels had any effect on the mainland. Germination success was substantially lower on the mainland, primarily because of high seed predation from the native bush rat, *Rattus fuscipes*. When caged to exclude vertebrates, 44% of seed were damaged over time by pathogens and invertebrates, with losses greater in sunlight than in shade. Results from the present study indicate that freshly buried seed with the mesocarp removed would have the greatest potential success in promoting the restoration of *L. australis* at degraded sites.

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Introduction

The maintenance of populations of long-lived plants is dependent on occasional recruitment events to replace individuals that die. Factors controlling the timing and magnitude of germination, early seedling establishment and growth are important drivers of plant recruitment (Baskin and Baskin 1998). Limiting factors may work on both a spatial and temporal scale (Eriksson and Ehrlen 1992) and for species such as palms that lack dormancy, timing may be crucial in their establishment. Palm seedling establishment can be promoted by large- or small-scale disturbances (Svenning 1998; Wright and Duber 2001; Beard et al. 2005), with the factors affecting germination being complex and varied. Moisture, temperature, light, salinity, predation and seed age have all been shown to influence palm germination (Brown 1976; Clancy and Sullivan 1988; Forget et al. 1994). The longevity of palm seed in the field is poorly known, although there is anecdotal evidence that seeds can persist in the ground for many years, sprouting after fire or similar disturbance (Anonymous 1999).

In coastal eastern Australia, several palms can be significant components of the mid- or upper canopy of moist eucalypt forest and rainforest. In such habitats, both large disturbances (such as fire) and small-scale disturbances (such as tree fall) may be important for recruitment of new individuals. One such palm, the cabbage tree palm, *Livistona australis* (R.Br.) Mart. has populations at risk from harvesting (during land-clearing) to provide plants for landscaping purposes, or from predation of

seed and seedlings by exotic mammals (Orscheg and Parsons 1996; Priddel *et al.* 2000; Carlile and Priddel 2009). In New South Wales (NSW), they form a significant component of swamp sclerophyll forest, an endangered ecological community (Keith 2004). A population on Cabbage Tree Island, NSW, provides habitat for a threatened seabird Gould's petrel, *Pterodroma leucoptera* (Fullagar 1976); however, palm germination here has been suppressed for almost a century by European rabbits, *Oryctolargus cuniculus* (Werren and Clough 1991). The recovery of this palm population following the eradication of rabbits, the islands only ground mammal, is unclear because information on the germination response in wild populations is scant.

Germination of *L. australis* (fruit diameter 8–10 mm) can be influenced by temperature, seed age and the presence of the mesocarp (the fleshy fruit layer) in the laboratory, and seed predation in the field (Orscheg and Parsons 1996). It has been suggested that germination requires the removal of the mesocarp and a time lapse of 1–3 months after fruit fall (Floyd 1989), which generally occurs May to August (austral autumn to winter). Flesh left on the seed often encourages fungal or insect attack (Fox *et al.* 1987), thus reducing viability, although the extent of this is unknown. The removal of the fruit layer can occur naturally through decay or the foraging activities of frugivorous birds (Higgins *et al.* 2006).

The aim of the present work was to determine under what circumstances seed germination is most successful in wild populations of *L. australis*. In our specific example, we have a

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population re-establishing seedlings under a rainforest canopy. We would expect that shade not only reduces germination, but also affects seed viability. If germination is delayed, we would expect an increase in the likelihood of removal by frugivores or seed consumption by predators (particularly in a mainland context). Given that many palm fruits are not consumed by birds, what impact, if any, does the continued presence of the mesocarp have on seed viability and germination. The present study tests these hypotheses by examining seed viability, the timing of germination and the influence of light and mesocarp removal on germination in the greenhouse. In the field, we investigated the effect of the following four factors on germination success: light, removal of the mesocarp, burial and the presence of vertebrate seed predators. From these results, we then make recommendations about targeting conservation efforts to rehabilitate degraded palm populations or maintain existing populations.

Materials and methods

Study sites

Field experiments were conducted at the following two nearby sites in south-eastern Australia: Mungo Brush (MB) and Cabbage Tree Island (CTI), NSW. These two study sites differed in relation to the presence of seed-eating mammals, which were common at MB but absent on CTI.

MB (32°34'S, 152°16'E) is a rainforest-covered hill (25 m) rising out of swamp sclerophyll forest on the eastern shore of Myall Lakes, 500 m from the coast and within the Myall Lakes National Park (31 581 ha). Floyd (1990) classified the rainforest at MB as an intermediate type between the Dry Rainforest Suballiance 23 (Ficus-Streblus-Dendrocnide-Cassine) and Subtropical Rainforest Suballiance 19 Sarcomelicope-Cassine-Podocarpus). There is no record of fire penetrating the rainforest at MB, and the pattern of fire scarring on the palms (scars present on tall palms but absent on small palms) together with data on palm growth rates (Carlile 2002) suggest that the current period without fire may exceed 100 years.

CTI (32°41′S, 152°13′E) is a nature reserve ~18 km south-south-west of MB. Floristically, it contains rainforest similar to that in MB (Floyd 1990), being a combination of dry and subtropical rainforest, with patches dominated by *L. australis*. The CTI rainforest is a form of Dry Rainforest Suballiance 23 (Floyd 1990). Rock-scree gullies support mature rainforest that increases in height on deeper soils. Browsing by rabbits from 1906, until they were eradicated in 1997 (Priddel *et al.* 2000), has resulted in a severe reduction in rainforest undergrowth (Werren and Clough 1991). Some of the taller palms show evidence of past fire; however, none has been recorded within the past century (Hull 1911; Hindwood and Serventy 1943; Fullagar 1976).

Greenhouse experiment 1: seed germinability and viability A germination trial was conducted to determine the potential germinability of seed provided with higher moisture, humidity and temperature (Orscheg and Parsons 1996) than would be expected for $in\ situ$ seed, and to assess the time taken for these seeds to germinate. Freshly fallen fruit (n=280), being with undamaged mesocarp lacking desiccation, was sourced from

MB in May 1998 and, in the laboratory, the mesocarp was then removed from the seeds by scraping with a sharp knife. Technically, seed with the mesocarp intact are 'fruit'; however, for clarity, they are hereafter referred to as 'seed with mesocarp intact'. Care was taken not to damage the seed coat. In each of 14 replicate pots (15-cm diameter), 20 seeds were buried at a depth of 1 cm in 12 cm of commercial potting mix. The pots were then placed in a glass-panelled greenhouse and watered for 10 min twice daily. The number of germinated seeds in each pot was recorded weekly. Germination was assessed as occurring when the plumule emerged above the soil surface. Once counted, each seedling was removed to avoid established seedlings suppressing germination of other seeds. Pots were inspected weekly over a period of 17 months. Germination success was calculated as the percentage of seeds that germinated.

At the completion of the trial, any intact seed remaining was assessed for viability by cutting it open and examining the endosperm. For our study, a seed was considered 'viable' if the normally cream or white endosperm (Rodd 1998) was without discolouration, free of fungal infection and invertebrate holes. Viability was calculated as the germinable fraction plus the residual viable fraction.

Greenhouse experiment 2: effect of light and mesocarp on germination

We examined the effect of light and mesocarp removal on germination success by using two light intensities (shaded and sunlit) in combination with presence or absence of the mesocarp. Commercial shade cloth (70% cover) suspended over half the pots simulated shade conditions while still allowing water to penetrate. Exposed pots without shade cloth were considered to be in sunlit conditions. Replicates were positioned randomly within the two light intensities. The mesocarp was removed as described previously.

Fresh seed was sourced from MB in August 1999 and, in the laboratory, buried in pots. Pots were then transferred to the greenhouse and monitored monthly for 24 months. Each of the four combinations of the two factors (light and mesocarp) was replicated four times. Each replicate was established as before, but with 25 seeds in each pot. The number of newly germinated seeds in each pot was recorded at each visit. Once counted, each emergent seedling was cut and killed with undiluted (360 g L⁻¹) glyphosate (*N*-(phosphonomethyl)glycine)), a broad-spectrum systemic herbicide. Because this herbicide rapidly binds to soil and becomes inactive, its use here rather than physical removal of the seedlings, was to ensure that the other seeds remained undisturbed for the duration of the experiment.

Field experiments

An orthogonally designed field experiment to assess the impact of light, mesocarp removal, seed burial and caging on seed germination was conducted at each study site (MB and CTI). Seeds were sourced locally by removing the fruit-bearing inflorescences from three palms after the commencement of ripe-fruit fall. Two light intensities (shade and sunlit) were examined. Shaded plots were below a closed canopy and received no direct sunlight at any time of the day; sunlit plots were below natural gaps in the forest canopy. Plots were

positioned randomly, but were at least 5 m away from reproductive palms so as to reduce the possibility of additional seeds being inadvertently incorporated into the experiment. Seeds had their mesocarp either intact or removed and were either buried under 1 cm of soil (checked first for the remote possibility of soil seed-bank) or deposited on the soil surface. Cages were used to exclude vertebrates from consuming or removing seeds. The cages were made from 10-mm-square mesh, shaped into a $150 \, \text{mm} \times 150 \, \text{mm}$ top with 30-mm-high sides, and secured to the ground by two 150-mm steel pegs passing through the sidewalls. Uncaged plots were delineated by a strip of mesh (30 mm high) along the perimeter and held in place by a single steel peg. It was assumed that for both caged and uncaged plots, the mesh had no effect on germination, other than the exclusion of vertebrate predators from the caged plots.

The 16 treatment combinations of four fixed factors (light, mesocarp, burial, caging), each with two levels, were replicated four times (a total of 64 replicates) at each of the two sites (MB and CTI). Location was to be examined as an additional factor in the analysis; however, a severe rainstorm washed many seeds from the uncaged plots on CTI, removing caging as an experimental factor at that site. As a result, data from the two study sites were analysed separately.

Each plot contained 70 seeds (with or without mesocarp) at a density similar to that occurring naturally around fruiting palms (~3000 m⁻²). In total, 8960 seeds were used, 4480 at each study site. Seeds were then sorted, with only the larger (>8-mm-diameter with mesocarp, >5-mm-diameter seed), undamaged, ripe seeds being selected for the experiment.

The field experiments began in May 1998 and plots were monitored initially twice monthly for 2 months and then monthly until April 2000. The number of new seedlings was recorded at each visit. Once recorded, each seedling was killed with glyphosate as described previously. At the completion of the study, the soil in each plot was checked for seeds and seed remains. Intact seeds were later examined for viability as described earlier.

Seed predation/destruction

Seed predation/destruction was examined in both caged and uncaged plots at one site (MB). The number of seeds present was recorded periodically over a 2-year period, May 1998 to April 2000. The proportion of seeds remaining at the conclusion of the experiment was compared across treatments without a viability assessment.

Seed remains found within or nearby uncaged plots were collected and examined for mammalian incisor markings. Where present, these were measured to the nearest 0.05 mm with callipers. Nocturnal searches to assess the mammal fauna present at MB were conducted on a single night in each of the following months: May 1998, February, June and July 1999, and February 2000. The incisor markings were then compared with the dentition of species observed to be present.

Statistical analysis

Prior to analysis, all proportional data were checked for normality and tested for heterogeneity of variance using Cochran's C-test (Underwood 1981) and were arcsin

transformed where indicated. Germination success in the second greenhouse experiment was analysed using two-factor ANOVA (mesocarp removal and light). In the field experiment, germination at MB was analysed using a four-factor ANOVA (mesocarp removal, light, burial and caging), whereas germination at CTI was analysed using three factors (mesocarp removal, light and burial) after transformation. Seed predation/ destruction at MB was analysed by three-factor ANOVA (mesocarp removal, light and burial) after transformation. From uncaged plots, over-time assessment was made using a repeated-measures ANOVA (mesocarp removal, light and time). All ANOVAs were computed using Systat 10 for Windows at 95% confidence. Student-Newman-Keuls tests were applied in all multiple comparison tests at 95% confidence. All statistical tests performed were two-sided and, where means are presented, standard errors are included.

Results

Greenhouse experiment 1: seed germinability and viability

In total, 255 (91%) of the 280 seeds tested germinated over a period of 4–10 months. One-third of the remaining seed (i.e. 3% of seed planted) was still viable at the conclusion of the trial (17 months). Thus, 94% of seed was considered viable.

Greenhouse experiment 2: effect of light and mesocarp on germination

There was no significant interaction between mesocarp removal and light on germination rates ($F_{1,12}=1.75$, P=0.21), nor was there any significant first-order effects (mesocarp removal: $F_{1,12}=0.98$, P=0.34; light: $F_{1,12}=0.11$, P=0.75). Across all treatments, mean germination success was $74\% \pm 6\%$. Germination was equally successful with mesocarp intact ($68\% \pm 8\%$) or removed ($80\% \pm 9\%$), and in sunlight ($76\% \pm 8\%$) or in shade ($72\% \pm 10\%$).

Field experiment: Mungo Brush

At MB, there was no significant interaction among the factors (mesocarp, light, burial and caging). The only significant result was the effect of burial ($F_{1,48} = 25.50, P < 0.01$), which resulted in higher germination (mean = 29% \pm 5%) than did placement of seed on the surface (5% \pm 1%). The effect of caging was approaching significance ($F_{1,48} = 3.55, P = 0.06$), the trend being lower germination in uncaged plots.

Field experiment: Cabbage Tree Island

On CTI, there was a significant interaction between mesocarp presence and burial ($F_{1,24}=9.56$, P<0.01, Fig. 1), with the highest germination recorded for buried seed without mesocarp ($53\%\pm8\%$). Light, as a single factor, was significant in doubling germination success (sunlit: $26\%\pm7\%$; shade: $13\%\pm5\%$).

Comparative germination success

Germination of seed treated in the same manner as in the viability trial (mesocarp removed, buried 1 cm below the surface and in sunlight) was compared across experiments (Table 1). There

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was a significant difference in seed viability across the different experiments (single-factor ANOVA, $F_{4,936} = 31.209$, P < 0.01). MB had substantially lower germination than did either CTI or the greenhouse (Table 1). The proportion of seed lost at MB was more than twice that lost on CTI.

Timing of germination

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The time to germination was 4 months for both greenhouse experiments, 7 months on CTI and 8 months at MB. In the two greenhouse experiments and on CTI, 90% of seeds that germinated did so within 3 months of the onset of germination, whereas at MB this took 10 months.

Seed predation/destruction

The mean proportion of seeds destroyed within caged plots at MB was 0.44 ± 0.04 (range = 0.03–0.62). Vertebrate predators were excluded from these plots, so these losses were attributed

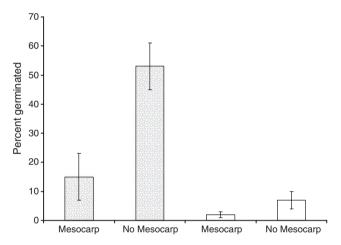


Fig. 1. The mean percentage germinated (with s.e. bars) from the significant (P < 0.01) interaction between mesocarp presence and burial resulting from a three-factor ANOVA (mesocarp, light and burial) of *Livistona australis* seed at Cabbage Tree Island; buried seed (stippled bars); unburied seed (open bars).

Table 1. Viability of *Livistona australis* seed from four separate germination experiments in which the mesocarp was removed, and the seed were buried in sunlit plots

In field experiments, caging was used to prevent access by vertebrate predators. GHE1, Greenhouse experiment 1; GHE2, Greenhouse experiment 2; FE_{MB} , field experiment at Mungo Brush; FE_{CTI} , field experiment on Cabbage Tree Island. Residual seeds recovered are expressed as a proportion of the original number of seeds. Significant differences in germination proportions are Student–Newman–Keuls results. Values with the same letters are not significantly different from each other

Parameter	GHE1	GHE2	FE_{MB}	FE _{CTI}
Sample size	280	100	280	280
Period of study (months)	17	21	24	24
Percentage germinated (mean \pm s.e.)	$91 \pm 3a$	$90 \pm 9a$	$19 \pm 8b$	$64 \pm 10a$
Residual recovered	0.09	0.10	0.13	0.11
Viable	0.03	0.06	0.01	0.05
Non-viable	0.06	0.04	0.12	0.06
Seed not recovered	0.00	0.00	0.68	0.25

to invertebrates and soil pathogens. The only significant factor affecting seed destruction was light intensity ($F_{1,24}$ =9.76, P<0.01), with losses greater in sunlight (0.54 ± 0.05) than in shade (0.33 ± 0.05).

There was a significant three-way interaction (time, mesocarp and light) in the persistence of surface seed in uncaged plots on MB (Table 2), following minimal germination. Seeds with an intact mesocarp remained longer than those with the mesocarp removed (Fig. 2). After 4 months, a proportion of just 0.02-0.03 of seed with the mesocarp intact had been displaced, compared with 0.20-0.30 of seed with the mesocarp removed. There was a significant interaction between light and mesocarp on seed persistence after 24 months ($F_{1,31}=10.38$, P<0.01). Seeds with mesocarp intact and in sunlit plots (0.53 ± 0.09) were at least twice more likely to be still present than those recorded in other treatments (Fig. 2).

The following mammals were observed within the palm forest at MB: bush rat, *Rattus fuscipes*; long-nosed bandicoot, *Perameles nasuta*; brush-tailed possum, *Trichosurus vulpecula*;

Table 2. Repeated-measures ANOVA (mesocarp, light and time) of the proportional raw data of *Livistona australis* seed remaining in uncaged plots at Mungo Brush over a 2-year period

Asterisk indicates a significant (P < 0.05) result

Factor	SS	d.f.	MS	F	P
Time	8.97	9	0.98	53.42	<0.01*
Time × mesocarp	0.51	9	0.06	3.01	<0.01*
$Time \times light$	0.10	9	0.01	0.59	0.59
Time \times mesocarp \times light	0.40	9	0.04	2.38	0.02*
Error	2.02	108	0.02		

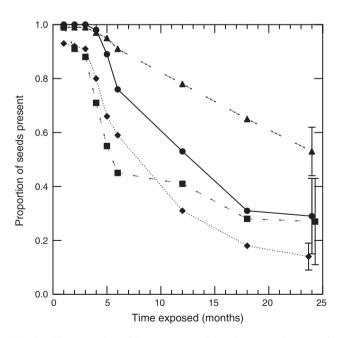


Fig. 2. The proportion of *Livistona australis* seeds present in uncaged plots at Mungo Brush over a period of 2 years. Data are the means of four replicates. Seed with mesocarp in sunlight (\spadesuit) and in shade (\spadesuit); and seed without mesocarp in sunlight (\spadesuit) and in shade (\blacksquare). Standard error bars are shown for final data points. The data are not corrected for the minimal germination ($5\% \pm 2\%$) here.

and dingo, Canis lupus dingo. Topknot pigeons, Lopholaimus antarcticus, and pied currawongs, Strepera graculina, were observed to feed on fruit hanging in the canopy; however, no birds were observed to take fallen fruit (seed with mesocarp intact) or seeds

Seed remains collected at MB from uncaged plots bore tooth marks matching those of broad, chisel-like mammalian incisors. In total, 26 examples of complete incisor pairs and seven examples of single incisors were discernible. The mean width of incisor pairs was 1.45 ± 0.05 mm (range = 1.00-1.85 mm) and the mean width of single incisors was $0.90 \pm 0.02 \,\mathrm{mm}$ (range = 0.75–1.30 mm). The incisor-pair width of an adult R. fuscipes measures 2.05 mm and a single incisor 1.10 mm (Triggs 1996). T. vulpecula has an incisor-pair width of 4.10 mm (Triggs 1996). One other species that was not observed in the nocturnal surveys, but which was likely to have been present is the introduced house mouse. Mus musculus. This species, however, has an incisor-pair width of just 1.1 mm (Triggs 1996), smaller than most of the indentations observed. Given that the seed remains are likely to have desiccated over time, the incisor spacing suggests R. fuscipes was the most likely predator responsible and that seeds were lost to predators rather than removed by dispersal agents.

Discussion

Under greenhouse conditions, more than 90% of fresh *L. australis* seed germinated, indicating high viability. Germination in the greenhouse commenced 4 months after sowing, whereas germination in the field commenced 7–8 months after sowing, all within the austral spring or early summer, with no apparent association to local rainfall. As found elsewhere (Orscheg and Parsons 1996), warmer temperatures within the greenhouse probably account for the faster germination, whereas in the wild, spring germination, with increasing ambient temperatures, appears to be the norm (Jakobasch 1981).

Seed viability is highly variable among palm species and may decline with increasing seed age (Agil *et al.* 2000). Seeds are likely to be attacked by pathogens in the field and may survive only up to 3 years, as recorded, under greenhouse conditions (Jakobasch 1981). Delayed germination can increase infection rates of seeds by up to 65% (Augspurger 1979). Species that have seeds that undergo long dormancy periods generally have mechanisms to protect the seed from pathogens (Augspurger 1990). Although dormancy has not been studied in *Livistona* (Dowe 2010), the members of the family Arecaceae generally have dormancy of only weeks to months (Orozco-Segovia *et al.* 2003). The destruction of *L. australis* seed by soil pathogens after extended periods within the soil suggests that dormancy mechanisms are not well developed in this species and a seed bank is unlikely to be established as a regeneration strategy.

Germination success in temperate rainforest trees is highly variable (e.g. 29.2%, Smythe 1989; 63.5%, Everham *et al.* 1996; 66%, Brewer and Webb 2001) and can be influenced by the presence of the mesocarp (Orscheg and Parsons 1996) or canopy gap (Figueroa 2003). In the present study, however, germination success of *L. australis* seed in the greenhouse was independent of both the presence of the mesocarp and light levels. In the field, the high seed viability and germinability, regardless of light levels,

may reflect a recruitment strategy whereby the population is characterised by a seedling or juvenile bank awaiting adult palm death or tree fall from storm damage to provide canopy gaps for successful growth to maturity (Silvertown 1982; Auld et al. 2010). Burial of seed increased germination success in the field, presumably because of decreased desiccation and predation (Smythe 1989). Natural mechanisms by which seeds become buried include soil movement as a result of surface runoff following heavy rain (as was the case in our studies), and removal and hoarding by seed-eating animals (see below). Mesocarp removal and sun light both increased germination success on CTI, but had no effect at MB, where germination success was substantially lower.

Caging improved germination rates at MB, although seed predation by vertebrates was not the prime cause of seed loss. Germination in caged plots at MB was just 19%, significantly less than that on CTI (64%). This difference cannot be explained by differing viability of sourced seed because seed germinated at MB also achieved in excess of 90% germination within the greenhouse within the same year and among different years. The two field sites are separated by less than 20 km, so climate is also unlikely to explain the difference in the germination success.

Seed destruction can significantly reduce the ability of a species to successfully reproduce. The destruction of L. australis seeds through soil pathogens and invertebrate attack was high, with a mean proportion of 0.44 of seed lost compared with caged plots at MB. The higher losses of seeds in sunlit patches is possibly due to insect attack being more prevalent at the higher temperatures that occur in such situations. However, pathogen damage is often most pronounced in cool, damp, shady situations (Foster 1986). Fox et al. (1987) suggested that removal of the mesocarp from the seed could discourage fungal or insect attack, and Smythe (1989) found that removing the mesocarp prevented palm seed from suffering attack from invertebrates that were contained as eggs within the skin. In uncaged plots, there was no significant difference in seeds destroyed with the mesocarp intact versus removed in shaded plots. However, in sunlight, removal of the mesocarp reduced this.

No avian consumers/dispersers of fallen seed were observed during the present study, and the two ground-foraging birds known to eat palm fruits – the brush-turkey, Alectura lathami (Marchant and Higgins 1993), and the cassowary, Casuarius casuarius (Willson et al. 1989) - do not occur in either study site. The only mammalian seed predator identified was the native rodent R. fuscipes. None of the teeth marks observed on seed remains belonged to the larger T. vulpecula, despite this possum having been implicated as a predator of large seed in other studies (Ballardie and Whelan 1986; Orscheg and Parsons 1996). The absence of disturbed soil in the experimental plots suggested that rats did not unearth and consume buried seed. A similar result was obtained in a study of a tropical forest palm, Astrocaryum mexicanum, in Central America, where burial of seed was also found to greatly increase survival to the seedling stage (Brewer and Webb 2001).

The impact of rats as a seed predator is variable, and can be particularly severe in isolated palm populations (Orscheg and Parsons 1996; Billing 1999; Auld *et al.* 2010). However, not all palm seed eaten by rats was necessarily consumed on site, some may have been carried away. A portion of this seed may have

survived being moved, and subsequently germinated some distance away from the parent. Studies have shown that removal and 'scatter-hording' can increase germination when compared with seeds left near the adult palm (Forget and Milleron 1991; Silva and Tabarelli 2001).

Implications for restoration and management of palm populations

Within NSW, L. australis can form a significant component of swamp sclerophyll forest, which is an endangered ecological community (NSW Scientific Committee 2004) that has undergone a 70% reduction in area since European settlement (Keith 2004). Threats, other than continued clearing for development, include an increased frequency of fire, weed invasion, as well as grazing and soil disturbance by domestic stock and feral herbivores. Changes in land-management practices can alleviate some of these threats and, in extreme cases, fencing and regeneration techniques for individual species can be applied. However, in the case of L. australis, the establishment of reproductive individuals takes many decades (Carlile and Priddel 2009) and introduced herbivores can dramatically suppress regeneration (Priddel et al. 2000). Consequently, any restoration program that included L. australis would first need to remove or control exotic predators such as pigs or rabbits (as on CTI).

The L. australis population on CTI has been severely affected by rabbit grazing, with little or no recruitment occurring during the 90 years between when rabbits arrived (1906) and when they were eradicated (1997) (Priddel et al. 2000). Natural mortality of mature palms in the absence of regeneration has created gaps in the distribution of *L. australis* on CTI (Carlile and Priddel 2009). The only published example of the impact of rabbit removal on an island-limited palm is on Round Island, Mauritius (Merton 1987). Here, natural regeneration has commenced since the eradication in 1986; however, such was the devastation by rabbits that there are few competing canopy species (Asmussen-Lange et al. 2011). Breaks in the distribution of the palm on CTI have implications for the successful breeding of the Gould's petrel, which is nocturnal on land (Priddel and Carlile 1995a). Nesting densities increase considerably in areas of shed palm leaves because they provide cover over the petrels rock-scree habitat (Fullagar 1976). To restore the original distribution and juvenile seedling bank (Silvertown 1982), additional plantings may be necessary on CTI, particularly where canopy gaps now exist. Results from the present study indicate that buried fresh seeds with the mesocarp removed would have the greatest potential for successful germination. Maintaining or restoring the distribution and abundance of L. australis on CTI has important conservation benefits for Gould's petrel. The seabird population here is recovering following a steep decline in recent decades (Priddel and Carlile 1997) and significant efforts have been made to provide quality habitat for their breeding (Priddel and Carlile 1995b). Following the removal of rabbits, the restoration of this nature reserve through a process of natural regeneration has commenced (Priddel and Carlile 2009). However, restoring the palm canopy will require ongoing monitoring and potential management through regeneration efforts, such as suggested here, well into the future.

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References

- Agil MR, Jurado E, Sánchez-Ramos G, Trejo-Hernández L, Rios FL (2000) Rapid viability loss in seeds of palmilla (*Chamaedorea radicalis* Mart.) from el Cielo Biosphere Reserve. *The Southwestern Naturalist* 45, 373–375. doi:10.2307/3672848
- Anonymous (1999) 'Palms may grow again'. St George & Sutherland Shire Leader. Hurstville.
- Asmussen-Lange CB, Maunder M, Fay MF (2011) Conservation genetics of the critically endangered Round Island bottle palm, *Hyophorbe lagenicaulis* (Arecaceae): can cultivated stocks supplement a residual wild population? *Botanical Journal of the Linnean Society* **167**, 301–310. doi:10.1111/j.1095-8339.2011.01175.x
- Augspurger CK (1979) Irregular rain cues and the germination and seedling survival of a Panamanian shrub (*Hybanthus prunifolius*). *Oecologia* 44, 53–59. doi:10.1007/BF00346397
- Augspurger CK (1990) The potential impact of fungal pathogens on tropical plant reproductive biology. In 'Reproductive ecology of tropical forest plants'. (Eds KS Bawa, M Hadley) pp. 237–245. (The Parthenon Publishing Group: Paris)
- Auld TD, Hutton I, Ooi MKJ, Denham AJ (2010) Disruption of recruitment in two endemic palms on Lord Howe Island by invasive rats. *Biological Invasions* 12, 3351–3361. doi:10.1007/s10530-010-9728-5
- Ballardie RT, Whelan RJ (1986) Masting, seed dispersal and seed predation in the cycad *Macrozamia communis*. *Oecologia* **70**, 100–105. doi:10.1007/BF00377116
- Baskin CC, Baskin JM (1998) 'Seeds: ecology, biogeography, and evolution of dormancy and germination.' (Academic Press: San Diego, CA)
- Beard KH, Vogt KA, Vogt DJ, Scatena FN, Covich AP, Sigurdardotti R, Siccama TG, Crowl TA (2005) Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs* 75, 345–361. doi:10.1890/04-1114
- Billing J (1999) 'The management of introduced rodents on Lord Howe Island.' (Lord Howe Island Board: Lord Howe Island)
- Brewer SW, Webb MAH (2001) Ignorant seed predators and factors affecting the survival of a tropical palm. *Oikos* 93, 32–41. doi:10.1034/j.1600-0706.2001.930103.x
- Brown KE (1976) Ecological studies of the cabbage palm *Sabal palmetto*. III. Seed germination and seedling establishment. *Principes* **20**, 98–115.
- Carlile N (2002) Demography of the cabbage tree palm *Livistona australis*. MSc Thesis, University of Technology, Sydney.
- Carlile N, Priddel D (2009) Mortality of adult *Livistona australis* on Cabbage Tree Island, Australia. *Palms* **53**, 46–50.
- Clancy KE, Sullivan MJ (1988) Some observations on seed germination, the seedling, and polyembryony in the needle palm *Rhapidophyllum hystrix*. *Principes* **32**, 18–25.
- Dowe JL (2010) 'Australian palms: biogeography, ecology and systematics.' (CSIRO Publishing: Melbourne)
- Eriksson O, Ehrlen J (1992) Seed and microsite limitation of recruitment in plant populations. *Oecologica* **91**, 360–364. doi:10.1007/BF00317624
- Everham EM, Myster RW, Vandergenachte E (1996) Effects of light, moisture, temperature and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany* 83, 1063–1068. doi:10.2307/2445996
- Figueroa JA (2003) Seed germination in temperate rainforest species of southern Chile: chilling and gap-dependency germination. *Plant Ecology* 166, 227–240. doi:10.1023/A:1023286521721

- Floyd AG (1989) 'Rainforest trees of mainland south-eastern Australia.' (Inkata Press: Melbourne)
- Floyd AG (1990) 'Australian Rainforests in New South Wales. Vol 2.' (Surrey Beatty: Sydney)
- Forget PM, Munoz E, Leigh EG Jr (1994) Predation by rodents and Bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* 26, 420–426. doi:10.2307/2389236
- Forget PM, Milleron T (1991) Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87, 596–599. doi:10.1007/BF00320426
- Foster SA (1986) On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* 52, 260–299. doi:10.1007/BF02860997
- Fox J, Dixon B, Monk D (1987) Germination in other plant families. In 'Germination of Australian native plant seed'. (Ed. P Langkamp) pp. 211–233. (Inkata Press: Melbourne)
- Fullagar PJ (1976) Seabird islands no. 35: Cabbage Tree Island, New South Wales. Australian Bird Bander 14, 94–97.
- Higgins PJ, Peter JM, Cowling SJ (2006) Strepera graculina Pied Currawong. In 'Handbook of Australian, New Zealand and Antarctic birds. Vol 7'. (Eds PJ Higgins, JM Peter, SJ Cowling) pp. 529–563. (Oxford University Press: Melbourne)
- Hindwood KA, Serventy DL (1943) The Gould petrel of Cabbage Tree Island. *Emu* 72, 273–329.
- Hull AFB (1911) Description of the nest and egg of white-winged petrel Estrelata leucoptera, Gould. Emu 10, 252–253. doi:10.1071/MU910252
- Jakobasch E (1981) Some notes on two native palms of south-eastern Australia. Principes 25, 130–132.
- Keith DA (2004) 'Ocean shores to desert dunes: the native vegetation of New South Wales and the ACT.' (NSW Department of Environment and Conservation: Sydney)
- Marchant S, Higgins PJ (1993) Alectura lathami Australian brush-turkey. In 'Handbook of Australian, New Zealand and Antarctic birds. Vol. 2'. (Eds S Marchant, PJ Higgins) pp. 341–353. (Oxford University Press: Melbourne)
- Merton D (1987) Eradication of rabbits from Round Island Mauritius: a conservation success story. *Dodo* 24, 19–43.
- NSW Scientific Committee (2004) Swamp sclerophyll forest on coastal floodplains endangered ecological listing. Office of Environment and Heritage. Available at http://www.environment.nsw.gov.au/determinations/SwampSchlerophyllEndSpListing.htm [Verified 20 February 2011]
- Orozco-Segovia A, Batis AI, Rojas-Aréchiga M, Mendoza A (2003) Seed biology of palms: a review. *Palms* 47, 79–94.
- Orscheg CK, Parsons RF (1996) Ecology of Livistona australis (R.Br.) Martius (Arecaceae) at its southern limit, south-eastern Australia. Part II. Phenology, germination, herbivory, regeneration and fire effects. Mooreana 6, 36–50.
- Priddel D, Carlile N (1995a) Mortality of adult Gould's petrel *Pterodroma leucoptera* at the nesting site on Cabbage Tree Island, New South Wales. *Emu* 95, 259–264. doi:10.1071/MU9950259

- Priddel D, Carlile N (1995b) An artificial nest box for burrow-nesting seabirds. *Emu* 95, 290–293. doi:10.1071/MU9950290
- Priddel D, Carlile N (1997) Conservation of the endangered Gould's petrel Pterodroma leucoptera leucoptera. Pacific Conservation Biology 3, 322–329
- Priddel D, Carlile N (2009) Key elements in achieving a successful recovery programme: a discussion illustrated by the Gould's petrel case study. *Ecological Management & Restoration* **10**, S97–S102. doi:10.1111/j.1442-8903.2009.00460.x
- Priddel D, Carlile N, Wheeler R (2000) Eradication of European rabbits (Oryctolargus cuniculus) from Cabbage Tree Island, NSW Australia, to protect the breeding habitat of Gould's petrel Pterodroma leucoptera leucoptera. Biological Conservation 94, 115–125. doi:10.1016/S0006-3207(99)00155-X
- Rodd AN (1998) Revision of *Livistona* (Arecaceae) in Australia. *Telopea* 8, 49–153.
- Silva MG, Tabarelli DM (2001) Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. *Acta Oecologica* 22, 259–268. doi:10.1016/S1146-609X(01)01117-1
- Silvertown JW (1982) 'Introduction to plant population ecology.' (Longman Press: London)
- Smythe N (1989) Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica* **21**, 50–56. doi:10.2307/2388441
- Svenning J-C (1998) The effect of land-use on the local distribution of palm species in an Andean rain forest fragment in northwestern Ecuador. *Biodiversity and Conservation* **7**, 1529–1537. doi:10.1023/A:1008831600795
- Triggs B (1996) 'Tracks, scats and other traces: a field guide to Australian mammals.' (Oxford University Press: Melbourne)
- Underwood AJ (1981) Techniques of analysis of variance in experimental marine biology and ecology. *Oceanographic Marine Biology Annual Review* 19, 513–605.
- Werren GL, Clough AR (1991) Effect of rabbit browsing on littoral rainforest, Cabbage Tree Island, New South Wales with special reference to the status of the Gould's petrel. In 'The rainforest legacy: Australian national rainforests study, vol. 2 flora and fauna of the rainforests'. (Eds G Werren, P Kershaw) pp. 257–277. (Australian Government Publishing Service: Canberra)
- Willson MF, Irvine AK, Walsh NG (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographical comparisons. *Biotropica* 21, 133–147. doi:10.2307/2388704
- Wright SJ, Duber HC (2001) Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33, 583–595.