Demography of the Cabbage Tree Palm, *Livistona australis*

By

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Certificate of Authorship/Originality

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

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Nicholas Carlile

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Abstract

This thesis, the demography of the Cabbage Tree Palm, *Livistona australis*, investigated some of the vital statistics concerning seed production and germination, seedling establishment and survival, time taken to reach reproductive maturity, longevity and population structure of the species. Seed survival, germination and seedling establishment was studied at two sites, one mainland location and one on a predator-free island. Greenhouse germination returned 91% success, but this was reduced to 19% by invertebrate attack and infection from soil pathogens *in situ*. The germination of *in situ* seed was not significantly affected by light levels, but burial of seed increased germination threefold (from 17% to 52%) compared to seed on the soil surface. Germination rates were higher with the removal of the mesocarp, but only on an island. At the mainland site mesocarp removal reduced germination success due to predation by the Bush Rat, *Rattus fuscipes*. These same predators did not reduce seedling survival by the end of a 30-month study. Evidence suggested, however, that low seedling survival at this mainland site (20-34%) was caused by insufficient light for photosynthesis after exhaustion of resources from the seed. Less dense seedlings on an island had much higher survival (62%).

Two additional study sites were included in the investigation that compared rates of trunk growth, approximate age based on these growth rates and the flowering and fruiting patterns within and between the four populations. Morphological measurements showed that the taller the palm the larger the crown. The overall size of adult palms was strongly influenced by the local environment. In general, growth was fastest and more variable prior to palms reaching reproductive age, after which the rate of growth declined and stabilised. The oldest palm was estimated to be 392 years old, and had a crown height of 14.9 metres. The mean age to first flowering from four populations was 170 years. Observations of senescence suggest that accident, by structural failure or breakage of the trunk, is the prime cause of death in natural palm populations. Between the four study sites there was differing distribution of the size classes of palm trunks. Two of the four populations indicated that any disturbance had not yet impacted on the distribution of trunk size classes at these sites. Of the other two sites one presented trunk frequencies that indicated a complex disturbance history while the other, an island study site, indicated that the impact brought about by 90 years of rabbit grazing had not yet become apparent.

This information can provide a basis from which to better manage populations of the species, particularly those at risk of decline due to isolation, harvesting of reproductive adults, frequent fires or other disturbance. Future research would be benefited from larger samples sizes than used here and by a more long-term study of seedling development. The estimation of the time taken for the development of the basal bulge remains the most difficult aspect of palm demographics.

1. Introduction to the Cabbage Tree Palm, *Livistona australis*

1.1 Introduction

Livistona australis, the Cabbage Tree Palm, is a common palm distributed over much of the eastern seaboard of Australia ranging from the Paluma Range in Northern Queensland to Cabbage Tree Creek in East Gippsland, Victoria (Brooks 1993). In the southerly limits of this distribution the species withstands cooler temperatures than almost any other Southern Hemisphere palm. Only the New Zealand Naipia Palm, *Rhopalostylis sapida,* grows at higher latitudes (Enright & Watson 1992). *L. australis* is found in near-coastal wet sclerophyll forests and in gallery rainforest and their margins (Rodd 1998) and is also conspicuous in swamp forests dominated by Paperbark, *Melaleuca quinquenervia*. It is considered indifferent to soil type with often locally dominant populations on exposed slopes above the sea growing in softer sediments (Rodd 1998).

Despite the relative frequency of *L. australis* within the forests of the eastern seaboard very little is known about this, the most common species of the genus. Australian palms, like most palms of the world, are generally understood taxonomically while little is known of their ecology (Tomlinson 1979). This thesis attempts to elucidate some of the broader aspects of the ecology of *L. australis*.

The Australian mainland has 53 species of palms comprising 19 genera. The genus *Livistona* is represented by 16 species in Australia of which 14 are endemic, including the species under study (Rodd 1998). With one exception, all other members of the genus are to be found in the Southeast Asian region and in the near Pacific. A single species recently placed in this genus (Dransfield & Uhl 1983) is located in a number of isolated patches in the Horn of Africa and Yemen. The discovery of this isolated species gives further support to the ancient origins of the genus (Rodd 1998) arising from vicariance biogeography. While no detailed records of this genus appear in the Australian fossil record (Dowe 1995) this disjunct distribution may be the result of a distribution that originated from the Gondwana landmass, which began breaking up in the mid-late Cretaceous.

Rodd (1998) places *L. australis* in an informal grouping of palms within the genus that are found in rainforest margins, wet sclerophyll and swamp forest on the east coast and along river channels flowing west from the Great Dividing Range in Queensland. This 'East Coast Group' also includes: *L. benthamii*, found in gallery rainforest from Cape York Peninsula westward across the Northern Territory and into southern Papua New Guinea; *L.drudei*, found in coastal lowlands of northern Queensland between Cooktown in the north and Proserpine in the south; *L. nitida*, a subcoastal species of south-eastern Queensland in the catchments of the Dawson and Comet Rivers; *L. decipiens*, a coastal species between Townsville and Maryborough in Queensland; and *L. fulva*, found only at Blackdown Tableland in central eastern Queensland.

1.2 Description of the species

The following information on the morphology of the genus and in particular *L. australis*, comes largely from the revision by Rodd (1998) of the Australian members of this genus.

1.2.1 Growth habit and trunk

In Australia all of the mature individuals of this genus develop distinctive solitary narrow trunks and fan-like foliage. One species, *L. inermis,* which is found in the north and north-east of the Northern Territory and north-west Queensland, can also produce suckers from the basal area.

Trunk diameters can be divided into three classes of circumference: 80 mm, 150 mm and 300 mm at 1-2 metres above ground with, *L. australis* belonging to the latter group. Observations have been made of some individuals in a stand of *L. australis* that have access to water, nutrients and light in greater amounts than other specimens in the same stand. In this situation Rodd (1998) reports that their girth in the lower part of their stems can be double that of the less well-nourished individuals.

The genus displays a trunk patterning that is related to the processes undergone of leaf aging, drooping and abscission. In *L. australis* this is overlayed by numerous vertically aligned fissures. Rodd (1998) considers that these arise from a tangential shrinkage of this dead outer zone of the trunk tissue over time.

1.2.2 Leaf morphology

For the purpose of this review a broad overview of features will be examined. The overall leaf shape is described as costapalmate, referring to the fact that not all segments radiate from the petiole apex. The leaf can be sub-divided into three parts: sheathing base, petiole and lamina or leaf blade.

The sheathing base is the point where the pseudopetiole wraps around the trunk. A model has been developed providing a range of types to describe the way in which leaves attach to trunks in palms (Tomlinson 1990). *Livistona* leaf bases do not conform to this model, by way of having a sharp rather than gradual change to where the sheath wraps around the trunk (Figure 1.1).

The transverse section of the petiole is characteristic to *Livistona*. The petiole tapers abruptly into the hastula and provides some morphological features for descriptive purposes. Petiole length is measured on only the lower leaves of the crown as those that have recently emerged continue to expand their petiole for sometime after the leaf has expanded. The length may be governed by adverse environmental conditions such as wind shear, which ultimately give rise to more compact crowns in the palm. In the case of *L. australis,* prickles along the petiole are more predominant in palms under 5 m in trunk height and can persist, to a lesser degree, in canopy palms of over 20 m.

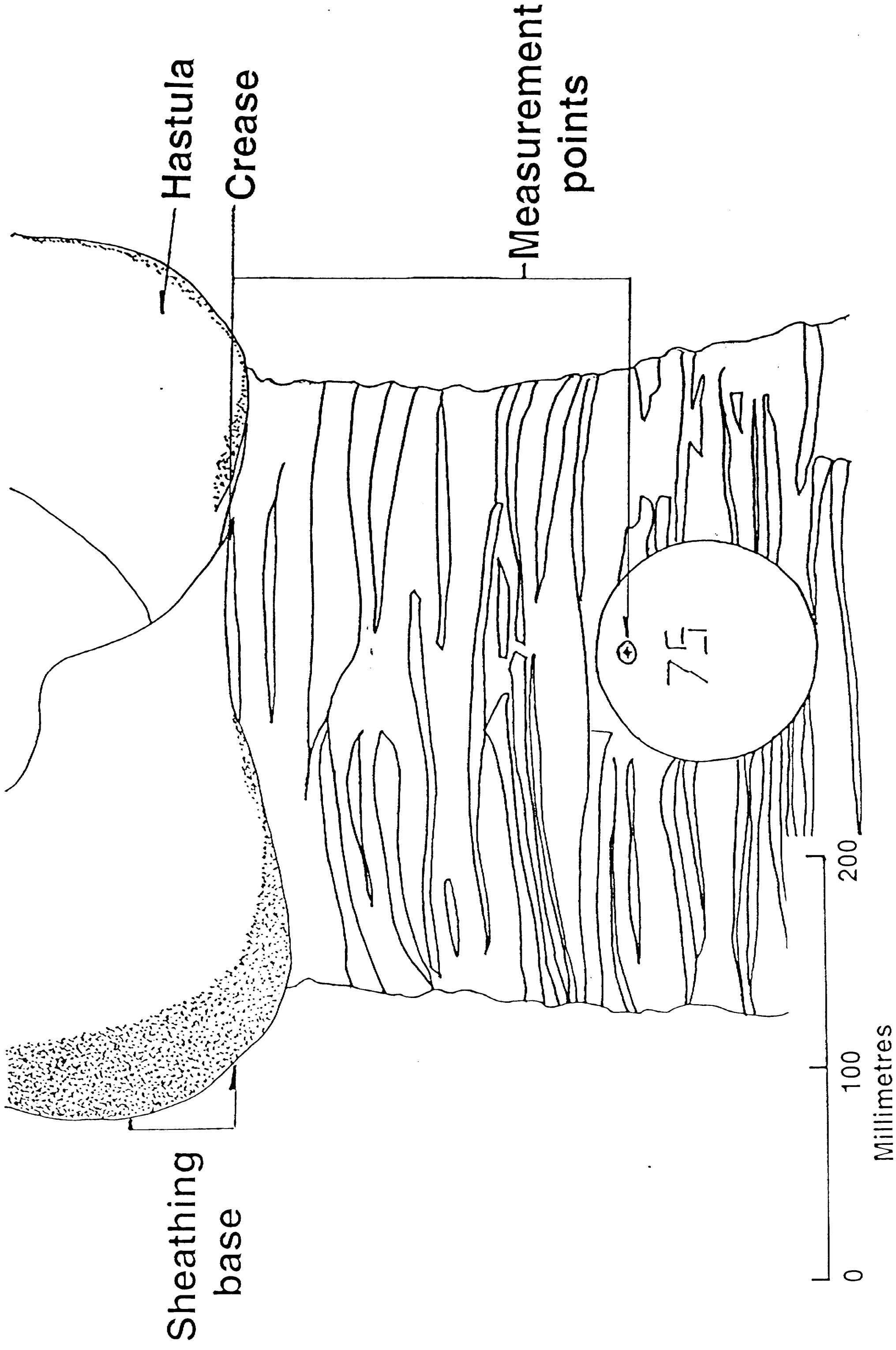

Figure 1.1: Sketch of the lower crown of *Livistona australis* showing leaf attachment to the trunk and points of measurement.

The lamina appears to have no characteristics by which it can be distinguished from that of several other genera of the Livistoninae. Within the genus the character and character states can be used for differentiation in such details as size, outline, undulation, thickness, rib-profile, colour and texture. Within the definition of costapalmate, for the leaf shape, some segments arise from a continuation of the petiole along the costa, or central rib. This varies between species and *L. australis,* along with *L. himilis* and *L. nitida,* is considered to be moderately costapalmate.

1.2.3 Inflorescence

Livistona produce several intrafoliar infloresences that arise, fruit and die all while within the crown of the palm. *L. australis* has the highest amount of branching within the infloresence for the genus, with 4 or 5 distinct junctions. The flower structure is uniform across the genus in Australia and follows the general pattern in the 12 genera of Livistoninae. The calyx is always shorter that the corolla, and the sepals are much thinner than the petals and fuse into a shallow cup at the flowers base. Flowers are either male or female with *L. australis* having the largest flowers within the genera in Australia, ranging from 2.5 mm to 3.5 mm long. The fruit shape is mostly globose but varies in size considerably between species and within individuals of a species. In *L. australis* the fruit is generally 13-22 mm in diameter, and black or brownish-black in colour when ripe. The seed itself is sub-spherical to moderately ellipsoid.

1.3 Review of research

Rodd (1998) produced the first comprehensive revision of the genus Livistona covering all the currently recognised species occurring in Australia. This revision, while providing much new information on many of the species, also highlighted the dearth of research pertaining to many of the species in this genus. This sentiment is echoed on a global scale with palms as a group being well known taxonomically, but with little knowledge on their ecology and physiology (Tomlinson 1979). The species *L. australis* has been the subject of two short papers (Orscheg & Parsons 1996a, 1996b) which have been described as the most comprehensive ecological and phenological studies carried out on any Australian palm (Rodd 1998). These studies on *L. australis* attempted to cover two broad areas of research. Firstly, they looked at whether the fragmented populations of *L. australis* in its southern distribution had sufficient allozyme variation when compared to more northerly stands in an effort to gain an indication of their relationship (Orscheg & Parsons 1996a). The results of this were inconclusive. The second study (Orscheg & Parsons 1996b) covered broader ecological issues such as field germination, the effects of disturbance on seedling survival and the rate of palm growth. They then attempted to age the larger members of known populations. These studies were extremely limited in their scope, with varying results that will be discussed in more detail later as part of this thesis.

Most of the published accounts of the genus *Livistona* take the form of observations and notes (e.g. Lothian 1959; Moore 1973; Latz 1975; Tucker 1980; Jakobasch 1981). Research within the genus of *Livistona* is confined to Australia (Hnatiuk 1977; Birch & Dowe 1989; Wuschke 1999), where the majority of the species occur, with studies by O'Brien & Kinnaird (1990) and Weiner & Corlett (1987) in Asia being the exceptions.

1.4 Research justification

Palms generally make ideal subjects for demographic studies as their single stems are easily recognisable, age determination is more simple when compared to other trees and reproductive status and output easily discernible (Tomlinson 1979). In this study, the demography of *L. australis,* some of the vital statistics concerning seed production and germination, seedling establishment and survival, time taken to reach reproductive maturity and longevity of the species were elucidated. This information provides a basis from which to better manage populations of the species. This is particularly important for isolated stands that have little input by way of seedling recruitment from other populations.

The subject of this research is particularly relevant to an isolated population of palms that find themselves inextricably linked to the survival of an endangered seabird off the coast of NSW, Australia. Cabbage Tree Island (CTI) is offshore from Port Stephens on the mid-north coast of NSW. *L. australis* is one of the dominant species on this unique offshore island rainforest. CTI is the principal breeding site in the world for Gould's Petrel, *Pterodroma leucoptera*, Australia's rarest endemic seabird. On CTI the palm has a close association with the breeding of the petrel as the species nests almost exclusively in cavities within the rock scree on the western side of the island where the palms dominate two steep rocky gullies. The shed leaves of the palms provide important covering to the petrel's shallow surface and sub-surface nest sites. The covering of dead leaves provides protection to the petrels, their eggs and developing young from adverse weather conditions, avian predators and the unwanted attentions of conspecifics nesting nearby. Some breeding pairs often choose nest sites within the mass of fallen palm leaves regardless of the substrate, such is the suitability of these leaf piles for nesting. Additionally the straight, rough trunks of adult palms provide an excellent structure for the petrels to climb to effect an easy departure through the thick forest canopy. In some cases the fallen and decaying trunks of the palms develop hollows that are also utilised by the petrels as nesting sites for several seasons until they decay and collapse.

The rare Gould's Petrel has been the subject of intensive management for almost a decade to attempt to reduce its likelihood of extinction. Management action to ameliorate threatening processes that had reduced adult survivorship and successful breeding were implemented from 1992 onwards. These have led to an increase in breeding pairs of petrels from 250 to 850 over this time. Breeding success has risen from 20% to stabilise at approximately 60%.

One underlying threatening process that not only affected the petrels but the entire island ecosystem was the presence of the introduced European Rabbit, *Oryctolagus cuniculus*. From 1906 the flora on CTI was subjected to the damaging activities of rabbit browsing. No inventory was documented of the island flora prior to the release of rabbits so the full impact of their activities has been difficult to gauge. However, when compared with similar vegetation communities on the adjacent mainland, CTI species had a greater tendency to coppice (Werren & Clough 1991) suggesting extreme levels of browsing over an extended period. The presence of complex ground covers and dense, low to medium shrub layers at mainland sites was also in distinct contrast to the structure of the rainforest vegetation on CTI. Rabbits are not generally associated with rainforest environments (Williams *et al.* 1995) and survived on the island only in low numbers. As part of the management of Gould's Petrel the rabbits were eradicated from CTI by September 1997 using a range of mortality agents applied sequentially (Priddel *et al.* 2000).

Anecdotal evidence suggested that in the time rabbits were present on CTI very few palm seedlings survived to become established (Priddel *et al.* 2000). Most multi-leaved juvenile palms were only to be found growing in areas inaccessible to rabbits such as in the hollow depressions of tree trunks, isolated steep rock stacks or other elevated locations. Palms in most of these locations fail to properly establish due to insufficient moisture or physical instability of the site. No species of *Livistona* in Australia is epiphytic. Trial studies of seedling survival demonstrated that 100% of palms that germinated at ground level were eventually destroyed by rabbit browsing (Priddel *et al.* 2000).

The close link between Gould's Petrel and *L. australis* on CTI dictates that for the petrels' ongoing survival it is important that the palm population at this site be appropriately conserved and managed.

A further consideration for research into this palm species relates to the aesthetic nature of the plant. *L. australis,* like most other palm species, is easily transplanted as an adult specimen, and is in demand for use in streetscapes and landscaping in major urban and tourist developments. In almost all such circumstances plants are sourced from wild populations. This is apparent from the evidence of fire scars on commercial plantings (personal observations). Elsewhere, this has been found to have serious consequences for many palm species, both common and rare (Lippincott 1995; McPherson & Williams 1998). The dearth of information available on the longevity of palms and their ability to regenerate indicates that caution should be exercised if these removal activities are to continue or become even more widespread. As this study will indicate, because of their great age, removal of mature *L. australis* would not reflect a sustainable harvesting regime but would be more akin to mining. It is important for the conservation of populations of this species, particularly in areas of discontinuous distribution (Orscheg & Parsons 1996a), that sound management practices are observed if this trend of the removal of mature palms is to continue into the future.

1.5 Thesis aims

This thesis addresses several areas of Cabbage Tree Palm demography, broken up into one chapter outlining the study sites followed by five chapters of specific research;

Chapter 3: Factors affecting seed germination in the Cabbage Tree Palm

The aim of these experiments was to gather basic information regarding germination. In a viability trial and greenhouse experiments the study aimed to determine what level of germination can be expected from seed under ideal conditions. In the short period of this study the germination rate between different years of planting was also be investigated. The study also aimed to look at the timing of germination to see whether it is seasonally affected or based on time lapsed following planting.

Using a comprehensive set of field experiments the study's aim was to test the influence of five factors on seed germination: site, with CTI characterised by the absence of surrounding undergrowth; light level; burial in soil; presence of the mesocarp; and predation exclusion by caging.

Chapter 4: Seedling survival in the Cabbage Tree Palm

The aim of this study was to follow the fate of seedlings at both a mammal-free site, Cabbage Tree Island, and on a mainland site, Mungo Brush, to determine their survivorship and some of the reasons for losses within the study populations. The study also aimed to monitor leaf production to test whether the number of leaves may provide an indication of the age of establishing seedlings.

Chapter 5: Estimate of the age of Cabbage Tree Palm based on growth rates

The aim of this study was to develop methods to estimate the age of *L. australis* palms based on direct measurement of growth rates at different stages of a palms development. The stages targeted were seedling to trunk development, trunked juveniles for two height classes, and reproductive adults from four height classes with observations at four sites over three growing seasons. In the course of this study basic morphological information was gained on the structure of adult palms. As part of morphological examination it was also an aim to determine what change if any, occurs in trunk girth during adult life of *L. australis*. The causes of senescence within the palm populations under study were examined. The conservation implications of the results of this study were also assessed.

Chapter 6: Age structure of Cabbage Tree Palm populations

This study looked at the structure of four populations of *L. australis* based on plant size. It considered the impact of a range of disturbance factors on the structure of these populations and draws conclusions regarding their long-term viability under current management regimes.

Chapter 7: Flowering and fruiting ecology of the Cabbage Tree Palm

This study aimed to better understand the reproductive functioning of *L. australis* by conducting the most detailed and long-term research yet carried out on this species. The study examined several aspects of phenology including: frequency of flowering; the number and sex of inflorescences; height of palms at first flowering; and the relationship between plant height, reproduction and leaf production. Four disjunct populations of varying latitude were studied.

Other aspects of reproduction examined included: the sequence of flowering and fruiting; the period between successive flowerings; and the quantity of fruit produced. An innovative approach, involving tracking inflorescence scars that appear as a series of bulges along the trunk of the palm, was used to determine flowering frequency. The distance between each bulge provides a measure of the period between successive flowering events. These data can then be used to determine the approximate date of each flowering, thus providing an opportunity to look back at the patterns of flowering that have occurred over much of the last century.

2. Study sites

2.1 Study sites

Four populations of *L. australis* within coastal New South Wales (NSW) were studied. They were, north to south: Mungo Brush (MB), in Myall Lakes National Park on the mid-north coast; Cabbage Tree Island (CTI), offshore from Myall Lakes National Park; Wyrrabolong National Park (WNP), north of Gosford; and the Royal National Park (RNP), south of Sydney (Figure 2.1). These were located over a distance of 215 km of the NSW coast ranging in latitude from 32°30' in the north to 34°10' in the south. This places them in the most southerly 25% of the species' distribution (Brooks 1993). CTI was chosen because of the ecological questions pertaining to the long-term damage arising from rabbit browsing of the palm population (see Chapter 1). MB provides a replication of most site attributes for CTI but has not suffered the long-term rabbit damage. The other two sites were selected to gain some information on any cline that may exist within the species along part of its north-south distribution. Additionally both WNP and RNP are also considered representative of the more common habitats where palms are found, coastal sands and moist gallery forest.

2.1.1 Cabbage Tree Island (CTI)

CTI, also known as John Gould Island Nature Reserve, provides a mammal free environment with a significant component of the rainforest vegetation being dominated by *L. australis*. The island is approximately 1 km long by 450 m wide and rises to a maximum height of 123 m (Fullagar 1976). The island's 30 ha comprises 18 ha of vegetation, of which 12 ha is rainforest and 6 ha open sedge and coastal heath. The remaining 12 ha is bare rock. The western side slopes at 30 degrees and is dominated by two gullies formed along eroded basalt dykes (Priddel *et al* 1995).

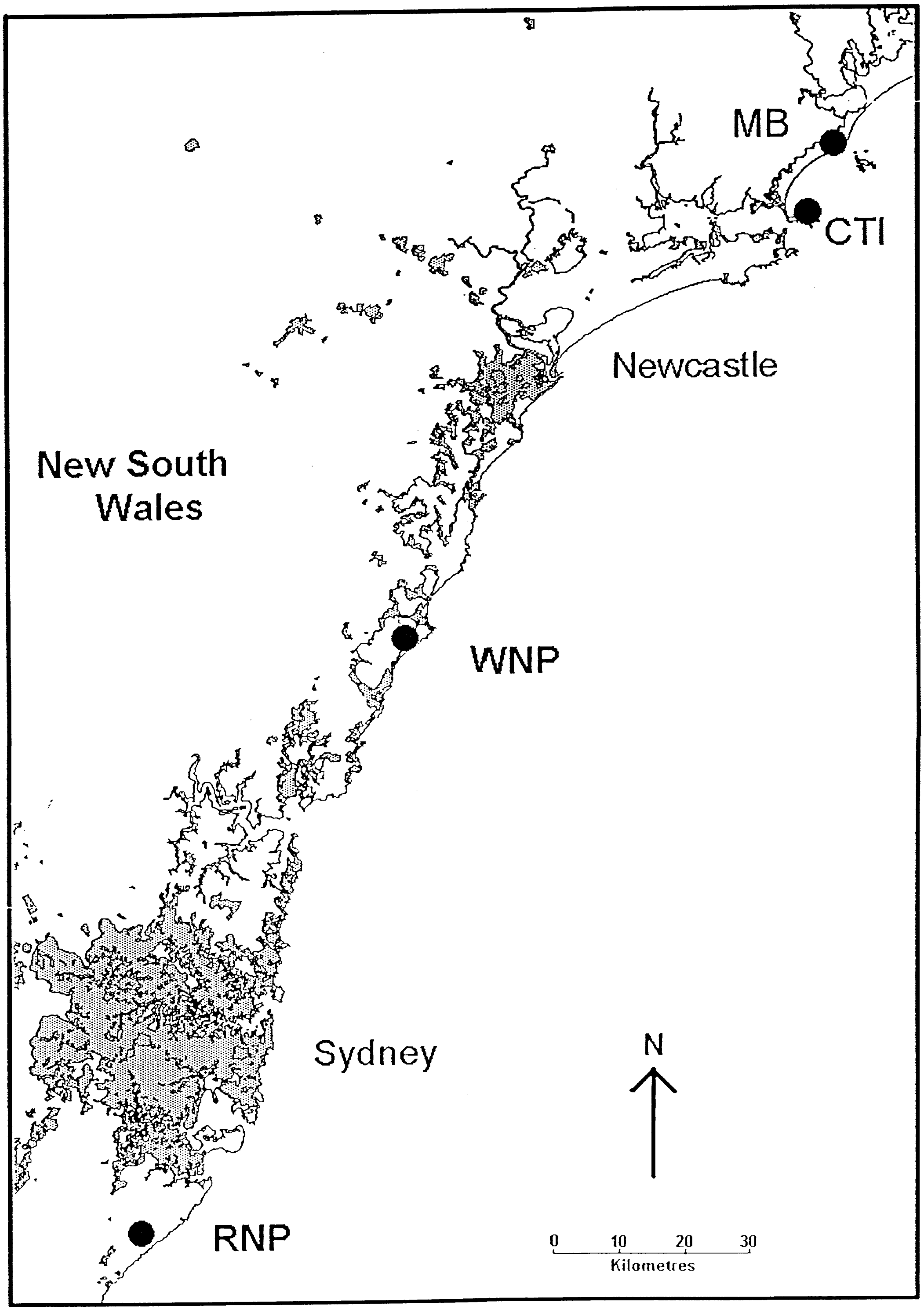

Figure 2.1: Map of localities mentioned in the text. Inset shows study sites where *Livistona australis* was regularly sampled: Mungo Brush (MB), Cabbage Tree Island (CTI), Wyrrabolong National Park (WNP) and Royal National Park (RNP).

The island is composed of the granitic rock tosconite, which occurs as rock outcrops over much of the island and rock scree slopes within the gullies. The CTI rainforest is a form of Dry rainforest Suballiance 23 (*Ficus-Streblus-Dendrocnide-Cassine*). Despite the rock scree, the gullies support mature rainforest that increases in height on deeper soil on the lower reaches of the island's western side. The study site on CTI was within the gullies in areas dominated by palms. No complete yearly records of rainfall exist from CTI, however there are island rainfall records from continuously monitored shorter periods. When these were compared to the same periods from those on the nearby mainland at Hawkes Nest, 2 km west of CTI, it appears that the island receives approximately 65% of any rainfall events experienced by the mainland (Priddel & Carlile, unpublished data). From this it can be estimated that the annual rainfall for CTI, based on regular data collected over an 11-year period at Hawkes Nest, is approximately 900 mm.

CTI has never been affected directly by European activities but has had the pressure of rabbit browsing between 1906 and 1997 (Priddel *et al.* 2000). The island contains evidence of past fire, but none have been recorded within the last century (Bassett-Hull 1911; Chisholm & Cayley 1929; Hindwood & Serventy 1943; D'Ombrain 1964; Fullagar 1976). At both CTI and MB, some of the taller palms show evidence of fire scars, whereas these are missing from smaller palms.

2.1.2 Mungo Brush (MB)

MB, within the greater 31,581 ha of Myall Lakes National Park, is located 18 km NNE of CTI. The 2 ha area of MB is a 25 m hill rising out of coastal heath on the eastern shore of Myall Lakes, 500 m from the coast. Floristically it contains a similar rainforest environment to CTI (Floyd 1990) being a combination of Dry and Subtropical rainforest with patches dominated by *L. australis*. Floyd (1990) classified the rainforest at MB as an intermediate type between the Dry rainforest Suballiance 23 and Subtropical rainforest Suballiance 19 (*Drypetes-Sarcomelicope-Cassine-Podocarpus*).

The study site was on the western side of MB with an 8 degree slope that, while not as steep as CTI, still maintained similar soils with the parent material being tosconite. The soil here is deeper than at CTI with only occasional floating rocks and boulders. The nearest rainfall records are for Hawkes Nest, 15 km to the south, and average approximately 1400 mm per annum.

Parts of MB have been the subject of clearing in the early to mid twentieth century (P. Short personal communication) but the history of fire incursion is more difficult to determine. It appears that the current period without fire may be of a similar duration to that of CTI and may exceed 100 years. There is no record of fire penetrating the rainforest at MB.

2.1.3 Wyrrabolong National Park (WNP)

WNP is a thin strip of reserve 620 ha in size divided by The Entrance township on the NSW Central Coast. Totalling 480 ha, the narrow northern section lies between Tuggerah Lakes and the coastal beach strip, south of the village of Norah Head. The topography is undulating vegetated dunes with swales dominated by littoral rainforest understorey overtopped by tall Bangalays, *Eucalyptus botryoides* (Lyons 1984). While not surveyed as part of Floyd's (1990) rainforest inventory for NSW, being only incorporated into the National Parks system in 1991, it is comparable to sites within the region that were classified as forms of Littoral rainforest Suballiance 20 (*Acmena smithii-Ficus-Livistona-Podocarpus*). The site meets the criteria for this Suballiance by its proximity to others from this grouping and being within range of salt-laden winds and on sandy soils derived from sand or sandstone (Floyd 1990). The dune swales nearest the lake edge, at Eel Haul Bay, have an understorey dominated by *L. australis*. It is within one of these swales that a study site was chosen, adjacent to the Lilly Pilly Walking Track on the edge of Tuggerah Lakes. The nearest rainfall records are from Munmorah State Recreation Area, 10 km to the north, and average 1155 mm per annum.

Up until 1981 this site had a recent history of frequent low intensity fires (Lyons 1984) but specific dates are unavailable. Since 1990, when the area was gazetted as a National Park, there has been only a single fire of low intensity in 1991 (Andrew Jones, personal communication.).

2.1.4 Royal National Park (RNP)

The RNP covers an area of 15,069 ha and contains a wide range of vegetation types (Keith & Tozer, unpublished data). The park is dissected by the Hacking River draining south to north. The middle reaches of the river are dominated by warm temperate and subtropical rainforest. This vegetation association is the result of the steep valley, rich alluvial soils and protected aspect. The parent material for the soil is Hawkesbury Sandstone. The study site was 2 km west of the junction of Stevens Drive and McKell Avenue on the south-western bank of the Hacking River. The vegetation here is wet sclerophyll with an open canopy of Blackbutt, *Eucalyptus pilularis*, and Turpentine, *Syncarpia glomulifera*, with rainforest understorey dominated by *L. australis*. The forest merges into rainforest along the river margin and is described as a Warm-temperate rainforest Alliance 9 (*Ceratopetalum apetalum*) Suballiance 34 (*Ceratopetalum-Diploglottis-Acmena*) (Floyd1990). The annual rainfall for the area is approximately 1200 mm and distributed evenly throughout the year (Thorvaldson 1978). Fire has encroached onto the site twice since records began in 1965, once in 1988 and again in 1994 (Ferguson 1997).

2.2 Additional localities

The most southerly populations of *L. australis* were also investigated. A large disjunction occurs in the distribution of the species in the most southern part of its range (Figure 6.1). The most southerly population is located at Cabbage Tree Creek near Orbost in East Gippsland, Victoria (37°47’, 148°28’) (Brooks 1993). This stand is in riparian forest dominated by *Eucalyptus botryoides* (Orscheg & Parsons 1996a). The species next appears north of Bega in southern NSW with small stands near Tilba, both in farmland (36°24’ 150°02’) and within Gulaga National Park (36°24’ 150°00’). These three sites along with three locations further north, two on the Illawarra Escarpment at Fox Ground (34°43' 150°45') and Stanwell Park (34°14' 150°59'), and one north of the study sites within Booti Booti National Park (32°18' 152°31'), were briefly surveyed for reproductive success during 2000 when fruit production had failed within the main study sites.

3. Factors affecting seed germination in the Cabbage Tree Palm, *Livistona australis*

Abstract

This study investigated two aspects of seed germination of the Cabbage Tree Palm, *Livistona australis,* the viability and timing of germination and the germination response of factors known to provide a varied success on germination. The study was carried out within a greenhouse and at two field sites, one on the mainland at Mungo Brush NSW with intact undergrowth and the other on the island of Cabbage Tree where undergrowth has been disturbed. In greenhouse trials 91% of seed of the germinated and 90% of all germination occurred within four months. *In situ* germination was reduced to 19% and this took up to 11 months. Temperature appears to be the principal factor controlling the timing of seed germination. The germination of *in situ* seed was not significantly affected by light levels, but burial of seed increased germination threefold (from 17% to 52%) compared to seed on the soil surface. Anecdotal evidence suggests that seed naturally moves into the soil as a result of the action of water run-off. The absence of a mesocarp increased germination rates only when tested on an island free of seed predators. There was some evidence to suggest that in the presence of predators, seed that remained on the surface with its mesocarp intact was more likely to germinate than seed that had the mesocarp removed. Under greenhouse conditions neither light levels nor the presence or absence of the mesocarp significantly affected germination (mean 74%). Seed loss from damage by pathogens and invertebrates affected 43% of caged seed in the field at Mungo Brush. The highest losses of seed were from replicates below canopy gaps, suggesting that temperature may influence seed loss. Topknot Pigeon, *Lopholaimus antarcticus,* and Pied Currawongs, *Strepera graculina,* were observed to feed

on fruit hanging in the canopy, but no avian predators were observed to take fallen seed. Mammalian predation of seed was minor. The Bush Rat, *Rattus fuscipes,* was the sole predator of fallen seed. There was no evidence of Brush-tailed Possums, *Trichosurus vulpecula,* taking *L. australis* seed from the forest floor. From these results it is not clear whether the disturbed forest environment of the island, where the undergrowth is not intact, hampered germination of palm seed. If accelerated germination was desired on Cabbage Tree Island, *in situ* results from this study indicate that buried seed with the mesocarp removed would have the greatest potential for success. In the absence of vertebrate predators on the island seed survival would be maximised.

3.1 Introduction

Elucidating the factors that influence seed germination in palms can assist in understanding why seedlings emerge in some situations and not in others. The timing of seedling emergence and the germination success rate, together with possible ways in which these parameters can be enhanced, can be determined from germination studies. For a palm population where regeneration has been suppressed for long periods and whose continued survival is in jeopardy (see Chapter 1), understanding seed germination is particularly relevant.

The factors affecting seed germination in the Cabbage Tree Palm, *Livistona australis*, are not well understood. Studies carried out on a number of palm species from several genera (e.g. Brown 1976, Clancy & Sullivan 1988, Forget *et al.* 1994) indicate that factors affecting germination are complex and varied. Factors known to affect germination include available moisture, temperature, light, salinity, predation and seed age. *L. australis* is the only palm species in

Australia for which seed germination has been investigated, albeit only cursorily. In a laboratory trial conducted by Orscheg & Parsons (1996b), germination was influenced by temperature, seed age and the presence of the mesocarp (the fleshy fruit layer). In a five-month field trial conducted by the same workers during autumn and winter, no seeds germinated and predation was found to be high.

It is a commonly held belief that palm seed can lay dormant in the ground for many years, sprouting after fire or similar disturbance (Anonymous 1999). It also has been suggested that germination of *L. australis* seed requires the removal of the fleshy fruit layer and a time lapse of 1- 3 months after fruit-fall (Floyd 1989). Flesh left on the seed often encourages fungal or insect attack (Fox *et al.* 1987) reducing viability, but the extent of this is not known. The removal of the fruit layer in *L. australis* can occur naturally through the foraging activities of Topknot Pigeons, *Lopholaimus antarcticus* (Gould 1865) and Pied Currawongs (personal observations).

The process of seedling emergence following germination is well understood. When palm seeds germinate the cotyledonary stalk, containing the ligule and seedling, first grows downward from the seed then splits. The plumule then grows upwards producing the seedling, and the root mass develops with the apical bud buried deep within the soil (see Brown 1976, Figure 6). This is called cryptogenial germination and is considered a critical adaptation for surviving fire or grazing (Tomlinson 1990).

This study investigated two aspects of *L. australis* seed germination. First, an examination was made of the viability of fresh seed and the seasonal timing of germination. Knowing the potential viability of seed allows a better understanding of germination response when tested under different environmental conditions. Second, the influence on germination was investigated for five factors: site, light level, burial in soil, presence of the mesocarp, and predation. The testing of site as an influence on germination provided a comparison of germination success between palm forests with contrasting understorey, one with healthy undergrowth (Mungo Brush) and another heavily disturbed (Cabbage Tree Island). To assess whether light levels affected seed germination two extremes of light were investigated: below a gap in the canopy, and a shaded position below a closed canopy. To assess the effect of soil covering, the seed was either buried or sown on the soil surface. Another factor to be tested was removal of the mesocarp . Removing the mesocarp mimicked the process that happens when seed is consumed by frugivores such as the Topknot Pigeon. The extent to which germination was reduced by predation was examined by comparing germination rates from two different environments, one with ground dwelling mammals present and the other without.

If germination is enhanced by removal of the mesocarp then this would provide a key technique for use in any regeneration program to rehabilitate degraded palm populations. Additionally, the placement of seed in appropriate locations within a palm forest may be used to obtain a favourable germination response.

3.2 Methods

3.2.1 Viability trial

A viability trial (hereafter referred to as VT) was conducted to determine the potential maximum germination rate of seed in an environment where the seed had ample moisture and favourable levels of humidity and temperature.

Freshly fallen seed was sourced from Mungo Brush (see Section 3.2.3) in May 1998. The mesocarp was removed from 280 seeds by scraping with a sharp knife. Care was taken not to damage the seed coat. In each of 14 replicate 15 cm diameter plastic pots, 20 seeds were planted at a depth of one centimetre in 12 cm of commercial grade potting soil.

The pots were then placed in a glass-panelled greenhouse. The greenhouse used an automatic watering system twice daily for 10 minutes each period, spraying mist from elevated lines. The number of germinated seeds in each replicate was recorded at each visit. Germination was recorded when the plumule emerged above the soil surface. Each seedling was then removed to avoid established seedlings suppressing later germinations. Once the first germination was detected, pots were checked weekly until no new germination had occurred during a four–week period.

At the completion of the trial, any remaining seed was assessed for viability by cutting it open and examining the endosperm. If the endosperm was without discolouration (normally cream or white in fresh seeds; Rodd 1998), free of fungal infection and otherwise intact, the seed was considered still viable.

3.2.2 Greenhouse experiment

A greenhouse experiment (GE) was conducted to test for the effect of the factors of light and mesocarp removal on germination rates under ideal conditions. Two light levels (shaded and sunlit) were examined in a glass-panelled greenhouse. Suspending a double thickness of shade cloth over half the pots simulated shade conditions and this still allowed water to penetrate. Exposed pots without the shade cloth cover were considered to be in sunlit conditions. The second factor in this experiment involved removal of the mesocarp. The mesocarp was removed as in VT, by scraping the seed coat with a sharp knife. Technically, seed with the mesocarp intact are "fruit", but for simplicity are hereafter referred to as "seed with mesocarp intact".

Freshly fallen seeds were sourced from Mungo Brush in August 1999, and following establishment of trials in the greenhouse were monitored monthly for two years. Each of the four combinations of the two factors was replicated four times. Each replicate in a 15-cm diameter pot was filled with commercial grade potting mix and 25 seeds, either with the mesocarp intact or removed, and was then covered by one centimetre of soil. The pots were watered twice daily by an automated system as described in Section 3.2.1. The number of new germinated seeds in each replicate was recorded at each visit. Germination was assessed as occurring when the plumule emerged above the soil surface. Each emergent seedling tip was cut and treated with undiluted glyphosate (360 g / l) in order to kill the seedling. This action, rather than the physical removal of the entire seedling, was used to ensure the other seeds within each pot remained undisturbed for the duration of the experiment. Care was taken to ensure that the glyphosate was applied only to seedling tips and that none came in contact with the soil.

At the completion of GE the seeds remaining within each pot were examined for viability. The remains of those seeds that had germinated were counted. A comparison was then made between the known number of seeds that germinated and reached the soil surface and the quantity of seed remains showing evidence of germination having occurred. The difference between these parameters provided an estimate of the number of seeds that germinated but which failed to produce a plumule above the soil surface.

3.2.3 *Field experiments*

An orthogonally designed field experiment (FE) was conducted in which three further factors (site, burial and caging) were added to those already examined in GE (light and mesocarp removal). The factors of light, mesocarp removal, burial and caging were each replicated at two sites, Cabbage Tree Island (CTI) and Mungo Brush (MB). The two study sites, details of which are included in Chapter 2, differ in regard to the presence or absence of undergrowth as a result of the disturbance history of the two sites.

Two light levels (shade and sunlit) were examined. Shaded areas were below a closed canopy and received no direct sunlight at any time of the day, whereas sunlit areas were below natural gaps in the forest canopy and received sunlight for at least part of the day. As before two levels of mesocarp cover were examined. Seeds had either their mesocarp intact or removed with a knife. Two levels of burial were examined. Seeds were either buried within one centimetre of soil or left exposed on the soil surface. Burial was achieved by removing 1 cm of the soil within the area bounded by the wire fencing or caging (see below), laying the seeds evenly within this area and re-covering with the overburden. Two levels of caging were examined. The presence or absence of cages was used to exclude or expose seed to the possibility of predation by vertebrates. The cages were fabricated from 10-mm-square mesh, shaped into a 150 mm x 150 mm upper surface with 30 mm high sides. These were secured to the ground by two 150 mm steel pegs passing through the sidewalls of the cage. The area of uncaged seeds was delineated by 5-mm-square mesh with a wall 30 mm high and held in place by a single 150 mm steel peg. It was assumed that in both caged and uncaged replicates the mesh had no measurable effect on germination other than the exclusion of vertebrate predators from the caged plots.

The 32 treatment combinations (orthogonal combinations of five factors, each with two levels) were replicated four times (a total of 128 replicates). Each replicate contained 70 seeds at a density of about 3000 seeds per square metre, similar to that occurring naturally around the base of fruiting palms (personal observation). A total of 8960 seeds were thus used, 4480 at each study site. Numbered replicates were positioned randomly, but were at least five metres away from reproductive palms in order to reduce the possibility of additional seed being inadvertently incorporated into the experiment.

Seed for this experiment was sourced locally. At both CTI and MB the fruit-bearing inflorescences were removed from three palms at a time when ripe fruit had begun to fall to the ground. Palms were climbed using an abseiling technique known as prussiking (see Chapter 5). Depending on the size of the individual crop, 2-3 inflorescences were cut from each palm crown using extendable parrot-beaked lopping shears. The fruit was stripped either by the impact of the inflorescence falling onto a tarpaulin spread on the ground below the palm or by shaking the inflorescence afterwards. Fruit still attached to the stem after this process was discarded. Fruit was then sorted, with only the larger, undamaged seeds selected for the experiment.

FE began in May 1998 and was monitored initially twice monthly for two months and then monthly until April 2000. Germination was taken to have occurred when the plumule tip appeared above the soil surface. The number of new germinated seeds in each replicate was recorded at each visit. Each seedling tip was then cut and treated with glyphosate as in Section 3.2.2. At the completion of the study the soil in each plot was examined for remaining seeds and seed remains. Intact seeds were later examined for viability as described in Section 3.2.1.

For each replicate, germination success (G) was expressed as: $G = N_G / (N_G + N_i)$ where N_G = the number of seeds that germinated and N_i = the number of intact seeds remaining at the conclusion of the experiment. This calculation of germination success allowed for comparison to be made between the two sites (MB and CTI) as the latter suffered substantial loss of seeds from numerous replicates due to them being washed out during a period of exceptionally high rainfall. This method of calculation and subsequent analysis did not measure the effect of predation on germination. Seed that had neither germinated nor was present as intact seed at the end of the experiment was effectively lost from the analysis. This "lost" seed included seed that had been washed out and seed that had been taken by predators. This has been termed germination excluding predation (G_{EP}). A second analysis of the germination data was applied to the MB site only where germination success (G) was expressed as: $G = N_G / N_T$ where N_G = the number of seeds that germinated and N_T = total number of seeds in the sample i.e. 70 per replicate. This has been termed germination including predation (G_{IP}).

3.2.4 *Seed loss*

Uncaged replicates were initially monitored fortnightly for two months, and thereafter monthly. At each inspection, seed was counted in each replicate. Additionally, any seed remains found within or nearby any uncaged replicate were collected and later examined for incisor markings. Where incisor markings were present, these were measured to the nearest 0.05 mm using calipers. Any signs of interference with the replicates, including digging or other signs of foraging, were noted. Throughout the experiment, casual observations were made to identify potential avian and mammalian predators of palm seed after it had fallen to the ground. Nocturnal surveys were carried out at MB within areas dominated by *L. australis* to assess the mammal fauna.

3.2.5 Analysis

The data was tested for heterogeneity of variances using Cochran's C-test to determine whether transformation was necessary (Underwood 1981), and where necessary these are indicated. A comparison of seed viability was analysed using one-factor analysis of variance (ANOVA). Germination response in the greenhouse experiments was analysed using two-factor orthogonal ANOVA. In the field experiments, germination response (G_{EP}) was analysed using multi-factor orthogonal ANOVAs. G_{IP} was analysed using two-factor orthogonal ANOVA. All ANOVA were computed using Systat 10 for Windows at 95% confidence. Student-Newman-Keuls tests (SNK) were applied in all multiple comparison tests at 95% confidence. All statistical tests performed were two-sided unless stated otherwise. Where means are presented, standard errors are included.

3.3 Results

3.3.1 Viability trial (VT)

The VT was conducted using seed without mesocarp, buried in soil and sunlit. After a period of 17 months, 255 of the 280 seeds (91%) had germinated. Of the remaining 9%, eight seeds (3%) were still viable. Timing of germination is described in Section 3.3.6.

3.3.2 Greenhouse experiment (GE)

Analysis of germination from GE looked at the effect of the factors light and mesocarp. A third factor (burial) was included in the original experimental design but later had to be discarded as Black Rats, *Rattus rattus*, removed or destroyed most seeds that were not buried (see Section 3.3.4). Data from all non-buried seeds were omitted from the analysis.

The results of analysis of the germination response from seed in GE are presented in Table 3.1. The mean proportion of germination was 0.74 (s.e. = 0.06). There was no significant interaction between the factors of light and mesocarp removal on germination rates (replicated two factor ANOVA $F_{1,7}=$ 1.75, $P = 0.21$). There was no significant difference in germination in relation to the presence or absence of the mesocarp ($F_{1,7}= 0.98$, $P = 0.34$) or light levels ($F_{1,7}= 0.11$, $P = 0.75$). Germination was as successful with mesocarp ($\bar{x}$ = 0.68, s.e. = 0.08) or without mesocarp ($\bar{x}$ = 0.80, s.e. = 0.09) and in sunlit ($\bar{x}$ = 0.76, s.e. = 0.08) or shaded ($\bar{x}$ = 0.72, s.e. = 0.10) situations.

3.3.3 Field experiments (FE)

Analysis of germination from FE was restricted to 8 treatment combinations at each site with caging removed as a factor at both sites. Seed losses at CTI substantially reduced the number of available seeds in many of the uncaged and some of the caged replicates when they were washed out during heavy rain. These substantial losses at CTI removed the ability to test the effect of caging between sites. If the sample size was reduced to less than 30 then the replicate was rejected in the analysis (ie, where $N_G + N_i < 30$); however, the removal of caging as a factor potentially doubled the original seed replicates available. Data from MB, including data from caging trials, were analysed separately to determine any possible affect on germination of the various factors including predation (G_{IP}) (see below).

Table 3.1: Two-factor (mesocarp, light) ANOVA of *Livistona australis* seed germination from greenhouse experiments. Significant results ($P < 0.05$) are underscored.

Factors	SS	df	MS	*F*	*P*
Mesocarp	0.06	1	0.06	0.98	0.34
Light	0.01	1	0.01	0.11	0.75
Mesocarp x Light	0.10	1	0.10	1.75	0.21
Error	0.70	12	0.06		

A four-factor ANOVA (site, mesocarp, burial and light) was applied to determine the relationships between germination and each experimental factor in the absence of predation (G_{EP}) (Table 3.2). The analysis showed that the only significant interaction between factors was the combination of site (CTI or MB) and mesocarp (intact or removed) ($P < 0.01$). At the 95% probability there was no significant interaction between mesocarp and burial ($P = 0.06$). Germination was significantly affected if the seed was buried or left exposed on the soil surface irrespective of the other factors ($P < 0.01$). Applying an SNK test, the proportion of germination between the two sites was similar when the mesocarp was intact (CTI $\bar{x}$ = 0.36 and s.e. = 0.09, MB $\bar{x}$ = 0.38 and s.e. = 0.06). The germination rate at CTI increased when the mesocarp was removed ($\bar{x}$ = 0.51 and s.e. = 0.07), but decreased at MB when the mesocarp was removed ($\bar{x}$ = 0.22 and s.e. = 0.05). The high germination rate of seed with the mesocarp removed at CTI indicated that here, the removal of the fruit flesh assisted germination. In contrast, the removal of the mesocarp at MB caused a reduction in germination. The poor germination of seed with the mesocarp removed at MB can be explained by the removal of seed from replicates exposed to rats (see Section 3.3.4), the removal of the mesocarp presumably making the seed more attractive to these predators.

At the 5% level of probability there was no demonstrable interaction between mesocarp and burial, but at $P = 0.06$ suggest it may have been a Type 1 error. The exclusion of burial as a factor due to rat predation within the GE precludes the comparison of the G_{EP} result with highest potential germination of the greenhouses seed trialed using the same combination of factors.

Table 3.2: Four-factor (site, mesocarp, light and burial) ANOVA of *Livistona australis* seed germination. Significant results (*P* < 0.05) are underscored.

Factors	SS	df	MS	*F*	*P*
Site	0.01	1	0.01	0.21	0.63
Mesocarp	0.16	1	0.16	2.75	0.10
Light	0.05	1	0.05	0.93	0.34
Burial	1.64	1	1.64	28.01	<0.01
Site x Mesocarp	0.59	1	0.59	10.12	<0.01
Site x Light	0.04	1	0.04	0.64	0.43
Site x Burial	0.01	1	0.01	0.21	0.65
Mesocarp x Light	0.01	1	0.01	0.15	0.70
Mesocarp x Burial	0.22	1	0.22	3.71	0.06
Light x Burial	0.01	1	0.01	0.09	0.76
Site x Mesocarp x Light	0.02	1	0.02	0.42	0.52
Site x Mesocarp x Burial	<0.01	1	<0.01	0.01	0.92
Site x Light x Burial	0.13	1	0.13	2.14	0.15
Mesocarp x Light x Burial	0.04	1	0.04	0.77	0.38
Site x Meso x Light x Burial	<0.00	1	<0.00	<0.01	0.97
Error	3.17	54	0.06		

The single factor of burial was significant. Germination was greater when seed was buried ($\bar{x}$ = 0.52, s.e. = 0.04) than when left on the surface ($\bar{x}$ = 0.17, s.e. = 0.04). This result is not unexpected, as most plant species require seed to be covered with soil for germination. Observations of seeds washed out of replicates at CTI suggest a mechanism by which such relatively large seed can be moved into the soil.

A four-factor ANOVA (mesocarp, soil, light and caging) was applied to the germination results at MB to determine what effect predation, in particular, may have had on germination (G_{IP}) (Table 3.3). The analysis showed that at MB there was no significant interaction between factors. The only significant result was the effect of seed being buried ($P < 0.01$), as with the previous result. At the 5% level of probability there was no demonstrable effect of predators (i.e. caged verses uncaged replicates) on germination, but this may be the result of the small number of replicates (Type one error). Some seed loss from uncaged plots was observed and this warrants further investigation.

3.3.4 Seed loss

Loss of buried seed in caged replicates at MB was attributed to the effect of soil pathogens and invertebrate attack, as there was no evidence of wash-out of seed at this site. This seed loss eventuated in the seed no longer being recognisable at the completion of the experiment. There was a high proportion of seed remains where it was not possible to distinguish between decomposing seed remains from previously germinated seed and decomposing seed that had not germinated and had suffered severe damage from invertebrate or fungal attack. Some seed remains were so advanced in decomposition that any attempt to reconcile the total number of seeds originally placed in replicates (n = 70) was not possible. The mean proportion of seed lost from caged

Table 3.3: Four-factor (mesocarp, light, burial and cage) ANOVA of *Livistona australis* seed germination at Mungo Brush. Significant results (*P* < 0.05) are underscored.

Factors	SS	df	MS	*F*	*P*
Mesocarp	0.04	1	0.04	1.70	0.20
Light	0.02	1	0.02	1.03	0.32
Burial	0.52	1	0.52	<u>25.50</u>	<<u>0.01</u>
Cage	0.07	1	0.07	3.55	0.06
Mesocarp x Light	0.01	1	0.01	0.53	0.47
Mesocarp x Burial	<0.01	1	<0.01	0.05	0.83
Mesocarp x Cage	<0.01	1	<0.01	0.17	0.68
Light x Burial	0.04	1	0.04	1.87	0.18
Light x Cage	<0.01	1	<0.01	<0.01	0.95
Burial x Cage	0.06	1	0.06	2.71	0.11
Mesocarp x Light x Burial	0.02	1	0.02	0.78	0.38
Mesocarp x Light x Cage	<0.01	1	<0.01	0.03	0.87
Mesocarp x Burial x Cage	<0.01	1	<0.01	<0.01	0.98
Light x Burial x Cage	<0.01	1	<0.01	0.15	0.70
Meso x Light x Burial x Cage	0.02	1	0.02	0.98	0.33
Error	0.98	48	0.02		

replicates at MB was 0.44 (s.e. = 0.04, range = 3 – 62).

Therefore a three-factor ANOVA (mesocarp, light and burial) was applied to the recorded losses of seeds from caged replicates at MB (Table 3.4). The analysis showed that there was no significant interaction between factors affecting seed loss. The only significant result was the effect of the single factor of light on seed loss ($P < 0.01$). Seed loss was greater when seed was sunlit ($\bar{x}$ = 0.54, s.e. = 0.05) than when seed was in shade ($\bar{x}$ = 0.33, s.e. = 0.05). It is possible that pathogen and insect attack is more prevalent at the higher temperatures provided in sunlit forest patches than in shade, but more research is necessary to clarify this.

Predation was recorded from uncaged replicates at MB. The proportion of seed remaining while being exposed to predation was recorded over a two-year period (Figure 3.1). Seed loss was examined in terms of the effect of the combined factors of light (sunlit or shade) and mesocarp (intact or removed). The results are shown monthly for the initial six months and at six-monthly intervals thereafter and indicate a decline over that time.

The data in Figure 3.1 was analysed by a repeated measures ANOVA (Factors: time, mesocarp and light) and the results are presented in Table 3.5. There was significant interaction between factors (Table 3.5) indicating that the replicates varied differently over time in relation to mesocarp and light. Figure 3.1 indicates that intact seed survived longer when exposed to predators than seed with mesocarp removed. The light levels on the seed may have influenced this result, particularly for seed in exposed plots.

The results of analysis of the germination response from seed exposed to predation at MB are presented as G_{IP} in Table 3.6. Germination in replicates

Table 3.4: Three-factor (mesocarp, light and burial) ANOVA of *Livistona australis* seed loss from caged replicates at Mungo Brush. Significant results ($P < 0.05$) are underscored.

Factors	SS	df	MS	*F*	*P*
Mesocarp	148.78	1	148.78	0.75	0.39
Light	1937.53	1	1937.53	<u>9.76</u>	<<u>0.01</u>
Burial	175.78	1	175.78	0.88	0.36
Mesocarp x Light	34.03	1	34.03	0.17	0.68
Mesocarp x Burial	166.53	1	166.53	0.84	0.37
Light x Burial	399.03	1	399.03	2.01	0.17
Mesocarp x Light x Burial	148.78	1	148.78	0.75	0.39
Error	4766.25	24	195.59		

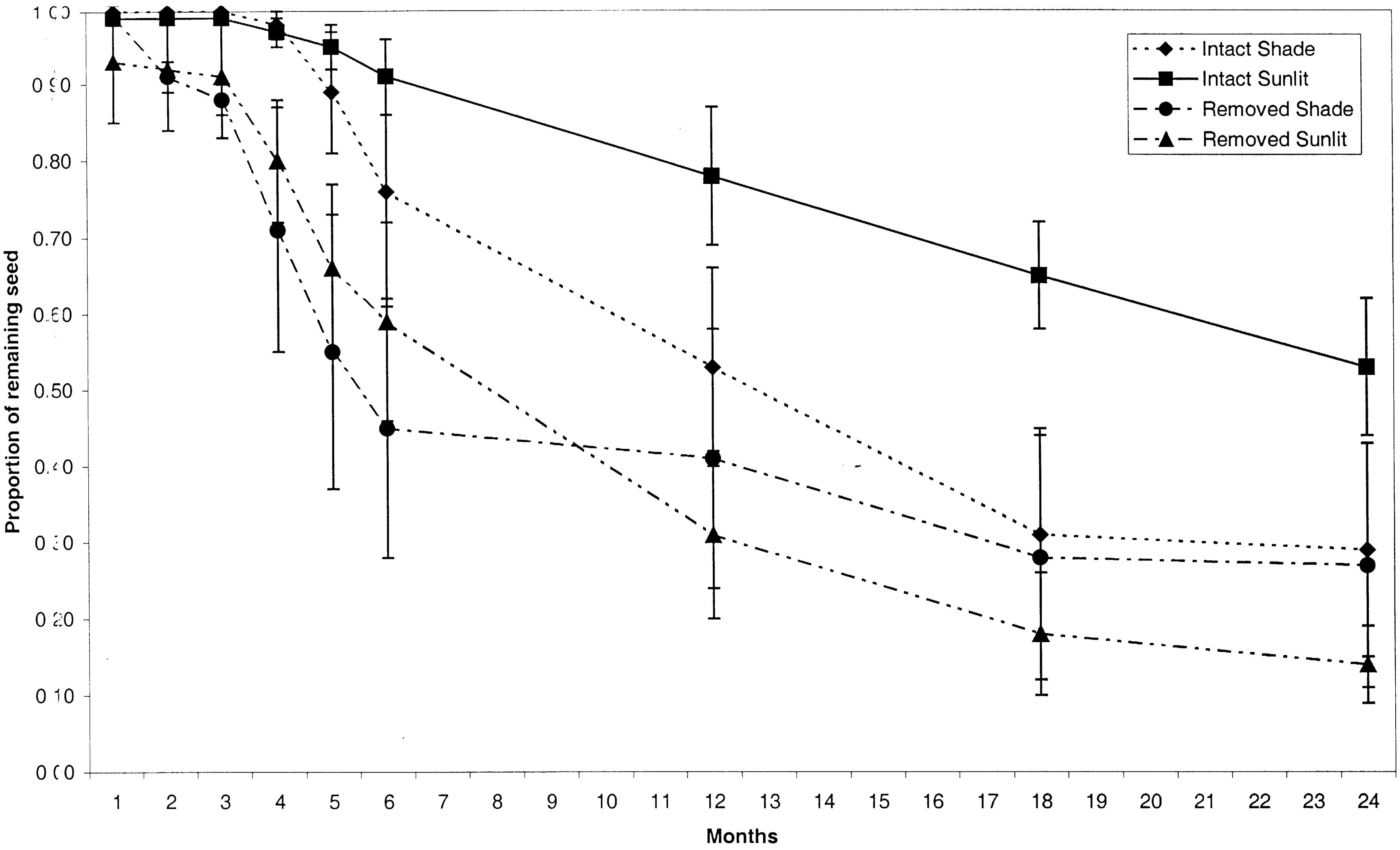

Figure 3.1: The proportion of *Livistona australis* seed remaining while exposed to predation at Mungo Brush over a period of two years. Data are the means of four replicates. Standard error (S.E.) bars are shown.

Table 3.5: Repeated measures ANOVA of the proportion of uncaged *Livistona australis* seed remaining at Mungo Brush over a two-year period. Significant results (*P* < 0.05) are underscored.

Factors	**SS**	**df**	**MS**	***F***	***P***
Time	8.97	9	0.98	53.42	< 0.01
Time x Mesocarp	0.51	9	0.06	3.01	< 0.01
Time x Light	0.10	9	0.01	0.59	0.59
Time x Mesocarp x Light	0.40	9	0.04	2.38	0.02
Error	2.02	108	0.02		

Table 3.6: Two-factor (mesocarp, light) ANOVA of *Livistona australis* seed germination exposed to predation at Mungo Brush. Significant results (*P* < 0.05) are underscored.

Factors	SS	df	MS	*F*	*P*
Mesocarp	0.002	1	0.002	<u>5.59</u>	<u>0.04</u>
Light	0.001	1	0.001	3.75	0.08
Mesocarp x Light	0.003	1	0.003	<u>10.39</u>	<u>0.01</u>
Error	0.003	12	<0.001		

exposed to predation was low ($\bar{x}$ = 0.01, s.e. = 0.006). There was significant interaction between the factors of light and mesocarp on germination rates (replicated two factor AVOVA: $F_{1,31} = 10.38$, $P < 0.01$). Applying an SNK test, the greatest germination of seed was in shade with the mesocarp intact ($\bar{x}$ = 0.05, s.e. = 0.01). Germination failed in shaded replicates where the mesocarp was removed ($\bar{x}$ = 0.00, s.e. = 0.00). The level of germination between the sunlit replicates with the mesocarp intact or removed was similar (sunlit and mesocarp intact: $\bar{x}$ = 0.003, s.e. = 0.003, sunlit and mesocarp removed $\bar{x}$ = 0.01, s.e. = 0.006).

Topknot Pigeon, *Lopholaimus antarcticus,* and Pied Currawongs, *Strepera graculina,* were observed to feed on fruit hanging in the canopy, but no avian predators were observed to take fallen seed.

Nocturnal searches for potential mammalian predators of seed were carried out at MB on a single night in each of the following months: May 1998, February, June and July 1999, and February 2000. Bush Rat, *Rattus fuscipes*, Long-nosed Bandicoot, *Perameles nasuta*, Brush-tailed Possum, *Trichosurus vulpecula,* and Dingo, *Canis familiaris,* were seen foraging within the palm forest at night.

Seed remains collected between May 1998 and April 2000 from uncaged, exposed (i.e. non-buried) experimental replicates at MB were examined. The remains of 13 seeds bore broad, chisel-like incisor tooth marks with the majority of the seed having been consumed by a species of unknown mammal. This dentition pattern excluded *C. familiaris* and *P. nasuta* as being responsible for the tooth marks found (refer to Triggs 1996). From the seed remains, 26 examples of the indentation of complete incisor-pairs and seven examples of single incisors were discernible. The mean width of incisor-pairs was 1.45 mm (s.e. = 0.05 mm, range = 1.00 – 1.85 mm) and the mean width of single incisors was 0.90 mm (s.e. = 0.02 mm, range = 0.75 – 1.30 mm). For comparative purposes, 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 is likely to be present is the introduced House Mouse, *Mus musculus*. This species, however, has an incisor-pair width of 1.1 mm (Triggs 1996), smaller than the indentations observed. Given that the seed remains may have been desiccated between the time of collection and the time of measurement, the most likely predator responsible was *R. fuscipes*.

3.3.5 Seed viability

Seed viability was assessed as a component of the viability trial (VT), the greenhouse experiment (GE) and the field experiment (FE) using seed without mesocarp, buried in soil and sunlit (Table 3.7). The results of the viability trial can be compared to the results from the other experiments. After 21 months, 90 of the 100 seeds used in the GE (90%) had germinated. Of those seeds that had not germinated, 6% were still viable. From the field experiment conducted at CTI (FE_{CTI}) 179 of the 280 seeds germinated (64%) within 24 months. The proportion of intact residual seed remaining viable was 5%. Over the same time period, 53 of the 280 seeds in the field experiment at MB (FE_{MB}) germinated (19%). Less than 1% of the intact residual seed was viable. There was a significant difference between the viability of seed from the different experiments (single factor ANOVA, $F_{4,936} = 31.209$, $P < 0.01$). Applying an SNK test, germination rates in VT, GE and FE_{CTI} were not significantly different from each other but were all greater than the germination rate at FE_{MB}. The proportion of germinated seed at MB was substantially lower than germination rates at either CTI or in the greenhouse under ideal conditions.

TABLE 3.7: Viability of *Livistona australis* seed from four separate germination experiments: a viability trial (VT); greenhouse experiment (GE); and field experiment at Cabbage Tree Island (FE_{CTI}) and Mungo Brush (FE_{MB}). Residual seeds are expressed as a proportion of the original number of seeds.

	VT	GE	FE_{CTI}	FE_{MB}
Sample size	280	100	280	280
Period of study (months)	17	21	24	24
Germination proportion	0.91	0.90	0.64	0.19
S.E.	0.03	0.09	0.10	0.08
Residual intact	0.09	0.10	0.11	0.13
viable	0.03	0.06	0.05	<0.01
non-viable	0.06	0.04	0.20	0.68
SNK of germination	a	a	a	b

3.3.6 Timing of germination

Timing of germination was analysed utilising data collected as part of VT, GE and FE. Following sowing, germination was first recorded in October for VT (Figure 3.2a), December for GE and FE_{CTI} (Figures 3.2b & 3.2c) and January for FE_{MB} (Figure 3.2d). Within four months of the onset of germination, 94% of all seeds to germinate within VT and 91% of all seeds to germinate within GE had germinated. To obtain greater than 90% germination of all the successful seeds took 5 months for FE_{CTI} and 11 months for FE_{MB} (Figure 3.2d).

3.4 Discussion

3.4.1 Germination success

Under greenhouse conditions greater than 90% of seed germinated. Germination success was independent of light levels and the presence or absence of mesocarp. In the field, light levels had no significant effect on germination and germination success was generally lower and more variable. The effect of mesocarp removal was variable improving germination rate at CTI (mesocarp intact 36%; removed 51%) but not at MB (intact 38%; removed 22%). Burial of seed increased the germination success at both field sites and was likely to be due to the soil-cover decreasing desiccation and not requiring the seed's radicle the difficulty of penetrating the soil surface. The action of soil movement and surface run-off is probably an important mechanism whereby seeds naturally become incorporated into the soil; however, research into this aspect of seed transport is needed to clarify the importance of this.

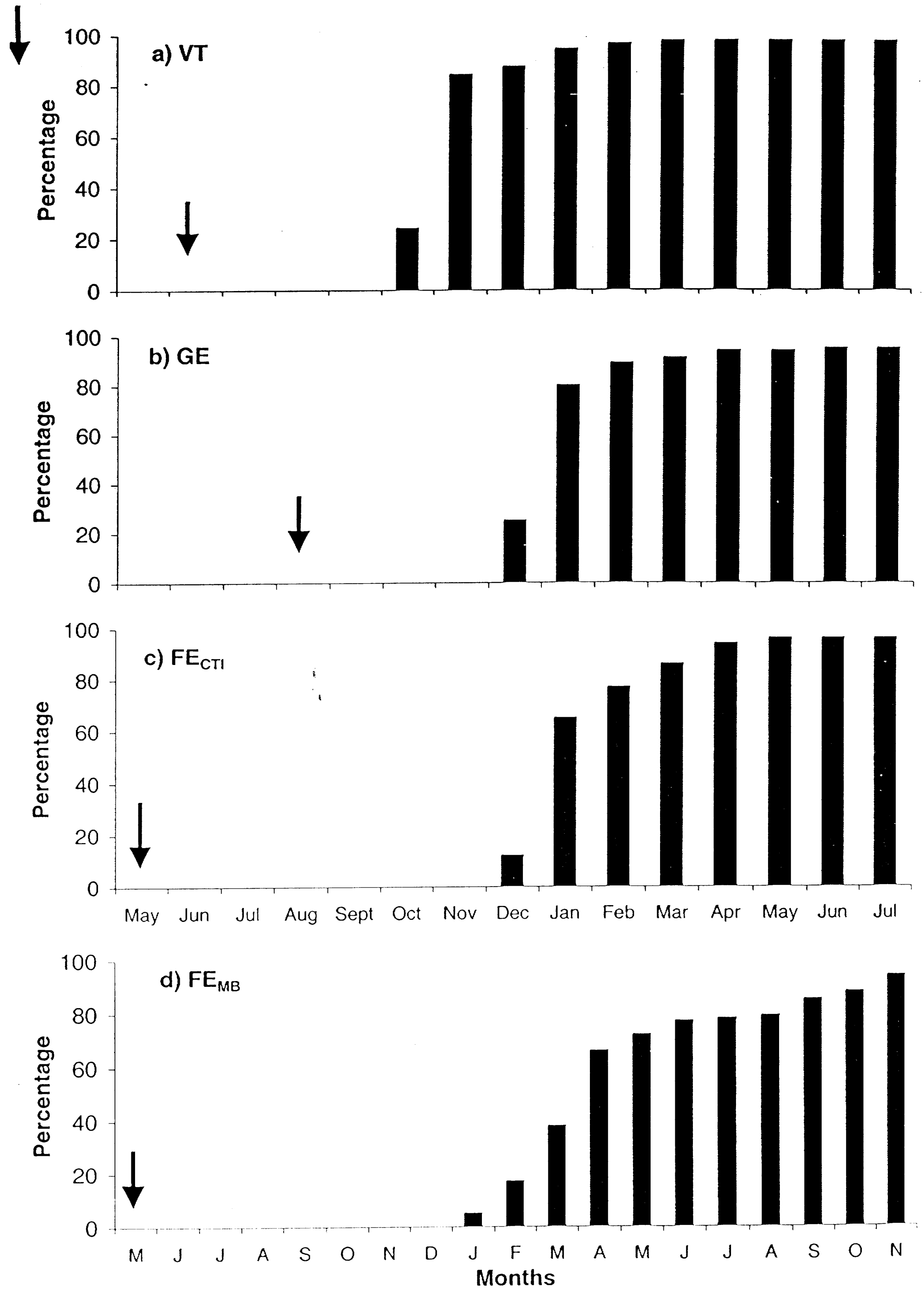

Figure 3.2. Cumulative percentage of *Livistona australis* seeds germinated over time from four experiments: a) viability trial (VT); b) greenhouse experiment (GE); c) field experiment at Cabbage Tree Island (FE_{CTI}); d) field experiment at Mungo Brush (FE_{MB}). Arrow indicates month of sowing.

3.4.2 Seed loss

Where it could be assessed, seed losses caused by the destruction of seed from soil pathogens and invertebrate attack was high with a mean of 43% lost from caged plots at MB. It has been suggested that the removal of the fruit from the seed could discourage fungal or insect attack (Fox *et al.* 1987), but from this study there was no significant difference in losses of seed with the mesocarp intact compared to seed with the mesocarp removed. In the Black palm, *Normanbya normanbyi,* insect predation by beetle borers and earwigs accounted for 24% of seed losses (Lott *et al.* 1995). No specific insect was noted damaging *L. australis* seed, but a large proportion of seeds had the seed coat removed. Although insect predators are generally the major cause of seed loss, in one study up to 25% of seeds were destroyed by pathogens (Kitajima & Augspurger 1989). More detailed studies are needed to verify whether it is pathogens or invertebrates that are most responsible for damage to *L. australis* seed.

Physical removal of unburied seed was recorded at MB, although the effect of this on germination rates was only significant at the 94% confidence level. The small number of replicates may have reduced the robustness of this result (Type 1 error). It was expected that over time seed predation would become equal between treatments as predators would eventually find all edible seed. If light levels were to effect seed survival then larger sample sizes may be necessary to prove this. Light levels had no significant effect on seed predation over time, but light did affect the rate of germination. When exposed to predation, unburied seed germinated most successfully in shaded areas with the mesocarp intact (5%), but totally failed under the same conditions with the mesocarp removed. Knowing that seed with the mesocarp intact survived longer when exposed to predation than seed with the mesocarp removed

(Table 3.3) explains the success of the germination in this instance. Seed exposed to predation in sunlit areas had germination rates of less than 1%, regardless of the status of the mesocarp. It has been found elsewhere that the average germination of palm seed exposed to light is five times less and time to germination is twice as long as for seed in darkness (Brown 1976). Sunlit seed with the mesocarp removed but exposed to predation survived long enough to have some germinate (albeit less than 1%). This observation is in contrast to the failure of similarly treated seed in the shade, and may indicate a preference of the seed predators to initially forage in environments with canopy cover (Begon *et al.* 1990; Orscheg & Parsons 1996b). More research, however, is necessary to fully explore the extent of the relationship of seed survival and germination when exposed to predators.

3.4.2.1 Avian predation

No avian predators of fallen seed were observed during the course of this study. Two ground-foraging birds have been recorded as eating palm fruit—the Australian Brush-turkey, *Alectura lathami* (Marchant & Higgins 1993) and the Southern Cassowary, *Casuarius casuarius* (Willson *et al.* 1989). The Australian Brush-turkey is a ground-feeding megapode that occurs throughout most of the range of *L. australis,* but none have been recorded at MB (David Turner, personal communication). Palm fruit is a component of the diet of the Southern Cassowary in northern Queensland, where there is some overlap with the distribution of *L. australis.* These ground-feeding birds act not as consumers of palm seed but as potential dispersers, as the hardness of the seed coat means the seed is ejected from the bird's crop undamaged (Harper 1977).

3.4.2.2 Mammalian predation

The only mammalian predator of seeds identified from seed remains recovered at MB was the Bush Rat, *Rattus fuscipes.* None of the teeth marks observed belonged to the larger potential predator — the Brush-tailed Possum, *Trichosurus vulpecula.* This latter species has been implicated as a predator of large seed in other studies (Orscheg & Parsons 1996b; Ballardie & Whelan 1986).

Undisturbed soil in the experimental replicates containing buried seed indicated that these did not suffer from rat predation. A similar result was obtained in a study of a tropical forest palm in Central America, *Astrocaryum mexicanum,* where the artificial burial of seed was also found to greatly increase survival to the seedling stage (Brewer & Webb 2001). It has been found elsewhere that *R. fuscipes* has been more attracted to areas containing the highest concentrations of seed (Ballardie & Whelan 1986). In this study the location of experimental replicates was chosen specifically to be away from fruiting palms so as to reduce the chance of additional seed being inadvertently incorporated into the study. This precaution may have resulted in lowering the overall potential for seed predation by *R. fuscipes.*

Germination was low at MB in uncaged replicates, but that which occurred provides some insight into possible predator behaviour. The highest germination was in shaded replicates with the mesocarp intact indicating that the seeds were less likely to be removed by predators and this long-term survival enabled some germination. The total failure of seed to germinate in shaded replicates with the mesocarp removed may indicate that the seed represents an attractive source of food for predators in areas where there is canopy cover. The similar germination response, albeit at very low levels, in seed in sunlit areas with the mesocarp either intact or removed is unexplained by this study. The seed with mesocarp removed may have, however, achieved some success in germination in this instance as the seed predators could be displaying an aversion to foraging in areas of canopy gap as a form of predator avoidance behaviour (Begon *et al.* 1990).

Not all palm seed eaten by rats was necessarily consumed on site, some may have been carried away. It is feasible that some of this seed may have survived being moved, and germinated some distance away. Anecdotal evidence from the germination of the Kentia Palm, *Howea forsteriana,* on Lord Howe Island indicates that some fruit removed by Black Rats remains viable, germinating in localised sites where seeds are regularly consumed (Larry Wilson, personal communication). The impact of *R. fuscipes* as a seed predator appears to vary from low, as in this study, to severe in isolated palm populations (Billing 1999; Orscheg & Parsons 1996b).

3.4.3 Seed viability

To better understand the results of any germination experiment it is essential that the background levels of seed viability are known. No studies have been published on the viability of the seed of *Livistona australis.* The only study attempted—a field trial at Cabbage Tree Creek in Victoria—ended when all seeds failed to germinate (Orscheg & Parsons 1996b). This may have been due to low field temperatures associated with the timing of the trial

This study showed that, under greenhouse conditions, greater than 90% of *L. australis* seed was viable. When seed was germinated *in situ* germination rates were highly variable. At CTI, germination success was not significantly different from that achieved under greenhouse conditions, whereas germination success at MB was considerably less (19%). The time taken for all germination to occur was similar between the greenhouse and the CTI field experiment but much longer at MB. The extended time taken for the seed to germinate at MB may have increased its exposure to soil pathogens, thereby reducing its viability. Elsewhere it has been shown that delayed germination increased infection rates of seeds by up to 65% (Augspurger 1979).

Germination within a single crop of *L. australis* seed may continue for up to three years (Jackobasch 1981). From this study, it can also be concluded that in a greenhouse, germination of all viable seed may take a full three years, but the major proportion of that seed will have germinated within the first year. It seems most unlikely that *in situ* seed would remain viable for three years, as it appears highly vulnerable to attack from soil pathogens. Species that have seeds that undergo long dormancy periods generally have mechanisms, still poorly understood, to protect the seed from pathogens (Augspurger 1990).

3.4.4 Timing of germination

The timing of germination in *L. australis* is not fully understood. Germination experiments of *L. australis* seed within a controlled environment found that higher temperatures reduced the time necessary for germination to commence (Orscheg & Parsons 1996b). Elsewhere spring germination of *L. australis* has been observed (Jakobasch 1981) and the onset of germination appears to be related to increasing ambient temperatures.

During this study, the onset of germination differed between experiments. There was some evidence to suggest that germination is temperature related as seed in the warmer greenhouse began germinating more quickly following sowing than did seed *in situ* (Figure 3.2). Faster germination at CTI than at MB could be linked to a difference in minimum ambient temperatures, with cooler temperatures at the mainland site of MB than at CTI, but comparative temperature data are lacking.

3.4.5 Implications of results

If the promotion of regrowth of *L. australis* was a goal of site management at CTI then the results of this study may assist. Generally if germination needed to be accelerated at CTI, *in situ* results from this study indicate that buried seed with the mesocarp removed would have the greatest potential for success. Germination may be higher if seed at CTI is not being predated, although predation was found to be significant only to 94% confidence. Overall, germination rates at CTI were not significantly greater than those at MB. At MB, the germination of seed caged against predation was not significant with 95% confidence ($P = 0.06$). From these results it is not clear whether the disturbed forest environment of CTI, where the undergrowth is not intact, hampered germination of palm seed.

In general the palms seed has a high viability when germination can occur within 12 months of seed fall from the canopy. While soil pathogens can be detrimental to seed longevity there impact on overall survival is as yet unclear.

4. Seedling survival in the Cabbage Tree Palm, *Livistona australis*

Abstract

The survival of *Livistona australis* seedlings, in the presence and absence of grazing, was monitored at two sites for two and a half years. Survival at Cabbage Tree Island (CTI) and Mungo Brush (MB) 12 months after germination was generally high, with greater than 84% survival for seedlings not exposed to rabbit grazing. Low rainfall during this initial establishment period reduced survival in one cohort to 65%. The proportion of seedlings surviving after 30 months at CTI, in the absence of rabbits, was 62% and at MB was 20-34%. The lower survival at MB may be attributed to lower levels of available light and greater intraspecific competition for other resources. It was concluded that sometime after 12 months the stored nutrient resource within the attached palm seed is exhausted and seedlings die if sufficient light is not available for photosynthesis. Survival of seedlings was low on CTI in the presence of the European Rabbit, *Oryctolagus cuniculus* (< 24% within 12 months of germination). Higher survival was obtained by preventing rabbit access to the plants through caging (68% survival within 12 months of germination) and by their eventual eradication. There was no evidence to suggest that at MB the Bush Rat, *Rattus fuscipes*, reduced seedling survival despite their continuous presence. The study provides a guide to aging seedlings up to six years following germination provided that they have not suffered defoliation from grazing or fire. In the absence of herbivores palm seedling survival following germination is high. Caging can improve survival where herbivores are abundant and will not, in itself affect palm survival. The aging of seedling palms is possible providing they have not had a history of defoliation.

4.1 Introduction

Knowledge of seedling survival in *Livistona* palms is scant. Research on the topic is limited to two cursory studies. Observations from a trial at Cabbage Tree Creek in Victoria found that, following transplantation to the study site, 90% of seedlings did not survive beyond one day (Orscheg & Parsons 1996b). Another study looked at the impact of rabbit grazing on *Livistona australis* seedlings on Cabbage Tree Island, New South Wales, and found that seedlings in wire cages had a higher survival rate than those left exposed (Priddel *et al.* 2000). European Rabbits *Oryctolagus cuniculus*, being so hardy and such prolific breeders, have had a profound effect on the flora and fauna, particularly on many islands around the world (Flux & Fullagar 1983). Seedling survival has been investigated in other palm species (e.g. Brown 1976; Ash 1988, Clancy & Sullivan 1988; Ataroff & Schwarzkopf 1992; Lippincott 1995; Cintra & Horna 1997). These studies demonstrate that seedling survival rates vary greatly due to a range of local factors, including temperature, moisture, salinity, predation, available light and a range of density dependent factors.

The development phase of *L. australis* seedlings is well understood. When palm seeds germinate the cotyledonary stalk containing the ligule and seedling first grows downward. After attaining a length of 30 mm or more (personal observation) it splits. The plumule then grows upwards producing the seedling and the root mass develops below the apical bud that remains buried deep within the soil (see Brown 1976, Figure 6). This process is called cryptogenial germination and is considered a critical adaptation for survival during fire or grazing (Tomlinson 1990).

For *L. australis*, the most conspicuous emergence of seedlings occurs when the growing tips appear after fire. This observation has led some observers to suggest that the seed needs to be heated to break dormancy (Hnatiuk 1977). It is more likely that observers have been viewing the resprouting of the apical bud (Orscheg & Parsons 1996b).

Palm seedlings grow quickly in greenhouse environments (Orsheg & Parsons 1996b Figure 21) where growth rates can be more than eight times faster than can occur *in situ* (McPherson & Williams 1996). The slow rate of *in situ* growth of seedlings lengthens the period of time during which they are vulnerable to vertebrate grazers. Vulnerability to grazers can be a problem for small populations of endangered palms (Lippincott 1995; Ratsirarson *et al.* 1996). Long-term demographic studies have shown that survival of seedlings is very low, even with common species in undisturbed habitats (Ash 1988).

This study tracked the fate of seedlings at a mainland site (Mungo Brush) and at an island recently made mammal-free (Cabbage Tree Island). The study aimed to i) determine the proportion of survival of the seedlings in each of the two habitats, ii) identify the reasons for any mortality, and iii) compare the findings between habitats. The study also monitored leaf numbers to test whether this was a useful indicator of seedling age. Published and unpublished data on palm survival collected from Cabbage Tree Island when rabbits were in abundance were considered in the context of this study.

As with many rainforest plants, seedlings of *L. australis* are likely to remain at the seedling stage for considerable periods until the formation of a gap in the canopy. The protracted period of slow development precludes this short study from following seedlings through to the time at which they develop into a larger, trunked palm. This study of early growth is important in that it provides some understanding of initial survivorship and the length of time that the seed can sustain the seedling. It also gives an indication of the effect of mammals on the survivorship of seedlings.

4.2 Methods

At Mungo Brush (MB) and Cabbage Tree Island (CTI) (see Chapter 2 Study Sites for details) 50 *in situ* seedlings were selected for treatment (caged) and 50 for a control (uncaged). For the caged treatment the seedlings were enclosed in three-sided, wire cages made of 10-mm-square mesh, 20 cm in height with three flanges extending from the bottom of the cage and mesh across the top of the cage. The cages were held in place by stones weighing down the flange on each side. A numbered brass tag uniquely identified each cage. For the control seedlings, each was identified by an individual brass tag attached to a wire spike. Each caged seedling was paired with an uncaged seedling.

Seedlings were chosen randomly from those that had recently germinated. Determining whether the seedling was the result of a recent germination was based on several factors. A recently germinated seedling had the seed still attached by the cotyledonary stalk, with the seed lying on the soil surface. The seed remained firm when pressure was applied with thumb and forefinger. It was assumed that at this stage of development the seed still provided an energy source for the establishing plant. The cotyledonary stalk appeared fleshy, rather than dried and shrivelled, indicating that nutrient flow from the seed to the seedling was still occurring. Finally, the seedling contained a single leaf with no evidence of the remains of older grazed or withered leaves.

A cohort of seedlings were tagged and caged in January 1999 at both MB (MB_{1999}) and CTI (CTI_{1999}). This was at a time when seed from the previous season had just germinated. Seedlings were checked for survival monthly within the first year and three-monthly thereafter. At each inspection the number of leaves were counted.

This current study replicates, in part, a study carried out on the survival of two cohorts of palm seedlings on CTI from 1993 and 1994. The survival of these seedlings was followed until 1999. Only a portion of the data from this earlier study has been published (Priddel *et al.* 2000) and these data and further unpublished data from that study form some of the data used in this chapter. This earlier study utilised the same methods employed in this current study using caged and uncaged seedlings, but with 49 rather than 50 caged seedlings in the 1993 cohort. The first of the two cohorts was monitored from November 1993 (CTI_{1993}) and the second from November 1994 (CTI_{1994}). Both cohorts were monitored regularly during the first 12 months and thereafter irregularly on the occasions when other research was being carried out on the island.

4.2.1 Analysis

The data were tested for heterogeneity of variances using Cochran's test and none required transformation. The seedling survival was divided into two time periods: 0 - 12 months, where monitoring had been monthly and 0 - 30 months, with monitoring at one to four-monthly intervals. Seedling survival was analysed by determining the line of best fit using Systat 10 for Windows. The line of best fit was based on the greatest r^2 value for the data after examining logarithmic, exponential, linear and polynomial relationships. In most cases a log linear relationship provided similar or higher r^2 values, so this curve was selected to allow comparison between cohorts. For caged and uncaged seedlings after 30 months at MB, polynomial equations provided the best fit. Analysis of leaf number was by repeated measures analysis of variance (ANOVA), as the same individuals were sampled each year, and by regression. Student-Newman-Keuls (SNK) was applied in multiple comparison tests at 95% confidence. All statistical tests performed were two-sided unless stated otherwise. Where means are shown, standard errors are included.

4.3 Results

4.3.1 Seedling survival

Seedling loss was recorded in each cohort within the first month of monitoring. On those occasions when seedling death was not by grazing, withering and browning of the leaves always preceded death. Occasionally, seedlings were found to have stem bases that were decomposed at the time of withering, indicating sub-surface damage to the plant prior to death. This is consistent with the seedling having been attacked by a fungus, which damages stem tissue that has not fully lignified (Augspurger 1984a).

4.3.1.1 CTI caged seedlings

Survival of three cohorts of caged *L. australis* seedlings (CTI_{1999}, CTI_{1994} and CTI_{1993}) over their first 12 months of life are presented in Figure 4.1a. There was a significant difference between the slopes of the equations ($F_{2,33}$ = 83.27). The CTI_{1993} cohort was different to the CTI_{1999} (t_{22} = 10.73) and to CTI_{1994} (t_{22} = 9.89). After 12 months only 65% of seedlings remained alive in the CTI_{1993}. In comparison the CTI_{1999} and CTI_{1994} cohorts were similar (t_{22} = 1.54) and had both declined only to 84%. The lower survival of seedlings in the CTI_{1993} cohort compared to the CTI_{1994} cohort may be due to the lower annual rainfall in 1993 than at other times during the study period. Rainfall data are lacking from 1999 to verify this.

Survival of three cohorts of caged *L. australis* seedlings (CTI_{1999}, CTI_{1994} and CTI_{1993}) over 30 months are presented in Figure 4.1b. There was a significant difference between the slopes of the equations ($F_{2,48}$ = 28.00). The CTI_{1993} cohort was different to the CTI_{1999} (t_{32} = 6.36) and to CTI_{1994} (t_{32} = 2.81). After 30 months, survival was lowest in the CTI_{1993} cohort at 53%. The CTI_{1994} cohort was different to the CTI_{1999} (t_{32} = 8.33). Seedling survival in the CTI_{1994} cohort was 62% and in the CTI_{1999} cohort was 72%. It is not known what factors have influenced the differences in survival of seedlings at the same location.

4.3.1.2 CTI uncaged seedlings

Survival of three cohorts of uncaged *L. australis* seedlings (CTI_{1999}, CTI_{1994} and CTI_{1993}) over the first 12 months of life are presented in Figure 4.2a. There was a significant difference between the slopes of the equations ($F_{2,33}$ = 53.04). The CTI_{1993} cohort was different to the CTI_{1999} (t_{22} = 8.50) and to CTI_{1994} (t_{32} = 6.12). The seedling survival in the CTI_{1993} cohort was reduced to 24% at 12 months. The CTI_{1994} cohort was different to the CTI_{1999} (t_{22} = 6.00). In the CTI_{1994} cohort seedling survival was reduced to 60%. Rabbits grazed the leaf

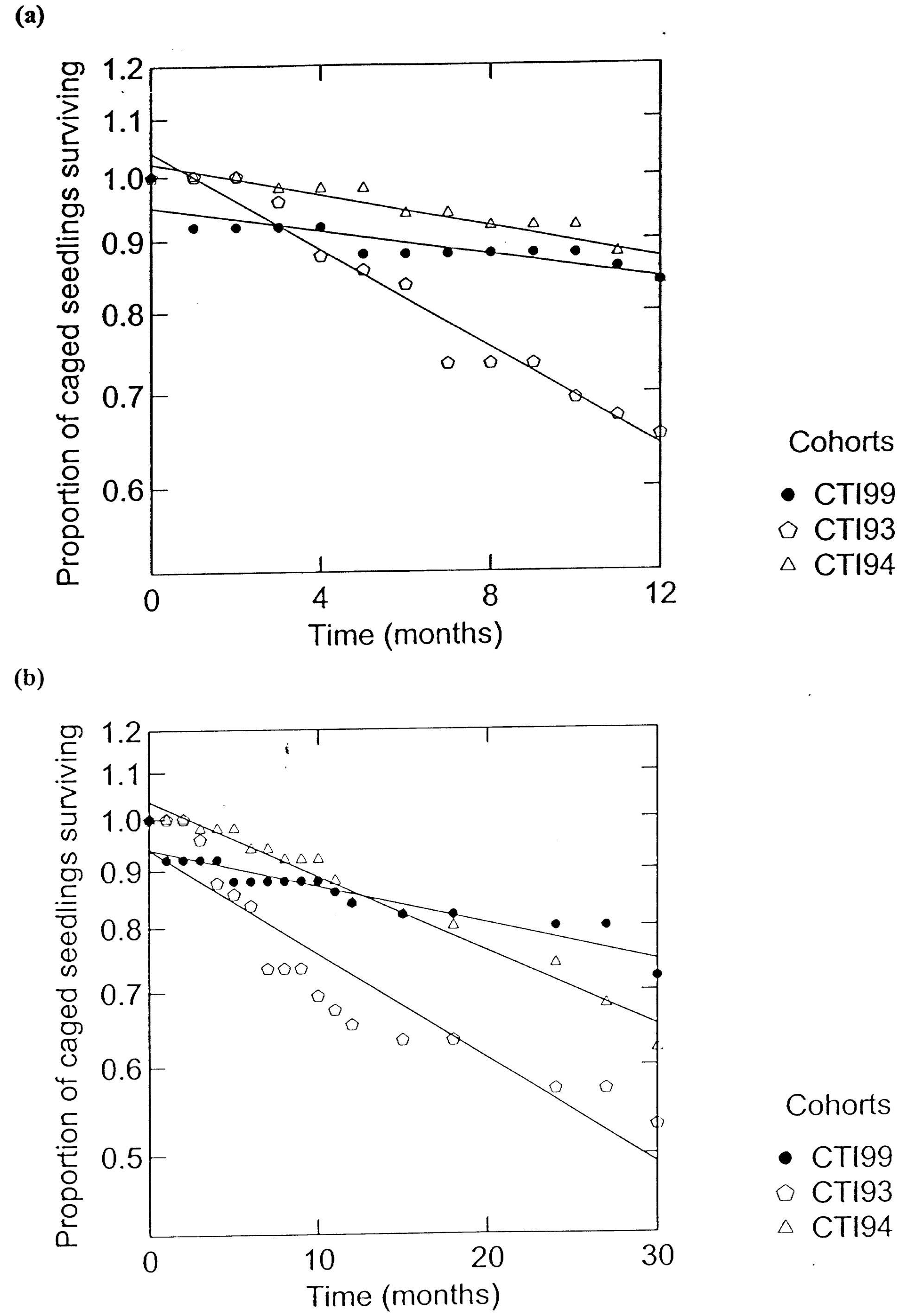

Figure 4.1: Proportion of three cohorts of caged *Livistona australis* seedlings surviving over 12 months (a) and 30 months (b) on Cabbage Tree Island (CTI). The log-linear equation for each cohort at 12 months is 1999: $y = -0.01x + 4.55$, $r^2 = 0.77$; 1993: $y = -0.04x + 4.65$, $r^2 = 0.96$; 1994: $y = -0.01x + 4.62$, $r^2 = 0.89$. The log-linear equation for each cohort at 30 months is 1999: $y = -0.01x + 4.54$, $r^2 = 0.88$; 1993: $y = -0.02x + 4.54$, $r^2 = 0.87$; 1994: $y = -0.01x + 4.64$, $r^2 = 0.97$. (Data from this study, Priddel *et al.* 2000 and Priddel & Carlile unpublished data).

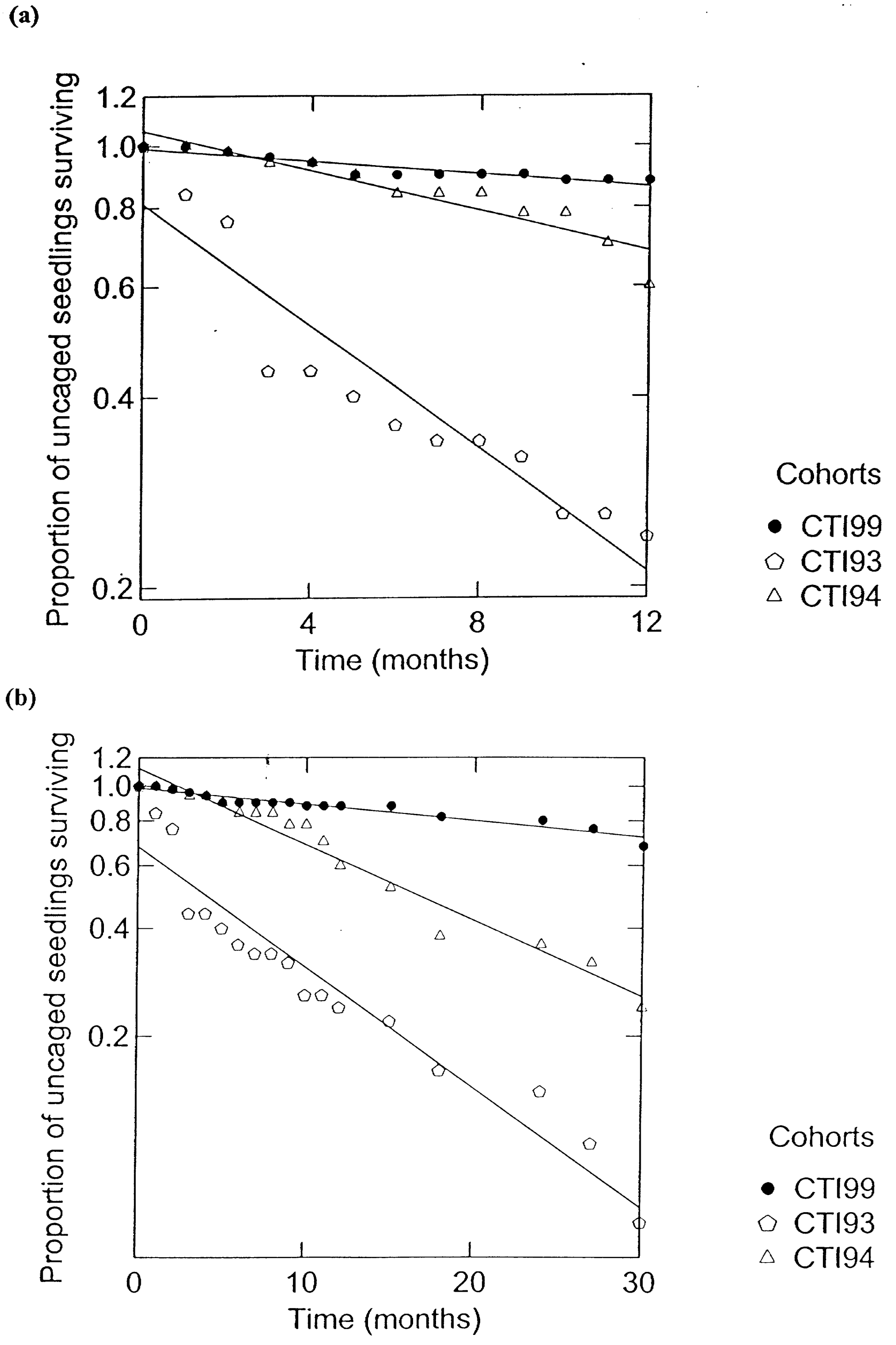

Figure 4.2: Proportion of three cohorts of uncaged *Livistona australis* seedlings surviving over 12 months (a) and 30 months (b) on Cabbage Tree Island (CTI). The log-linear equation for each cohort at 12 months is 1999: $y = -0.01x + 4.59$, $r^2 = 0.87$; 1993: $y = -0.11x + 4.40$, $r^2 = 0.89$; 1994: $y = -0.04x + 4.66$, $r^2 = 0.89$. The log-linear equation for each cohort at 30 months is 1999: $y = -0.01x + 4.59$, $r^2 = 0.93$; 1993: $y = -0.08x + 4.23$, $r^2 = 0.93$; 1994: $y = -0.05x + 4.72$, $r^2 = 0.97$. (Data from this study, Priddel *et al.* 2000 and Priddel & Carlile unpublished data).

tips of uncaged seedlings. In some, but not all cases the plant was pulled out of the ground and the swollen apical bud consumed, leaving only a short section of petiole at each marked site (D. Priddel personal communication). Rabbits were eradicated from CTI in 1997 (Priddel *et al.* 2000), hence palms in the CTI$_{1999}$ cohort were not subjected to rabbit grazing, unlike all seedlings prior to this event. Over the first 12 months, seedling survival for CTI$_{1999}$ was a high 88%. Loss of seedlings in the CTI$_{1993}$ cohort (76%) was almost double that of the CTI$_{1994}$ cohort (40%). This may have been caused by differences in rainfall between years, or by a fluctuation in the rabbit population on the island.

Low rainfall in any one year may have affected rabbit foraging, providing added pressure on seedling survival. Dramatic fluctuations in rabbit numbers had been observed even in consecutive years (Priddel & Carlile unpublished data).

Survival of three cohorts of uncaged *L. australis* seedlings (CTI$_{1999}$, CTI$_{1994}$ and CTI$_{1993}$) over 30 months are presented in Figure 4.2b. There was a significant difference between the slopes of the equations ($F_{2,48} = 98.42$). The CTI$_{1993}$ cohort was different to the CTI$_{1999}$ ($t_{32} = 12.40$) and to CTI$_{1994}$ ($t_{32} = 4.90$) and the CTI$_{1994}$ cohort was different to the CTI$_{1999}$ ($t_{32} = 15.97$). After 30 months the survival of seedlings was lowest in the cohorts exposed to rabbit grazing, CTI$_{1993}$ with 6% and CTI$_{1994}$ with 24%, and was considerably higher when the island was free of rabbits, in the CTI$_{1999}$ cohort (68%).

For both caged and uncaged cohorts the number of seedlings surviving declined between the 12 month and 30 month period (Table 4.1). Caged survival in the CTI$_{1999}$ and the CTI$_{1993}$ cohorts fell by 12% and in the CTI$_{1994}$ cohort by 22%. Between the 12 and 30 month period the decline in survival in the uncaged CTI$_{1999}$ cohort was 20%, in the CTI$_{1994}$ cohort 36% and in the CTI$_{1993}$ cohort 18%. In CTI$_{1999}$, losses for both caged and uncaged seedlings over the first 12 months were 12% and 16% respectively. There was no significant difference between slopes of the equations ($t_{22} = 0.865$). Losses at 30 months were 28% and 32% respectively. This would indicate that for CTI$_{1999}$, carried out in a rabbit free environment, the caging itself had no

Table 4.1: The proportion of surviving *Livistona australis* seedlings from caged and uncaged experiments established in 1999 at Cabbage Tree Island (CTI_{1999}) and Mungo Brush (MB_{1999}) and two previous cohorts at CTI established in 1993 (CTI_{1993}) and 1994 (CTI_{1994}) (Priddel *et al.* 2000 and unpublished data). All results are significant except caged to uncaged survival at CTI_{1999} and MB_{1999} (see text).

	Seedling survival			
	Caged		**Uncaged**	
	12 mths	**30 mths**	**12 mths**	**30 mths**
CTI_{1993}	0.65	0.53	0.24	0.06
CTI_{1994}	0.84	0.62	0.60	0.24
CTI_{1999}	0.84	0.72	0.88	0.68
MB_{1999}	0.86	0.30	0.86	0.34

demonstrable effect on seedling survival. The losses of uncaged seedlings exposed to rabbit grazing were typified by a high initial loss in the first 12 months relative to the losses over the following 18 months.

4.3.1.3 *MB caged and uncaged seedlings*

The survival of a single cohort of caged and uncaged seedlings over 12 months at MB$_{1999}$ is presented in Figure 4.3a. There was no significant difference between the slopes of the equations ($t_{22} = -1.15$). The proportion of surviving seedlings declined by 14% for both treatments after 12 months (Table 4.1). Dead uncaged seedlings at MB$_{1999}$ were found *in situ* with none showing any sign of being grazed.

The evidence for the lack of grazing on seedlings is also supported by the trend equations for both the caged and uncaged seedlings being similar.

The survival of a single cohort of caged and uncaged seedlings over 30 months at MB$_{1999}$ is presented in Figure 4.3b. The best fit to describe caged seedling survival over 30 months was a polynomial. At 30 months the decline from the levels at 12 months for the caged seedlings was 30% the uncaged seedling was 34%. The polynomial trend equations describing losses between the cage and uncaged seedlings were similar, indicating factors other than grazing cause seedling decline at this site.

4.3.1.4 *Comparison between CTI and MB*

Seedling survival after 12 months at MB for both caged and uncaged treatments (86%) was similar to that recorded at CTI$_{1999}$ for caged (84%) and uncaged (88%) treatments ($F_{2,44} = 0.27$). The proportion of surviving seedlings after 30 months at CTI$_{1999}$ for both caged (72%) and uncaged (68%) was twice as great as that of seedlings at MB$_{1999}$ for caged (30%) and uncaged (34%). The similar level of decline at 12 months was likely due to the seedlings at both sites surviving on the resources of the attached seed. After 30 months, however, environmental factors may have separated the results between the

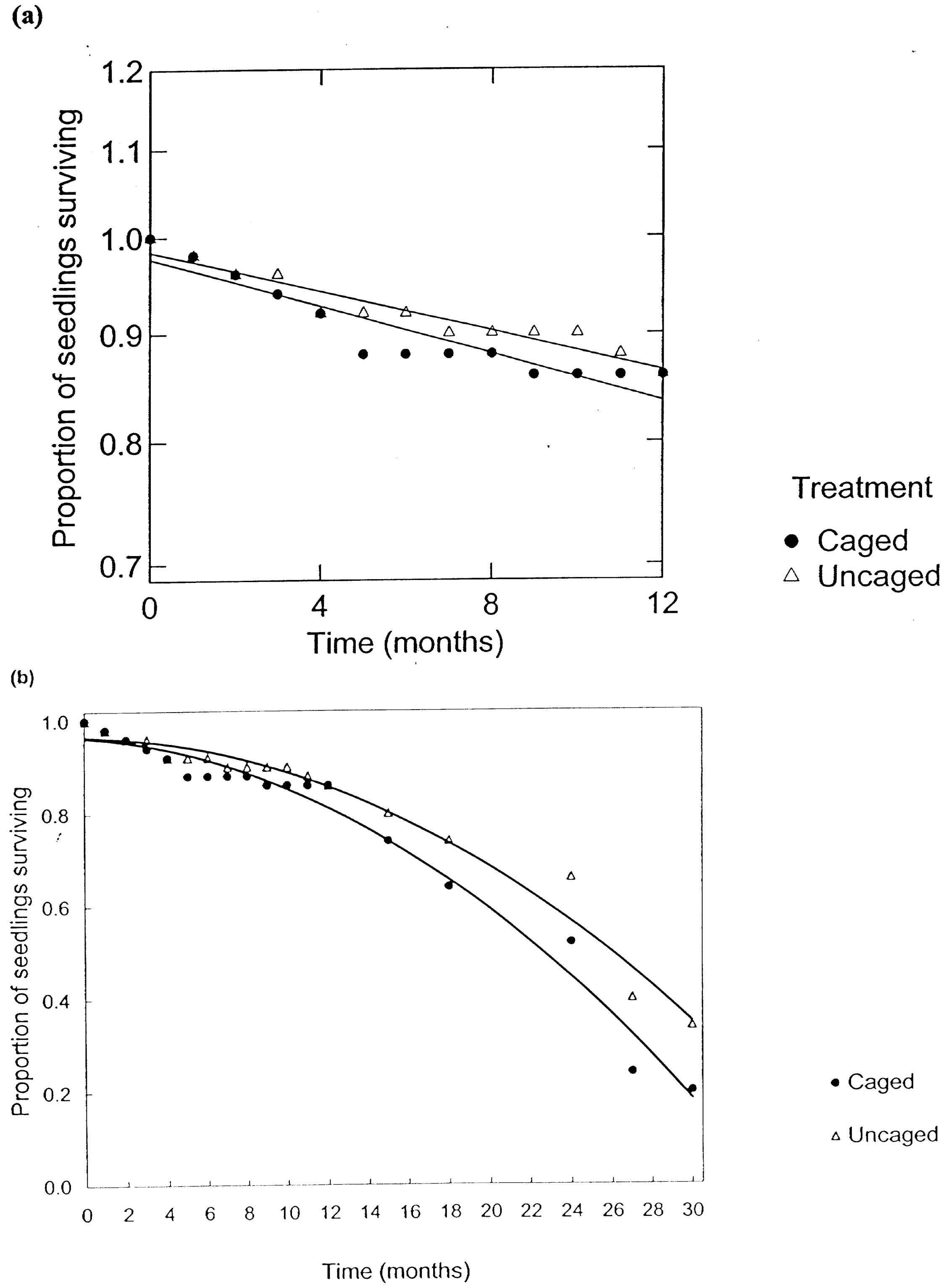

Figure 4.3: Proportion of a single cohort of caged and uncaged *Livistona australis* seedlings surviving over 12 months (a) and 30 months (b) at Mungo Brush (MB). The log-linear equation at 12 months for caged: $y = -0.01x + 4.58$, $r^2 = 0.87$ and uncaged: $y = -0.01x + 4.59$, $r^2 = 0.92$. At 30 months the polynomial equation for caged: $y < -0.0007x^2 - 0.0038x + 0.9639$, $r^2 = 0.9778$ and for uncaged: $y < -0.0006x^2 - 0.0012x + 0.9643$, $r^2 = 0.9710$.

sites with competition for available resources such as light and space probably higher at MB, giving the greater decline at this site. While this indicates that seedlings on CTI have a higher survival than at MB the extent of the relationship is unknown and requires further investigation.

4.3.2 Seedling age based on leaf number

Caged seedlings were protected from potential grazing whereas uncaged seedlings were exposed to grazing. As leaves may have been grazed from seedlings that where uncaged, these data were omitted from the analysis of leaf number. The numbers of leaves retained by caged seedlings over the period of the study are shown in Figure 4.4. The CTI_{1999} cohort had leaves counted only for the first two years. The leaves of the CTI_{1994} and CTI_{1993} cohorts were counted over five and six years, respectively. Applying an SNK test (Table 4.2), in the first year CTI_{1994} cohort had the highest number of leaves during the first year of growth, followed by CTI_{1999}, with CTI_{1993} and MB_{1999} having the least leaves. Applying an SNK test in the second year of growth, CTI_{1999} had more leaves than any other cohort. The number of leaves in both CTI_{1994} and CTI_{1993} cohorts were similar and greater than those in the MB_{1999} cohort. The marginal increase in the mean number of leaves in the MB_{1999} cohort between the first and second years (7%) may indicate a limitation in available light reaching the forest floor or a lack of other available resources for growth. In comparison, between the first and second year the CTI_{1999} cohort and the CTI_{1993} cohort increased by 60% and the CTI_{1994} cohort by 20%.

In the two years after germination all cohorts are represented. Using a repeated measures analysis of variance (ANOVA) over that period there was no significant interaction between the cohorts and years but there was a significant difference between years (Table 4.3). There was no significant difference between cohorts.

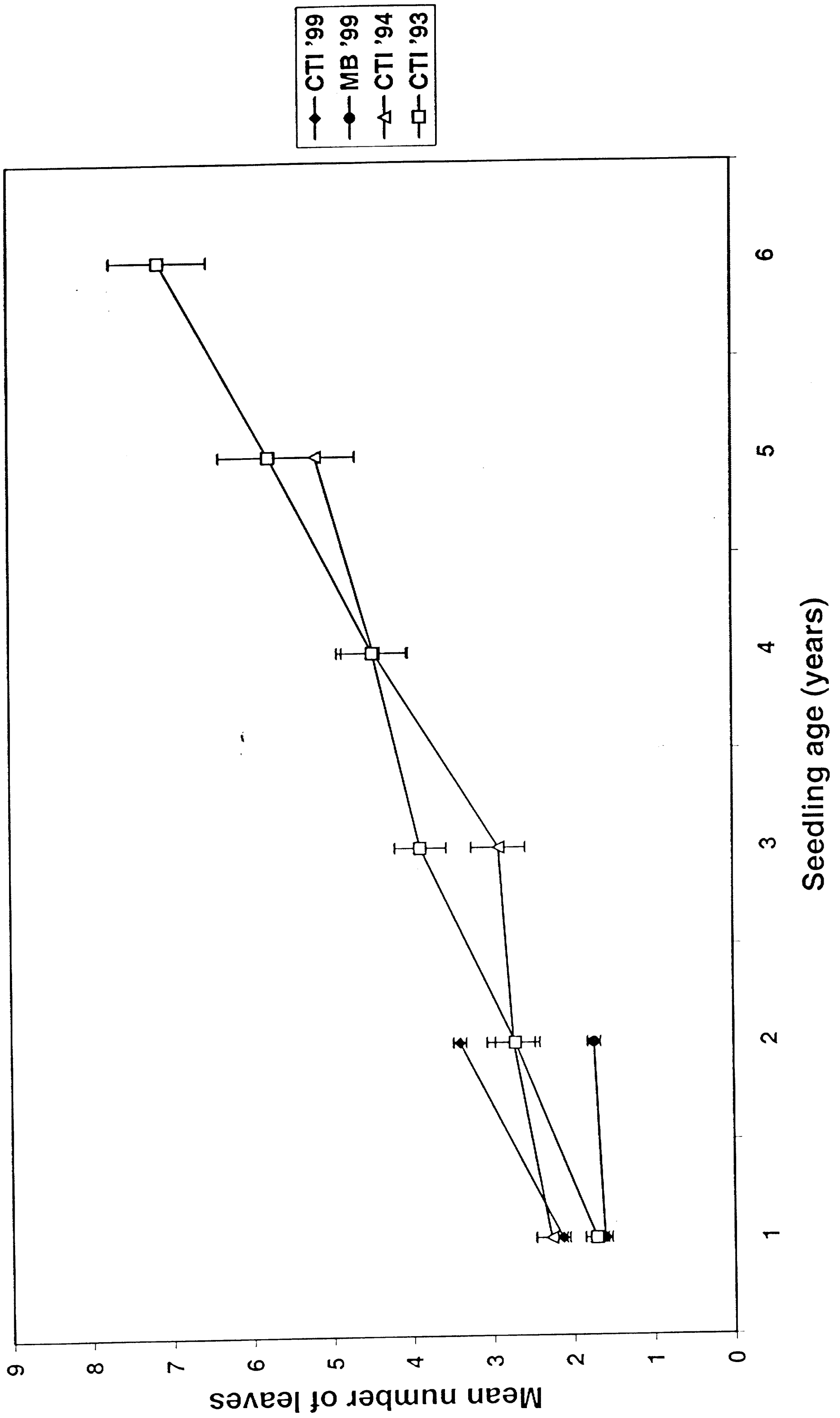

Figure 4.4: The mean number of leaves of *Livistona australis* retained by known age caged seedlings from four cohorts: 1999 at Cabbage Tree Island (CTI_{1999}) and Mungo Brush (MB_{1999}) and two previous studies on CTI commencing in 1993 (CTI_{1993}) and 1994 (CTI_{1994}).

Table 4.2: The mean number of leaves of *Livistona australis* retained by known age caged seedlings from four cohorts: 1999 at Cabbage Tree Island (CTI_{1999}) and Mungo Brush (MB_{1999}) and two previous studies on CTI commencing in 1993 (CTI_{1993}) and 1994 (CTI_{1994}). SNK results of within year comparisons are in italicised lower case letters.

		Seedling age (years)					
	(n)	1	2	3	4	5	6
CTI_{1999}	37	2.13 *b*	3.40 *a*				
S.E.		0.09	0.08				
MB_{1999}	26	1.61 *c*	1.73 *c*				
S.E.		0.09	0.08				
CTI_{1994}	11	2.27 *a*	2.73 *b*	2.91	4.45	5.18	
S.E.		0.19	0.33	0.34	0.41	0.50	
CTI_{1993}	17	1.71 *c*	2.71 *b*	3.88	4.47	5.76	7.12
S.E.		0.14	0.25	0.32	0.45	0.62	0.60
Total	91	1.92	2.71	3.50	4.46	5.54	7.12
S.E.		0.06	0.11	0.25	0.31	0.42	0.61

Table 4.3: Repeated measures ANOVA of the mean leaf number of *Livistona australis* seedlings from three cohorts at Cabbage Tree Island over a two-year period. Significant results (*P* < 0.05) are underscored.

Factors	SS	df	MS	*F*	*P*
Cohort	1.16	2	0.58	0.54	0.58
Time	15.26	1	15.26	28.87	< 0.01
Time x cohort	0.99	2	0.49	0.94	0.39

The number of leaves for the cohorts CTI_{1993} and CTI_{1994} were recorded for five years (Table 4.2). A repeated measures ANOVA over that period showed that there was no significant interaction between cohorts and years but a significant difference was found between years (Table 4.4). There was no significant difference between cohorts although the CTI_{1993} cohort was greater than the CTI_{1994} cohort in the third year. An exponential regression was found to best describe the relationship of the increasing number of retained leaves over time for the CTI_{1993} cohort: $y = 0.98e^{0.28x}$, $r^2 = 0.68$ and for the CTI_{1994} cohort: $y = 1.03e^{0.27x}$, $r^2 = 0.59$. The slopes for the exponential equations were similar and the regression value indicates this was a useful descriptive tool for aging *in situ* seedlings at these sites in these years.

4.4 Discussion

4.4.1 Seedling survival

4.4.1.1 Survival rates over 12 – 30 month periods

The survival of seedlings at 12 months following germination was generally high with less than 16% losses in both the caged and uncaged CTI_{1999} and MB_{1999} cohorts and caged CTI_{1994} cohort. Losses in the CTI_{1993} cohort were more pronounced (35%). When examined in association with rainfall data, the data suggests that if, within the first 12 months following seed germination, there is an extended dry period then survival is reduced. In the longer term (30 months) the mean survival of caged seedlings from all three cohorts on CTI was similar ($\bar{x}$ = 0.62, s.e. = 0.05). The mean loss of 38% of caged seedlings was due to factors other than grazing by vertebrates. The uncaged seedlings in the CTI_{1999} cohort were not subjected to rabbit grazing as rabbits were eradicated from CTI in 1997. Uncaged seedling survival in the CTI_{1999} cohort, after 30 months, was similar to the results of the caged palms in all three cohorts, indicating that caging had no measurable affect on seedling survival.

Table 4.4: Repeated measures ANOVA of the mean leaf number of *Livistona australis* seedlings from two cohorts at Cabbage Tree Island over a five-year period. Significant results ($P < 0.05$) are underscored.

Factors	**SS**	**df**	**MS**	***F***	***P***
Cohort	1.29	1	1.29	0.21	0.65
Time	204.88	4	51.22	42.97	< <u>0.01</u>
Time x cohort	9.45	4	2.36	1.98	0.10

The rate of seedling loss differed, with curves significantly different between each cohort. This would indicate the factors affecting survival differed for each cohort. In studies on other species, palm seedling survival has been found to be quite variable. In one cohort of the neotropical dioecious palm *Chamaedorea tepejilote* in primary forest, seedling survival was 40% (Oyama 1990). In contrast *Prestoea trichoclada*, used in harvesting of palm hearts, had high survival in primary forest when compared to that in pasture (Bonilla & Feil 1995). Three cohorts of seedlings of the tropical palm *Euterpe edulis* exhibited survival rates of between 57% and 81% (Matos *et al.* 1999). Seedling survival in mature palm forest for both the short and long-term is likely to be controlled by a complex range of factors meaning their elucidation will require future intensive research.

4.4.1.2 Comparison between habitats

Seedling survival in the MB$_{1999}$ cohort steadily declined after 12 months so that at 30 months it was less than half that recorded in the CTI$_{1999}$ cohort over the same time period. Seedling survival is influenced by a range of factors including seedling density (Webb & Peart 1999), distance from canopy gaps (Nadolny 1999) and the presence of selective herbivores (Terborgh & Wright 1994). The difference in survival of caged seedlings between the two study sites appears most likely due to the differences in available light. CTI has had much of the undergrowth removed by years of rabbit grazing (Floyd & Dodkin 1978). Shady, more moist conditions at MB probably provide for an increase likelihood of death due to fungal pathogens (Augspurger 1979; 1984b). Alternatively, another explanation for the differences in seedling survival between the two sites is competition from established seedlings. Transect surveys found that seedling density at MB was more than 20 times greater than at CTI (see Chapter 6). From a study of seedlings of 149 different species in Bornean Rainforest over a 19-month period, mean survival was 66%, with the most abundant species suffering higher mortality than less abundant ones (Webb & Peart 1999). The increased seedling loss beyond the first 12 months in the MB$_{1999}$ cohort compared to the CTI$_{1999}$ cohort may indicate that the energy resources available from the seed begin to decline at this time.

Elsewhere, seedling losses in the Needle Palm, *Rhapidophyllum hystrix*, have been attributed to the exhausting of food stores in the endosperm of the seed (Clancy & Sullivan 1988). Seedling mortality following the exhaustion of seed resources generally occurs in poor microhabitats (Nadolny 1999) and in sites of dense understorey, and is the likely cause of seedling failure (Orscheg & Parsons 1996b). The reason for difference in the decline over the longer timeframe of the caged CTI_{1993} cohort compared to the CTI_{1994} cohort is not clear. From available data the rate of decline after 30 months was less in the CTI_{1993} cohort when compared to the CTI_{1994} cohort, but the differences were significant. This highlights the need for research to determine the factors affecting seedling survival in rainforest environments.

4.4.1.3 Effect of grazers

In the presence of the European Rabbit, *Oryctolagus cuniculus,* loss of uncaged seedlings from grazing was dramatic and acute. From the CTI_{1993} and the CTI_{1994} cohorts that were exposed to only rabbits 6 – 24% of seedlings survived after 30 months. In comparison, the CTI_{1999} cohort had 68% of seedlings survive over the same period of time in the absence of rabbits. The dramatic effect of rabbit damage to palm seedlings has been reported from other studies. A reintroduction of Sargent's Cherry Palm, *Pseudophoenix sargentii,* to islands in Florida Keys, USA, suffered defoliation and sometimes total destruction of up to 30% of seedlings by rabbits (Lippincott 1995). On Round Island in Mauritius, rabbits were implicated in the reduction of three palm species and their associated plant communities (Merton 1987). It is clear that exotic herbivores, particularly rabbits, on islands are a source of damage and destruction to indigenous flora and fauna unless they are controlled or eradicated (Flux & Fullagar 1983).

From the only other study of *L. australis* seedling survival, involving a trial at Cabbage Tree Creek in Victoria, 90% of uncaged seedlings ($n = 90$) did not survive beyond one day following transplantion to the study site (Orscheg & Parsons 1996b). The remaining 10% were destroyed within 6 weeks. All seedlings had had their laminae bitten off and the seed removed from the site, possibly by Bush Rats, *Rattus fuscipes*. This study has shown that despite the continuously observed presence of *R. fuscipes,* at MB (see Chapter 3) and their potential threat to seedling survival, no loss of uncaged seedlings from rats or any other mammal was recorded. At 12 months following germination the number of surviving seedlings in the MB_{1999} cohort was equal to those in the CTI_{1999} cohort. Similar results have been found in seedling survival studies in neo- and paleotropical rainforest studies (Terborgh & Wright 1994; Webb & Peart 1999). In contrast, in a study of seedling survival in subtropical rainforest in northern NSW it was found that caging significantly improved seedling survival by protecting them from grazing animals (Nadolny 1999). It would appear that the impact of herbivores varies with location.

4.4.2 Seedling age based on leaf number

Seedlings retain leaves in increasing numbers with age to six years. This study suggests that while no equation could adequately predict the number of leaves retained in known age seedlings, leaf number could be used as a rough guide for seedling age. A larger sample of seedlings may be necessary to develop a more accurate predictive tool. Orscheg and Parsons (1996b) assumed that two-leaved *L. australis* seedlings recorded in a study in Victoria, were about 12 months old and reaching the limit of their seed resources. On the basis of this study, Orscheg and Parsons (1996b) were roughly correct in their estimation of age. Provided that seedlings have not suffered defoliation by grazing or fire, the results from this study could act as a rough guide in aging seedlings in a forested environment up until six-years post-germination until further research is carried out.

In the absence of herbivores palm seedling survival following germination is high. Caging can improve survival where herbivores are abundant and will not, in it self, affect palm survival. The aging of seedling palms is possible providing they have not had a history of defoliation.

5. Estimate of the age of Cabbage Tree Palms, *Livistona australis,* based on growth rates

Abstract

The aim of this study was to develop a method to age *Livistona australis* palms based on direct measurement of growth rates. Using leaf scars on palm trunks, an estimation of growth was obtained by yearly measurements over a range of hight classes. Morphological measurements showed that the size of a *L. australis* crown was strongly correlated to the height of the trunk; the taller the palm the larger the crown. The overall size of adult palms was strongly influenced by the local environment, with more sheltered sites producing taller, larger crowned palms. Growth can be highly variable between populations. Palms at Cabbage Tree Island and Mungo Brush, north of Newcastle, grew two to four times slower than those in the Royal National Park, south of Sydney. The tallest palm encountered in the study was in the most sheltered of the study sites—Royal National Park—and had a height of 26 metres. In general, growth was faster and more variable prior to palms reaching reproductive age, after which it declined and stabilised. Fire appears to stimulate growth of sub-adults, however, the effect of frequent fires is probably detrimental to the long-term viability of populations. The oldest palm was estimated to be 392 years old, and had a height of 14.9 metres. The mean age to first flowering from four populations was 170 years. Prior to reaching reproductive age, the basal area of the trunk swells, probably to strengthen the trunk to support the additional load caused by fruit hanging in the crown. This study describes a technique to determine the growth rates of palms by taking a repeated series of measurements immediately below the crown. Observations of senescence suggest that accident, by structural failure or breakage of the trunk, is the prime cause of death in natural palm populations.

5.1 Introduction

Estimating the age of palms has always been a difficult task. Lacking a vascular cambium the trunks do not produce growth rings, and many species are particularly slow growing. From studies of trees in tropical forests (including palms) long-lived species do not grow continuously, whereas short-lived species generally do (Lieberman & Lieberman 1985; Lieberman *et al.* 1988). Aging of palms by direct measurement of trunk growth has been attempted only in species that do not attain great heights (Oyama 1990; Pinero *et al.*1984) or estimated for individuals in a population that can be reached by a telescopic aluminum pole (Lieberman & Lieberman 1985). In an extreme case, palms were felled to obtain data (Ash 1988). The aging of palms has most often been attempted by indirect methods of estimating growth from counts of leaf scars.

Within Australia, an estimate has been made of the age of *Livistona eastonii* based on measurements taken during a single visit to a population combined with the reported time taken for a single leaf to emerge in a small palm of the same species (Hnatiuk 1977). The same methodology has been applied to the Cabbage Tree Palm, *Livistona australis*, but with the growth observations covering a full growing season (Orschegs & Parsons 1996b). Both these approaches involved estimating leaf production during a single season's growth. Leaf scars within a 30 cm section of the trunk, near ground level, were counted. Dividing the number of leaf scars by the total number of leaves produced in a season gave an estimate of the years of growth within this short section of the trunk. To age the adult palm this result was extrapolated over the total trunk height.

The most difficult aspect of aging palms is in determining the time it takes a seedling to increase its basal bulge sufficiently to produce a trunk. Estimates have been based on matrix modelling of data obtained by monitoring populations of Cabbage Palm, *Sabal palmetto,* seedlings over two years (McPherson & Williams 1996). The annual rate of increase in frond length provided first approximations of the time it took for trunk development in New Zealand's Nikau Palm, *Rhopalostylis sapida,* (Enright 1985) or a seedling's single-year leaf production of *Livistona* in Australia (Orscheg & Parsons 1996b; Hnatiuk 1977). Estimations have been made for *Livistona mariae* by either speculation (Lothian 1959) or by taking measurements based on historical photographs (Latz 1975). Other approximations of time taken for the formation of the basal bulge have been based on specimens growing in gardens and nurseries (Eagle 1978).

The aim of this study was to develop a method to age *L. australis* palms based on direct measurement of growth rates at different stages of a palm's development. The various stages targeted were: seedling to the formation of a trunk, trunked juveniles of two height classes and reproductive adults of four height classes. In the course of this study, basic morphological information was also obtained on the structure of adult palms. Part of this morphological examination aimed to determine what change, if any, occurs to trunk girth during adult life. The causes of senescence within the palm populations under study were also examined. The conservation implications of the findings of this study are then discussed.

5.2 Methods

Each year *L. australis*, like all other palm species, produce a small number of new leaves and shed an almost equal number of old leaves. The indirect method of age estimation based on the number of leaf scars and a single rate of leaf production does not take into account the variation in growth throughout the palm's juvenile and adult life stages. A more accurate estimation of growth can be obtained by measuring the yearly increment of trunk growth over a range of height classes.

5.2.1 Palm selection

In each of the four populations of Mungo Brush (MB), Cabbage Tree Island (CTI), Wyrrabolong National Park (WNP) and Royal National Park (RNP), 50 palms with formed trunks of varying heights were sampled. Within each site the first 50 trunked palms encountered during a random walk were selected. The criterion for acceptance of an individual palm was based solely on its suitability for climbing. If an individual was heavily entangled with vine, it was rejected. For safety reasons, palms with a deviation from the vertical of more than 1.5 m between the trunk base and crown were also rejected. Those palms that had suffered substantial damage to the trunk, either from arboreal termite mounds (see Section 5.5) or from friction with another tree, were also rejected. This selection process provided from each study site a sample that was assumed to be representative of the various height classes present in each population.

5.2.2 Measurement technique

Direct measurement of growth increments beneath the crown requires access to the top of the trunk. To reach the crown a specific climbing technique needed to be developed. The average trunk diameter of *L. australis* is 25-40 cm (Rodd 1998). Girths of this width preclude the more simple method of climbing using an ankle strap such as those used to climb Thatch Palm, *Howea fosteriana* (Larry Wilson, personal communication) and other palms of similarly narrow dimensions. Climbing palms of larger girth can be safely achieved by prussiking, an ascent method developed for abseiling. In abseiling, a climber ascends a rope by the use of foot-stirrups and a waist harness attached to the main line via a mechanical ascender or prussik cords. The climbing method developed for this study was based on this technique, but involved the use of a climbing harness, seat-belt webbing for stirrups and safety lines placed around the trunk. Despite repeated use of this technique no palm sustained any apparent trunk damage. With some practice the crowns of palms with trunks exceeding 10 m high could be accessed within five minutes.

5.2.3 Palms with trunks

A numbered aluminium disc was affixed to the trunk of each palm, immediately below the crown (see Figure 1.1). Measurements were taken with a retractable tape measure to 1 mm accuracy, from the point of attachment of the disc to the ventral side of the petiole of the photosynthetic leaf directly above it. A consistent morphological structure at the base of each petiole provided a standardised upper measurement point. This structure was a horizontal crease formed where the convex lower surface of the petiole joins the palm trunk. At this junction the petiole thins and broadens, wrapping itself in an interlocking manner with other petioles around the trunk as part of a phyllotatic spiral. In juvenile palms petiole stubs persisting from previously shed leaves often cover this crease. These required removal before a measurement could be obtained. Occasionally, in adult palms the crease can also become partly obscured by the upper petioles when the crowns sag under a heavy burden of fruit. Despite this, accurate measurements can still be achieved because the crease continues across the width of the petiole base. The breadth of this structure also ensured that, regardless of whether the fixed marker was directly below the middle of a leaf or near the edge of a leaf, there was a standard point to which the growth measurement could be taken.

As leaves are shed, the crown extends upwards away from the fixed aluminium disc. The increasing distance between the disc and the crown was used as a measure of trunk growth. This measurement has several underlying assumptions. It was assumed that the only height increases in trunk growth takes place at the apical bud, above the fixed aluminium disc. The rate of growth of the palm's apical bud was assumed to be reflected in the number of leaves produced in the crown and that these leaves are shed from the crown at a relatively constant rate and in relation to the rate of leaf production. It was also assumed that as the palm trunk contracts or expands, the marker disc will move only in a horizontal direction, leaving its relative vertical position from the crown unchanged. Individual measurements of palm growth were recorded annually over the 3-year period following placement of the markers.

The basic morphology of each palm was recorded by measurements of crown height, trunk height to immediately below the crown, crown depth, height of the lowest inflorescence scar (see Chapter 7 for description) and circumference of the trunk at 1.5 m above ground (girth). This last measure was not recorded in palms with trunk heights less than 1.5 m. Crown height was defined as the overall height of the palm. Trunk height was defined as the height to the bottom of the crown deemed to be the lowest photosynthetic leaf. All height measurements were determined by trigonometric calculations involving the distance from the palm, measured by a 30 m fibreglass tape, and the angle of elevation, measured with a clinometer. Crown depth was obtained by deducting trunk height from crown height. Trunk circumference was measured with a retractable tape measure to nearest 1 cm.

5.2.4 Basal bulge

The period of trunk growth is the first of two measurements needed to estimate the total age of an individual. The time taken from seedling germination through the expansion of the basal bulge to when a trunk is first formed also has to be determined. Fortuitously, past activities carried out during the recovery of the Gould's Petrel, *Pterodroma leucoptera,* (Priddel *et al.* 1995) provided a series of known-age palm seedlings from which the rates of initial growth could be measured. Palm seed had been removed from the island in early 1992, germinated and replanted within the rainforest as year-old seedlings in late 1993 (David Priddel, personal communication). Of the original 35 palm seedlings planted, 17 were still alive in 1998. The only intervention they had received, which promoted their survival, was a wire enclosure to exclude browsing rabbits. The caging was removed after rabbits were eradicated from the island in 1997 (Priddel *et al.* 2000).

At the commencement of this study the seedlings were 7 years old. They were individually tagged, and from 1999 to 2001 the circumference of the basal bulge at ground level was measured annually and the number of leaves recorded.

When measuring trunked palms the trunk is generally exposed and available for direct measurement. With seedlings no trunk is present, and the measurement at ground level had to be taken over the entire stem of the palm seedling including the petioles. This measurement—the basal bulge—is an over-estimate of the developing trunk and therefore requires a correction factor to be applied to calculate the true developing trunk circumference.

To develop such a correction factor a second group of young palms was examined. This group comprised juvenile palms with newly emerged trunks that were exposed beneath their low crowns. Such individuals are rare, as most recently emerged trunks are generally fully encased in dried petiole stubs which prevent any direct measurement of the trunk. After extensive searches were made of all study sites, 10 juvenile palms with exposed, newly emerged trunks were located within the vicinity of the MB study site. The trunk circumference and the associated circumference of the petioles over the trunk were measured. Leaf numbers were also recorded.

5.2.5 Estimate of time for trunk growth

By partitioning palms into various height classes any variation in growth rate between trunks of different heights could be determined. The height classes chosen were: trunks < 1 m; 1.0 – 4.0 m; 4.0 – 7.0 m; 7.0 – 10.0 m; 10.0 – 13.0 m; 13.0 – 16.0 m; 16.0 – 19.0 m. The size categories replicated those used in a similar study of *L. australis* (Orschegs & Parsons 1996b). Growth rates (GR) were estimated for each height class using the mean annual increment (from three years of data) for each palm in that class at each site. The time taken for a palm to grow through a height class was determined by extrapolating the mean distance grown in one year, over the entire length of the height class (1 m in the case of the lowest height class and 3 m for every other height class). For example, palms in one study site with trunk heights between 4.0 m and 7.0 m, were measured growing at an average rate of 113 mm per annum. This rate was divided into the total distance of the height class — 3000 mm. The resulting figure of 26.5 was the estimated number of years required for a trunk to grow from a height of 4.0 to 7.0 m at this site. The summation of the time taken to grow through each height class provides an estimate of the age of the palm's trunk.

For example:

If trunk height = 8.3 m

Trunk age = (1000 / GR: < 1 m) + (3000 / GR: 1.0 to 4.0 m) + (3000 / GR: 4.0 to 7.0 m) + (1300 / GR: 7.0 to 10.0 m)

While this method ages the trunk of a palm, the time taken for initial trunk development still needs to be added to give the total age of an individual.

5.2.6 Estimate of time for trunk development

After the initial measurement of the basal circumference of the 17 seedlings on CTI in 1999, two annual increments of growth were recorded (in 2000 and 2001). The mean growth increment of all seedlings over both years was determined. From the recently emerged trunks of the 10 juvenile palms, the over-petiole circumference and the direct trunk circumference were also determined. A correction factor was developed to compensate for the over-measurement of stem circumference that included petioles:

$$V / T = f$$

where V = mean over-petiole circumference; T = mean trunk circumference; f = correction factor. The correction factor is the proportional difference between the over-petiole circumference and the actual trunk circumference. It assumes that the proportion of the thickness of the petioles remains constant relative to the trunk circumference when measuring the basal bulge before trunk development.

The correction factor can then be applied to the following formulas to provide the estimated time required to grow from the time of germination (seven years before the seedlings where first measured) until the establishment of the trunk:

$$\mathrm{B} = T - \frac{C}{f}$$

and: Years to trunk establishment = $(\mathrm{B} / S_i) + 7$

where B = the basal bulge; T = mean trunk circumference; C = mean initial seedling circumference; f = correction factor; and $\mathrm{S_i}$ = mean seedling increment.

Using this method to estimate the number of years taken to produce a trunk assumes that the yearly increments from the 7-year old seedlings until the time when the trunk emerges remain constant. It is possible that this was not the case, but the obvious time constraints within the scope of this study restrict such measurements being recorded. In the light of this, the estimated time for trunk development should be seen only as an approximation.

5.2.7 Aging of palms

By combining estimates of the time taken for trunk growth and the estimate of the time taken for basal bulge expansion to produce a trunk from seedlings, the total age of any trunked palm can be estimated.

As part of an attempt to age the palms at each study site, a search was made within the immediate area of each site to locate any palm that was taller than those within each sample. This was to enable an estimate of the tallest and oldest palm at each study site. If such a palm was located the basic morphology was recorded, as with the sampled palms.

5.2.8 Canopy cover

It was assumed that growth rates would vary between sites and were likely to be strongly influenced by the amount of available light. At each of the four study sites canopy cover was measured, to provide a comparison of light penetration to the forest floor. Using a 3.34 megapixel digital camera (Nikon Coolpix 995) with a 38 mm lens, six 1600 x 1200 pixel-sized high contrast images were captured of the canopy cover at each site. The location of each image was randomly selected within the confines of each sampled palm population. The images were used to estimate canopy cover. Each image recorded the canopy cover as a percentage of the total sky that had light blocked out. By obtaining the mean of the canopy cover at each site a comparison could be made between sites.

5.2.9 Changes in the girth of adult palms

As a result of the 1994 fire at RNP all trunks below 9 m in height were heavily scorched and blackened. During the investigations of this study it was discovered that some trunks within the population showed unburnt fibre exposed within vertical fissures. The sampled population of 50 palms at RNP was surveyed to determine the prevalence of this feature. As each palm sampled was part of the population being climbed for the aging study, the whole length of each trunk was surveyed for developing fissures. For palms that showed evidence of the development of new fissures since the 1994 fire, the width of each fissure was measured in a band around the circumference of the trunk 1.5 m above the ground.

5.2.10 Senescence

Where possible, observations were made of the causes of death of adult palms. The period of observation covered not only this 4-year study, but also included the previous six years spent on CTI undertaking other studies.

5.2.11 Analysis

The data were tested for heterogeneity of variances to determine whether transformation was necessary before analysis was carried out (Underwood 1981) using Cochran's test. The relationship between crown height (CH) and trunk height to below the crown (TH) was analysed by linear regression. The attributes of CH and TH were compared across sites in two one-factor analyses of variance (ANOVA). All ANOVAs were calculated using Systat 10 for Windows. Girth was compared between sites by a one-factor ANOVA. Trunk growth across different classes of trunk height was analysed between sites using a replicated two-factor ANOVA. Growth rates were analysed using CurveExpert (Hyams 1995) to determine whether a mathematical predictor could be assigned to the patterns of growth observed. The distributions of results for basal growth increments were non-normal (Campbell & Gardner 1989) and medians and interquartile ranges were applied as non-parametric confidence intervals ($P = 0.05$). An age range was provided for palms, rather than a single definitive figure, because of error estimates on recorded attributes for the different size classes and pre-trunk plants. Leaf production of seedlings used for basal growth increments on CTI and MB was compared using a two-sample *t*-test, with the relationship between leaf production and growth of the CTI seedlings analysed by regression. Crown depth and age at first flowering were compared between sites by a one-factor ANOVA. As part of canopy estimation the high contrast digital canopy images were analysed using Idrisi for Windows (Eastman 1995), a Geographic Information System. Digital JPG images were converted into TIF format. Idrisi then counted the number of cells in each image that had data recorded in them. If the cell contained data of the canopy it was scored as containing an image. If the cell, however, had originally contained data on the sky, or a canopy gap, then the high contrast used in the original capture of the image would render this cell as empty, in contrast to the dark canopy cells. Statistical data were obtained on each image giving the mean of cell values. A higher mean cell value in the image indicated that there were fewer cells in the image containing data and therefore a greater canopy gap. In analysing the changes in trunk girth a regression was used to determine the relationship between trunk height and fissure development. Student-Newman-Keuls (SNK) test was applied in multiple comparison tests with 95% confidence. All statistical tests performed were two-sided unless stated otherwise. Where means are shown, standard errors are included.

5.3 Results

Trunk height (TH) was a good predictor of crown height (CH) (linear regression, $Y = 1.079x + 3.226$, $r^2 = 0.94$, $P < 0.01$). Both TH and CH were significantly different between sites (single factor ANOVA for CH: $F_{3,196} = 8.57$, $P < 0.01$, TH: $F_{3,196} = 4.30$, $P < 0.01$) (Table 5.1). SNK tests indicated that both CH and TH at RNP were greater than at all other sites. Both CH and TH at WNP were similar to MB and CTI. The girth of palms between the four sites was also significantly different ($F_{3,189} = 22.9$, $P < 0.01$). SNK tests indicated that the girths of palms in RNP and MB sites were similar but both were greater than at

TABLE 5.1: The mean, standard error, range and Student-Newman-Keuls (SNK) results for the trunk height (TH), crown height (CH) and girth of *Livistona australis* at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Measurements are in metres.

		CTI	MB	WNP	RNP	Total
TH	**Mean**	6.61	6.56	7.40	9.00	7.40
	S. E.	0.40	0.52	0.59	0.66	0.28
	Range	0.40 – 12.20	0.70 – 12.10	0.60 – 16.25	0.70 – 15.90	
	SNK	b	b	b	a	
CH	**Mean**	10.13	9.98	11.02	13.72	11.21
	S. E.	0.41	0.56	0.65	0.70	0.31
	Range	1.80 – 14.90	2.90 – 16.30	1.50 – 19.20	4.00 – 21.60	
	SNK	b	b	b	a	
Girth	**Mean**	0.67	0.87	0.81	0.90	0.81
	S. E.	0.02	0.02	0.02	0.02	0.02
	Range	0.44 – 0.95	0.50 – 1.10	0.47 – 1.10	0.11 – 1.08	
	SNK	c	a	b	a	

CTI and WNP. The girth was smallest at CTI.

5.3.1 Estimated time for trunk growth

Between 1999 and 2001 data on growth rates were collected from 200 palms across the four study sites (Table 5.2). Insufficient sample sizes in the lowest height class (trunks < 1.0 m) from all sites were due to the relative rarity of small-trunked palms. Small sample sizes in other height classes at sites reflected the relative lack of abundance of each height class within the population sample. The lack of data for height classes above 13.0 m at CTI and MB and above 16.0 m at RNP reflected the absence of these size classes in those samples. Logistic constraints precluded increasing sample sizes within height classes, and it is necessary to be mindful of the consequences of this in interpretation of the robustness of the results. During the course of this study no palm passed from one height class into the next.

Palms of the <1.0 m height class on CTI were extremely rare due to the long-term presence of grazing rabbits. The single palm from this height class at CTI did not record any discernable growth between 1999 and 2001. So that some measure of growth and therefore a time period for trunk development could be assigned to palms growing at this height at CTI, the three years of data from the single CTI palm was pooled with the slowest growing palm from the same height class at MB, where similar growth in all other height classes had been recorded (see SNK result Table 5.2). This probably provides an overestimate of growth rate and underestimate of time for trunk development. Zero annual growth rates for individual palms were not uncommon in some years, with 5% of all annual measurements (*n* = 600) between 1999 and 2001 recording no growth.

Excluding the height classes not replicated in all sites and the height class of trunks < 1.0 m (insufficient sample size; Table 5.2), a significant interaction was found when height class and site were tested in relation to rates of growth (replicated two factor ANOVA, $F_{3,174} = 3.65$, $P < 0.01$). Rates of growth varied according to trunk height, but the manner in which this varied was not

TABLE 5.2: Mean annual growth rates (mm) within height classes for trunks of *Livistona australis* from 1999 to 2001 at four sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Sample sizes in parentheses. Dashes (–) indicate no data.

Height Class	**Sites**			
	CTI	**MB**	**WNP**	**RNP**
< 1 m	28.5 (1)	85.8 (2)	71.7 (2)	579.0 (1)
S.E.	–	28.5	13.9	–
1.0 – 4.0 m	89.9 (8)	71.7 (13)	256.2 (12)	340.0 (11)
S.E.	13.1	13.9	43.6	45.0
4.0 – 7.0 m	134.7 (16)	225.9 (10)	415.0 (10)	425.4 (5)
S.E.	16.0	38.9	50.0	72.2
7.0 – 10.0 m	134.9 (20)	217.8 (14)	425.2 (10)	433.2 (4)
S.E.	10.8	26.4	31.3	42.4
10.0 – 13.0 m	141.6 (5)	230.0 (11)	381.7 (10)	339.6 (21)
S.E.	12.4	23.9	33.4	23.7
13.0 – 16.0 m	–	–	400.6 (5)	296.8 (8)
S.E.			90.7	70.0
16.0 – 19.0 m	–	–	217.0 (1)	–
S.E.			–	

consistent across sites. The general trend was for growth rates to increase with increasing height up to 10.0 m.

There were, however, a few exceptions to the general pattern of growth. The rates of growth in the 10.0 – 13.0 m height classes at WNP and RNP both fell in relation to the rates in two lower classes. Using the estimated growth rates, a comparison can be made of the estimated number of years required for palm trunks to grow through each height class at the four study sites (Figure 5.1).

Palm growth from each site was analysed using CurveExpert (1995). For individual sites the pattern of growth varied, requiring different curve formulas to best describe the data. The growth curves at CTI and MB were best described by an exponential relation ($y = a/1\text{-}e^{-bx}$). For CTI $a = 47.19$ and $b = 0.45$ with an $r^2 = 0.25$. At MB $a = 137.69$ and $b = 0.42$ with $r^2 = 0.51$. WNP had a curve of best fit described under a logistic model ($a / y = 1 + be^{-cx}$) where a = 76.78, $b = 10.65$ and $c = 0.83$ with $r^2 = 0.43$. For RNP no model could be fitted with better than 10% of the data being accommodated in any curve function. From the pooled results from all sites (not shown in the figure) a logarithmic scale provided the best fit ($y = a + b \cdot ln(x)$) where $a = 48.12$, $b = 20.2$, $x =$ height, with $r^2 = 0.22$. The low r^2-value indicates that the curve fit is poor, though it does in part describe, in part, the growth data from all sites.

5.3.2 Estimated time for trunk development

The rate of growth of the basal bulge was based on the mean annual increase of the circumference of 17 monitored seedlings on CTI. The mean circumference of the seedlings at the commencement of the study was 105 mm (s.e. = 19). The mean expansion rate from two years of data was 39 mm per annum (s.e. = 9). The large standard errors indicate that the seedlings had a high degree of variability in circumference and rate of growth with non-normal distributions. Applying medians and interquartile ranges, the developing trunks had median circumference of 85 mm (range = 55 – 120 mm) and a median growth rate of 30 mm (range = 15 – 60 mm).

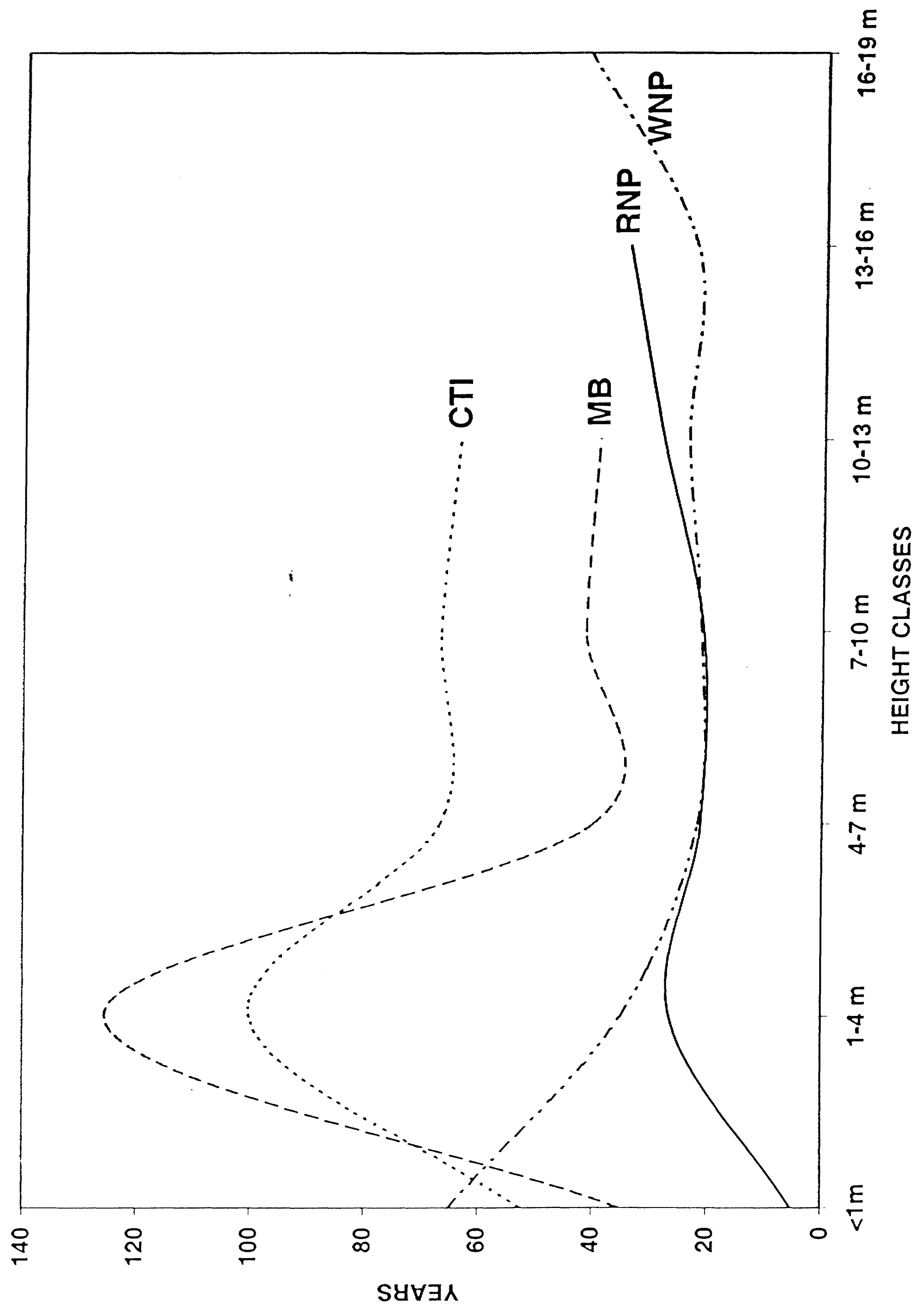

Figure 5.1: Comparison of the estimated number of years required for *Livistona australis* palm trunks to grow through a range of height classes at four sites: CTI, Cabbage Tree Island (dots ····); MB, Mungo Brush (dashes ---); WNP, Wyrrabolong National Park (dots with dashes ···-); and RNP, Royal National Park (solid line —).

Data collected from MB for 10 palms with recently exposed trunks found that the mean over-petiole circumference of the trunk was 1002 mm (s.e. = 63) and the mean trunk circumference was 824 mm (s.e. = 44). The correction factor developed to offset the error from over-measurement of seedling trunk circumferences that included petioles was then applied:

$$V / T = f$$

$$1002 / 824 = 1.22$$

The correction factor can be added to the formula to estimate the time required to grow from germination (seven years before the seedlings where first measured) until the basal bulge develops a trunk:

$$\mathrm{B} = T - \frac{C}{f}$$

$$\mathrm{B} = 824 - \frac{85}{1.22} = 754$$

and: Years to trunk establishment $= (\mathrm{B} / S_i) + 7$

$= (754 / 30) + 7$ years

$=$ 32 years (range 19 - 59 years)

Leaf counts were determined for the 17 known-age seedlings on CTI ($\bar{x}$ = 10.6 leaves, s.e. = 1.2, range = 3 - 21, n = 17) and from MB for 10 palms with recently exposed trunks ($\bar{x}$ = 14.1 leaves, s.e. = 0.8, range = 9 - 17, n = 10) and they were significantly different (two-sample *t*-test t = 2.88, d.f. = 9, P = 0.02). The known-age seedlings did not have crowns that were as well developed as the MB palms, and it is likely that this latter group were older as they had already developed trunks. The number of leaves on seedlings was a reasonable predictor of the increase in circumference recorded over the two years of monitoring (linear regression r^2 = 0.52, P = 0.01). As a palm produces more leaves it is likely that its girth will also increase.

5.3.3 *Aging of palms*

From the combined estimates of the number of years required for palm trunks to grow through each of the various height classes and the time taken for the basal bulge to produce a trunk, the ages of the palms at each study site were calculated. Using this data the estimated age for the tallest palms sampled within the study sites could be calculated (Table 5.3). In addition, within each study site any palm that was taller than those sampled has been included to give an approximate value for the oldest individual at each site.

At MB and RNP taller individual palms were found outside the samples. The tallest palm was located in the RNP, with a crown height of 26.1 m, and an estimated age of 231 – 271 years. The oldest palm within the study site on CTI had an estimated age of 352 – 392 years, with a crown height of 14.9 m. The lower crown height yet greater estimated age of the CTI palm in comparison to the RNP palm reflects the slower observed growth rates at CTI.

Crown depth of reproductive palms varied between study sites (Table 5.4). The sample sizes reflect the number of reproductive palms in each study site. There was a significant difference in crown depth between study sites (one-factor ANOVA, $F_{3,99}$ =12.8, $P < 0.01$). An SNK test indicated that the crown depth was greatest at RNP and smallest at MB and CTI.

Of the 50 palms selected at each study site, not all had reached reproductive age and non-mature palms lacked an inflorescence scar. This resulted in a reduced sample size available for estimating the age of palms at first flowering. The height of the lowest inflorescence scar was recorded as part of the morphological measurements of each palm (see Chapter 7). Utilising both the growth data of trunked palms and the estimated time for the basal bulge to produce a trunk, an approximate age for the first flowering from the four populations was estimated (Table 5.5).

For palms to become reproductive at CTI and MB they need to attain an approximate age exceeding 200 years. Palms in the RNP have been as young as 76 years when they first reproduced. The age at first flowering of palms was significantly different between the four sites ($F_{3,99}$= 238.8, $P < 0.01$). An SNK

TABLE 5.3: The trunk height, crown height and estimated age of the tallest *Livistona australis* within the sampled populations (sample) at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Any palm within the study site that was found to be taller than those in each sample has been included (site). Range of years in parentheses.

Location	Trunk Height (metres)	Crown Height (metres)	Estimated Age (years)	
CTI – sample	12.2	14.9	365	(352 – 392)
MB – sample	12.1	16.4	301	(288 – 328)
MB – site	17.4	19.6	358	(345 – 385)
WNP – sample	16.2	19.2	225	(212 – 252)
RNP – sample	15.9	21.6	168	(155 – 195)
RNP – site	22.7	26.1	244	(231 – 271)

TABLE 5.4: The mean crown depth of reproductive *Livistona australis* at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP) showing standard error and sample size. Student-Newman-Keuls (SNK) results are also shown.

	CTI	MB	WNP	RNP	Total
Mean	3.54	3.45	3.91	4.79	3.88
S.E.	0.12	0.14	0.14	0.26	0.10
n	28	28	22	24	102
SNK	c	c	b	a	

TABLE 5.5: The estimated age of *Livistona australis* at the time of their first flowering at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). The range of age is based on the 95% confidence interval. Standard error and sample size are shown.

	CTI	MB	WNP	RNP	Total
Mean	208	210	152	90	170
S.E.	3.74	4.38	2.56	2.61	5.17
Range	194-235	196-237	138-179	76-117	76-237
n	28	28	22	24	102
SNK	a	a	b	c	

test indicated that the age at first flowering of palms was similar between MB and CTI but significantly greater than at WNP which was greater than at RNP (Table 5.5).

5.3.4 Canopy cover

Measures of canopy cover were collected from the four study sites and analysed to provide a mean cell frequency for each site (Table 5.6). A higher mean cell frequency number indicates less canopy cover.

There was a significant difference in canopy cover between sites ($F_{3,21} = 9.291$, $P < 0.01$). An SNK test indicated that the canopy cover at RNP had a greater cell frequency and therefore less canopy cover than at all other sites. The RNP study site had almost half the canopy cover found at MB, CTI and WNP.

5.3.5 Changes in the girth of adult palms

The survey of palms to identify trunks showing signs of recent expansion was carried out within the study site at RNP (Table 5.7). Within the height range of the palms from which this data was obtained, one palm was within the sample under study but did not show signs of recent fissures (palm N°. 105: CH = 10.1 m, TH = 5.3 m). All palms that showed recent fissures had not yet reached reproductive size. No reproductive palms showed any sign of recent fissure development while 7 of the 26 (27%) of the non-reproductive palms showed fissures. From this it can be concluded that only palms yet to reach reproductive size were capable of expanding their girth, resulting in fissures such as those recorded in this study.

TH was a reasonable predictor of fissure size (linear regression, TH: $r^2 = 0.41$, $P = 0.07$). With a larger sample size it may be possible to show with some confidence that the taller the trunk the less well developed the fissures in the lower trunk were. CH was not a good predictor of fissure size (CH: $r^2 = 0.18$, $P = 0.18$). Palm girth was also not found to be a good predictor of fissure size (Girth: $r^2 = 0.04$, $P = 0.20$).

TABLE 5.6: The mean cell frequency from digital images of canopy cover at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Standard error and sample size are shown. Higher values reflect less canopy cover.

	CTI	MB	WNP	RNP
Mean	44.26	42.12	48.46	75.36
S.E.	5.29	3.17	7.10	3.73
n	6	6	6	6
SNK	b	b	b	a

TABLE 5.7: Measures of fissures within the trunks of *Livistona australis* following fire scarring at Royal National Park. Crown height and trunk height of individuals are also included.

Palm No.	Sum of fissures (mm)	Crown (m)	Trunk (m)
133	23	12.2	6.1
150	65	12.7	6.3
114	69	8.0	5.0
102	75	8.0	3.7
104	88	8.1	3.6
130	118	8.0	3.4
141	131	9.3	4.2

5.3.6 Senescence

Observations made on CTI over 10 years revealed a number of different types of accidents that have led to the death of individuals (Table 5.8). Six incidents were recorded where the subsidence of substrate caused palms to die after toppling over. Occasionally part of the trunk was encased by an arboreal termite nest (genus: *Nasutitermes*) 4 – 7 m above ground. On two occasions it appeared that the weight of the nest had contributed to the palm toppling over. When these termite nests are abandoned and eventually dislodge, their effect on the trunk is clearly visible. Their presence usually creates an indentation or scalloping of the trunk at the point of attachment. On three occasions palms were observed to snap at this weak point. No sign of arboreal termite nests had been recorded from any other palm sites surveyed. It is likely that this feature is unique to CTI, possibly due to reduced host availability due to island confinement of *Nasutitermes* sp. Other forms of trunk wear on CTI were caused by the constant abrasion of adjacent trees, resulting in a localised reduction in trunk diameter. Often the palm survived long after the tree that caused the wear had died and decomposed. One individual was found to have eventually succumbed to the weak point in the trunk and snapped during a period of high wind. Seven crownless adult palm trunks were encountered. These individuals died despite the trunk remaining upright. The apex of the remaining trunk extended to a narrow point just below where the crown had once sprouted. It is almost certain that these individuals had senesced rather than been killed by accident.

5.4 Discussion

This study shows that the size of the crown of *L. australis* is strongly correlated with the height of the trunk. The taller the palm the larger the crown. The overall size that an adult palm can reach was strongly influenced by the environment in which it was growing. The most sheltered site within this study was RNP within the deep valley of the Hacking River. The adult palms here were taller, had larger crowns and were of larger diameter than palms within

TABLE 5.8: Senescence and death by accident of adult *Livistona australis* on Cabbage Tree Island from 10 years of observations.

No. of Palms	Cause of death
6	Toppled from subsidence
2	Toppled from weight of termite nest
3	Snapped at narrow wear point from old termite nest
1	Snapped at narrow point from previous branch wear
7	Death of crown

any other site studied. The converse of this situation was the site at CTI.

On this exposed offshore island the adult palms had the lowest canopy height, the smallest crowns and the narrowest trunks. CTI also receives the least annual rainfall of the four sites studied (see Chapter 6). Further work is needed to fully understand the mechanisms involved in the relationship between palm morphology and environmental factors such as rainfall, soil type, depth, associated vegetation and exposure to wind.

5.4.1 Estimated time for trunk growth

This study describes a technique to determine the growth rates of palms by taking a repeated series of measurements immediately below the crown. This estimate of growth looked at a range of trunk height classes and was therefore more accurate than rates based on leaf scar frequency in the lower sections of the trunk. The method used in this study for measuring the expansion of the basal bulge leading to trunk development in palms was not entirely satisfactory. Only the chance availability of known-age seedlings growing *in situ* provided an opportunity to gain valuable data to estimate the time taken for this process to occur. Future studies will need to look at long-term data collection of a range of known-age seedlings to obtain accurate measurements of this process.

The development of a method to accurately measure trunk growth is of prime importance if populations of palms are to be adequately managed. From this study it was found that trunk growth showed substantial variation between the different sites. While the sample size for palms at one metre trunk height was very small, the divergent curves for the next largest size class, with a larger sample, maintained the variation seen between the populations (Figure 5.1). This variation was most prevalent during the period of trunk formation and prior to trunked palms reaching reproductive height. The divergent curves in the smallest size classes may be the result of small sample sizes (Figure 5.1), however the estimate of years for growth within the pre-reproductive palms provides some insight into the differences between the populations. The slowest overall growth rates were on CTI. Once the palms there had reached 1 m in height they averaged 25 years for the production of each subsequent metre in trunk height. In contrast, the fastest rates of growth were in WNP and RNP. At these two sites 1 m palms averaged 9 years for each subsequent metre of trunk growth. These rates are considerably slower than those estimated in a previous study of *L. australis* of 1 m every 6 years (Orscheg & Parsons 1996b) or for *L. mariae* of 1 m every 5 years (Latz 1975). The discrepancy in the rates of growth between the studies is related to the differing techniques used to obtain them. Orscheg and Parsons (1996b) based their predicted growth rates on leaf-scar frequency in the lowest section of palm trunks and annual leaf production of adult palms and therefore, did not take into account any variation in leaf production at different heights. Latz (1975), studying a different species, used photographs from two distinct periods to determine rates of growth for palms and used features of cliffs in the background of the images to determine changes in height. *L. mariae* may either have a faster rate of growth than *L. australis* or by not basing the rates of growth on direct measurements, the calculation may have given inaccurate results.

The slow growth rates recorded at CTI may be the result of poorer growing conditions on the island relative to the other sites. The rainfall there is lower, the soils skeletal, the vegetation has exposure to salt spray not found at other sites, and the winds are probably stronger than on the mainland. Similar observations of slow palm growth in harsh environments have been made in other studies (Orscheg & Parsons 1996b; Hnatiuk 1977).

Rates of growth at RNP were far in excess of all other sites for palms with trunks under 4 m (Table 5.2). The factors influencing these high rates of growth may be related to the structure of the forest, which allowed a greater level of light to penetrate to the forest floor compared to the other study sites. This site had significantly less canopy than at other sites studied (Table 5.6), and had also been burnt more recently and more frequently than any of the other sites. It can be argued that frequent fires have significantly changed the structure of this forest. The palms in the lower height classes here might have responded to this change by increasing their growth rates relative to the other sites studied

(Table 5.2). The dynamics of several species of tropical palms appear to be driven by the occurrence of light gaps within the forest canopy (Vandermeer *et al.* 1974). As an example, *Balaka microcarpa*, an understorey palm in Fiji, had faster growth rates under gaps in the tree canopy than those in shade (Ash 1988). It is to be expected that any small palm exposed to increased light level through a newly formed canopy gap would respond by elevated rates of growth. In the RNP it was not a single gap that had opened up but a forest-wide change in the canopy, brought about by frequent fires, that resulted in a widespread increase in light penetrating to the forest floor. It is probable that the 1994 fires resulted in the death of a number of mid-storey species (e.g. *Acacia* spp.) that take greater than 10 years to recover stature and close-up the mid-canopy (Tony Auld, personal communication). In this case it would be expected that the growth rates recorded will decrease from their current levels to reflect a decrease in light penetration.

After the most recent fire in the RNP (in 1994) 75% of palms smaller than 9 m at one particular site had all of their existing leaves killed without causing the death of any individuals (Orscheg & Parsons 1996b). This is regarded as a low-intensity fire (Gill & Moore 1997) which ultimately removed leaves from the lower palms and stimulated leaf growth. The total leaf numbers recorded at the RNP site (Chapter 7, Table 7.10) for palms with trunks < 1 m and between 1.0 and 4.0 m were much higher than at all other sites. Greater leaf numbers would increase the photosynthetic abilities of a palm, giving rise to the increase in growth rates recorded in this study. This study has shown that leaves remain in the crown for at least 5 years, and in younger palms possibly much longer (see Chapter 7, Section 7.3.2). At the completion of this study only 7 years had elapsed since the most recent fire in the RNP. The effects of this were still evident in the smaller trunked palms by way of high leaf numbers and accelerated growth rates when compared to the other sites in this study.

Despite the variability, it is clear from the study that once palms reach a height of greater than 4 m growth rates remain relatively constant throughout their adult life stage. The onset of this regular growth rate occurs at approximately the same time as reproduction first begins (See Chapter 7, Table 7.10).

High variability in annual growth rates is a feature of many long-lived tropical trees, including palms (Lieberman *et al.* 1988; Enright 1992). Consequently, it is acknowledged that the three years of data collected on growth rates in this study may not reflect the total variability in growth throughout the life of a palm. The estimation of age based on growth rates, therefore, will always be subject to some degree of error due to the high variation in rates of growth between years.

5.4.2 *Estimated time for trunk development*

The most difficult aspect of estimating the growth rate of palms was determining the rate of growth of the basal bulge that eventually produces a trunk. The use of seedlings planted a number of years before this study commenced greatly assisted in this estimation. The time taken for a trunk to form was estimated at 32 years (range: 19 to 59 years). While the lowest figure is comparable to estimates from other Australian studies on this genus (20 years, Orscheg & Parsons 1996b; 22 years, Hnatiuk 1977), the mean and higher end of the range are more consistent with overseas studies of other genera (59 years, McPherson & Williams 1996; 52 years, Enright & Watson 1992; 29 to 38 years, Anderson 1983).

5.4.3 *Aging of palms*

The ability to age palms is essential to developing management strategies for the safeguarding of any species that is considered threatened. Six species of *Livistona* are threatened within Australia (Rodd 1998) because they occur as either naturally isolated populations or their populations are now reduced and fragmented by extensive clearing. A common species like *L. australis* also has populations that are considered to be threatened. The Cabbage Tree Creek stand of *L. australis* in eastern Victoria, for example, is the only natural population of palms in that State (Conn and Walsh 1994). In a broader context the aging of palms has been used to determine environmental events that affect forest communities (Sarukhan *et al.* 1985). Palm trunks that have been bent to the ground by falling branches or trees, then regrown to an upright position, record stochastic events. When this is evident on a broad scale the dating of such events can lead to the understanding of regeneration within forests following significant disturbances to the canopy. Additionally, the presence of even-age stands of palms can be used to date major events within a forest that led to their establishment, such as high intensity fires.

This study has provided the most accurate technique for aging *L. australis* and similar species. The results indicate that *L. australis* is a long-lived species that is likely to require periods in excess of 150 years following germination to grow to reproductive age. Palms older than 300 years are commonplace and individuals approaching four centuries may well be possible under some circumstances. Aging of *Livistona* using a range of other techniques has indicated that they are much younger than this study has determined (25 m *L. mariae* was 100 – 300 years old, Latz 1975; 8 m *L. eastonii* was 280 years old, Hnatiuk 1977; 18.3 m *L. australis* was 132 years old, Orscheg & Parsons 1996b). If these studies were to reassess the ages of the palms in question it is highly likely that they would be much older than previously estimated.

In general, the height of an adult palm is not a good indicator of its age. The tallest palms in the study were in RNP but these were also determined to be the youngest. Height may be used to determine relative age between individuals in a single population but cannot be extrapolated to palms growing under different environmental conditions.

Crown depth was found to vary between study sites (Table 5.4). The increased crown depth at RNP may have been the mechanism by which faster rates of growth were recorded here. It was also found that the number of leaves in the crown was also significantly greater here than at the other sites (see Chapter 7, Section 7.3.9). Further research is necessary to determine the influence of the environment on crown size of palms.

From the sites chosen the rate of growth increased with increasing latitude, but the limited sample size precludes any prediction of definitive trends here. This trend may well be confounded by sampling sites of lower rainfall, poor soil fertility or with higher exposure. If any trends from latitude are to be explored then palm populations within forest gully sites may provide the best examples for comparison.

5.4.4 *Changes in the girth of adult palms*

While most of this study has concentrated on the vertical growth of *L. australis* there was also some evidence to suggest that expansion of the lower trunk occurs in individuals prior to reaching reproductive height. The absence of vertical fissures in reproductive palms suggests that this process does not occur subsequent to first flowering. The development of fissures probably occurs well before the palms reach reproductive height, but larger sample sizes are needed to clarify this aspect. It is likely that the swelling provides greater structural strength in the lower trunk. Such strength is needed by reproductive palms to not only support the weight of the upper trunk and larger crown, but also to support the additional weight of high fruit yields (Chapter 7). Further studies into the cell structure of palm trunks may uncover more detail as to the physiological explanations for this process.

5.4.5 *Senescence*

The process of senescence and death in natural populations of palms has never been studied in detail. Most observations have been restricted to cultivated palms. From studies in these environments the mechanism that leads to thinning, impoverished crowns in the tallest of palms and eventual malfunctioning in vascular bundles that transfer nutrients throughout the plant, has been documented (Tomlinson 1990). This is natural senescence, and the dead palm is characterised by the remaining trunk tapering to a narrow apex, where once the crown grew. From this study it is known that some palms in natural populations do survive long enough to reach this critical point.

This study reported several causes of adult mortality. The sloping rock-scree on CTI (Fullagar 1976) contributed to several deaths through the occasional subsidence of the substrate. *L. mariae* was also found to be prone to death from toppling following scouring of the surrounding soil (Latz 1975). The attachment of a termite nest, a dark and carton-like structure (Watson & Gay 1991), does not lead to the infestation of the trunk wood. Having a pithy core, the Palmae are not susceptible to internal attack. The sheer weight of these structures, however, may have caused some palms to topple. The mechanical effect of wear from the termites' presence may also have caused some palms to snap their trunk at the point of attachment. Some individuals managed to survive despite termite damage accounting for the loss of more than 75% of the trunk at the original point of nest attachment. These individuals were generally located among the expansive canopies of Deciduous Figs, *Ficus superba,* where they were protected from winds and extensive lateral movement.

From other studies it appears that accident from structural failure rather than senescence (Tomlinson 1979) determines the life span of a palm (Pinero *et al.* 1984; Enright 1992). Accidental deaths, accompanied by the immediate collapse of a trunk, are easily observed, as the results are dramatic. Palms that die through senesence or *in situ* require careful observation to be detected.

5.4.6 Conservation of palm populations

For the conservation of small populations it is likely that the removal of large reproductive individuals for commercial planting would not be sustainable. The yield of adult palms within most populations would be very slow. The recovery from harvesting of reproductive adults that leaves only the smaller, non-reproductive palms behind, would take many decades or possibly as long as a century to occur. This action may well be detrimental to the survivorship of that population, increasing the chance of its local extinction.

6. The structure of four Cabbage Tree Palm, *Livistona australis,* populations

Abstract

The structure of four Cabbage Tree Palm, *Livistona australis*, populations was examined; Mungo Brush (MB), Wyrrabolong National Park (WNP), Cabbage Tree Island (CTI) and Royal National Park (RNP). The mean seedling density was higher at MB (0.70 m^2, s.e. = 0.13) and WNP (0.55 m^2, s.e. = 0.17) than at CTI (0.05 m^2, s.e. = 0.02) and RNP (0.08 m^2, s.e. = 0.02). MB had a greater density of seedlings with 6 or more leaves ($P = 0.01$) compared to all other sites. The larger seedling classes (> 4 leaves) were missing from CTI as a result of the European Rabbit, *Oryctolagus cuniculus* , which occupied the island from 1906 until their eradication in 1997. The low density of seedlings at RNP may have been the result of two fires in the last 14 years and possibly grazing. Rainfall differed between sites ($P = 0.01$), but the small number of sites precluded using rainfall as a predictor of seedling density with any confidence. The distribution of size classes based on trunk height differed between the four sites. WNP, a disturbed site, had a similar population structure to the undisturbed site of MB. RNP, also a disturbed site, possessed relatively few individuals within the 1-10 m height class and a concentration of trunked palms in the 10-13 m height class. This indicated a complex history of disturbance beyond known records. Despite the presence of rabbits at the CTI site there was no significant difference between palm height here and at MB ($t_{(2)49} = 0.153$). It maybe that growth estimates for small palms (Chapter 5) may not be accurate and the impact of this grazing has yet to become apparent at this site.

6.1 Introduction

Population studies are important in understanding the dynamics of palm demography, particularly with regards to long-lived species such as *Livistona* (Hnatiuk 1977; this study Chapter 5). Problems in recruitment may take many years to become evident in long-lived species and the remedial effort needed to address imbalances within populations maybe difficult to effect. As an aging population begins to decline due to senescence it further reduces the ability of the population to be self-sustaining. Isolated palm populations, which have little chance of additional seed arriving from other sources, are particularly vulnerable to local extinction. Few studies have examined the structure of palm populations (Hnatiuk 1977; Savage & Aston 1983; Pinero *et al.* 1984; Sarukhan *et al.* 1985; Orscheg & Parsons 1996b; Barot & Gignoux 1999; Matos *et al.* 1999; Williams *et al.* 1995; Barot *et al.* 2000). This is despite many of the 2800 species within this particular sub-class of plants (Palmae) being ideal subjects for demographic studies (Tomlinson 1979). Two studies of population structure from the genus *Livistona* have been reported (Hnatiuk 1977; Orscheg & Parsons 1996b).

Livistona australis is found in the wetter coastal forest of Australia's East Coast. Throughout most of Queensland and in New South Wales to the Illawarra, south of Sydney the species is common, but becomes less so from this point south through to Victoria. The southern half of the range of *L. australis* is characterised by fragmented and isolated populations (Brooks 1993). These outlying populations are genetically similar to populations within the main geographic range of the species and their current distribution is a legacy of warmer and wetter palaeoclimates (Orscheg & Parsons 1996a). The conservation of these isolated stands may be difficult to effect without a better knowledge of the population dynamics of *L. australis*.

This study looks at the structure of four populations of *L. australis* based on plant size. It considers the impact of a range of disturbance factors on the structure of these populations and draws conclusions regarding their long-term viability under current management regimes.

6.2 Methods

Four populations of *L. australis* within coastal New South Wales (NSW) were studied. They were, north to south: Mungo Brush (MB), in Myall Lakes National Park on the mid-north coast; Cabbage Tree Island (CTI), offshore from Myall Lakes National Park; Wyrrabolong National Park (WNP), north of Gosford; and The Royal National Park (RNP), south of Sydney (see Chapter 2 for description). The MB site was considered to have the longest period free of disturbance in comparison to the other three sites. Fire had not encroached on the rainforest for more than 100 years and the site was not known to be under grazing pressure from exotic herbivores. The palm population at this site was used as a control for seedling density and the frequency of trunked palms.

All palms without an aboveground trunk were considered seedlings. The *L. australis* populations were divided into 13 size classes based on structure: 1 leaf seedlings; 2-leaf seedlings; 3-leaf seedlings; 4-leaf seedlings; 5-leaf seedlings, ≥ 6-leaf seedlings; trunks < 1 m; trunks 1.0 – 4.0 m; trunks 4.0 – 7.0 m; trunks 7.0 – 10.0 m; trunks 10.0 – 13.0 m; trunks 13.0 – 16.0 m; and trunks 16.0 – 19.0 m. These categories follow those used in other studies (e.g. Orscheg & Parsons 1996b).

6.2.1 Seedling density

A random point was selected at each of the four sites (see Chapter 2). From this point a 30 m transect was laid out in a random direction and 10 randomly selected quadrats (2 m x 2 m) were sampled along its length, without overlap. All palm seedlings within each quadrat were measured for total height and leaves were counted. Three additional transects running parallel to the first, each separated by a 10 m interval were also sampled. Therefore, each site had 40 samples (4 transects each containing 10 quadrats) comprising a total area of 160 m^2. Seedling density was calculated by dividing the number of seedlings from each of the six seedling size classes by the area of each plot (4 m^2). Leaf number from the five smaller size classes was used as a surrogate for approximate age (see Chapter 4). Several attributes were recorded at each site: rainfall, aspect, slope, associated vegetation communities, and evidence of disturbance such as fire or grazing. Data for CTI was collected in April 2000, for WNP in July 2001, and for MB and RNP in August 2001.

6.2.2 Relative frequency of trunked palms

At each study site the height of exposed trunks (trunked palms) was measured for a sample of 50 individuals. From a random point in each population the first 50 trunked palms encountered on a random walk were selected (see Chapter 5 for criteria). The sampled area at each site was estimated to be 400 – 600 m^2. It was assumed that the selected palms reflected the relative abundance of each trunk-height size class at each site. These samples were also used in studies of the rates of trunk growth, and the flowering and fruiting frequency of adult palms (see Chapters 5 & 7). Palm height was measured according to the method outlined in Chapter 5. The population structure was classified by the seven height classes of trunked palms (Section 6.2). Using information gained from aging techniques based on rates of growth (see Chapter 5), the approximate ages of each height class were estimated.

Rainfall data were sourced from locations as near as possible to the study areas and were collated from a variety of sources. Data for MB and CTI were determined from 10 years (1988–1997) of records from Hawkes Nest and seasonal records (1993–1997) from CTI (Chris Patterson, Priddel & Carlile unpublished data) (see Chapter 2 for explanation). WNP rainfall data was from 8 years (1991–1999) of records from Munmorah State Recreation Area (NPWS unpublished data). Rainfall records for RNP covered 17 years of data collected between 1979 and 2000 (Audley, Commonwealth Bureau of Meteorology unpublished data).

6.2.3 Analysis

Seedling density between each of the six size classes based on leaf number was analysed using one-sample *t*-tests. Rainfall was analysed using one-factor analysis of variance (ANOVA). The correlation between the mean annual rainfall and the mean seedling density was analysed. Student-Newman-Keuls (SNK) was applied in multiple comparison tests with 95% confidence. All statistical tests performed were two-sided unless stated otherwise. Where means are shown, standard errors are included.

6.3 Results

6.3.1 Seedling density

The mean seedling density from all sites was 0.37 m^2 (s.e. = 0.07) (Table 6.1). Seedling density was similar at MB and WNP. These were both greater than seedling density at RNP and CTI, which were similar. The density of *L. australis* seedlings of each size class (i.e. leaf number) appears in Figure 6.1. All size classes were present only in the MB and WNP samples. Seedlings with three leaves were absent at RNP and with five or more leaves were absent at CTI. The absence of the 3-leaf size class at RNP was probably a chance event of sampling in a population where densities were low for seedlings with more than two leaves. The missing classes in the CTI sample probably reflect an absence in the population of seedlings with more than four leaves. CTI has only recently reverted back to a mammal free island. The eradication of rabbits, 2.5 years previously, has removed the effect of rabbit grazing on seedlings. Of all four sites examined, seedlings at RNP were the only plants to show evidence of grazing, with associated scats identified as being that of Rusa Deer, *Cervus timorensis.*

One-sample *t*-tests were applied to the results of the seedling density data (Table 6.2). When comparing sites there were significant differences in the seedling density in all six size-classes. MB had a significantly greater density of seedlings with six or more leaves compared to all other sites. This indicates

Table 6.1: Mean density (m^2) of *Livistona australis* seedlings at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Student-Newman-Keuls (SNK) results are also shown.

	CTI	MB	WNP	RNP	Total
Mean	0.05	0.70	0.55	0.08	0.37
S.E.	0.02	0.13	0.17	0.02	0.07
Range	0.00 – 0.25	0.05 – 2.60	0.00 – 3.35	0.00 – 0.40	0.00 – 0.40
Total plants	16	339	265	41	661
SNK	b	a	a	b	—

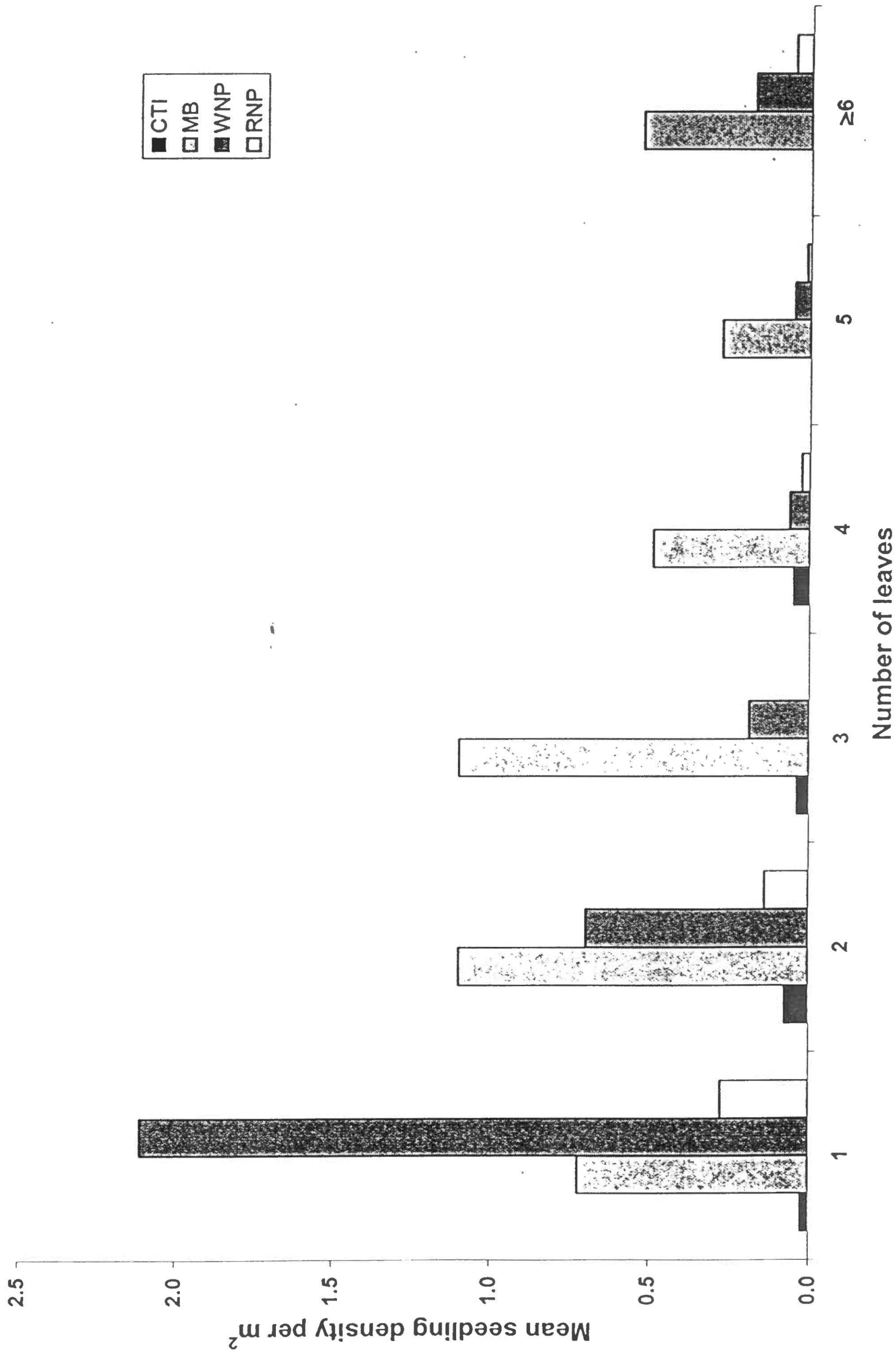

Figure 6.1: Comparison of seedling density of *Livistona australis* in each of six size classes (based on leaf number) at four sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP).

Table 6.2: One-sample *t*-test of the mean density (m^2) of *Livistona australis* seedlings of six size classes at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Underscored *P*-values indicate a significant result (*P*<0.05) for comparisons between sites within each size class. Student-Newman-Keuls (SNK) results are also shown. Dashes indicate no data for a size class.

		Number of leaves					
		1	**2**	**3**	**4**	**5**	**≥ 6**
CTI	***t***	- 52.58	-7.19	-12.26	-2.12	—	—
	P	< 0.01	< 0.01	< 0.01	0.12	—	—
	SNK	c	c	b	b	—	—
MB	***t***	- 0.23	1.50	1.53	1.13	1.97	5.36
	P	0.83	0.23	0.22	0.34	0.14	0.01
	SNK	b	a	a	a	a	a
WNP	***t***	3.08	0.65	- 1.40	- 1.50	- 0.68	- 0.15
	P	0.05	0.56	0.26	0.23	0.54	0.89
	SNK	a	b	b	b	b	b
RNP	***t***	- 9.78	- 7.09	—	- 5.24	- 5.72	- 6.76
	P	< 0.01	0.01	—	0.01	0.01	< 0.01
	SNK	b	c	—	b	b	b

that the site has the greatest potential to recruit individuals into the adult population when senescence or accident occurs, creating canopy gaps. WNP had a significantly greater seedling density in the 1-leaf size class compared to all other sites. The more open understorey at WNP compared to MB may account for this higher density. These data, combined with the low seedling densities at the latter sites indicate that site characteristics and/or disturbance factors are reducing seedling survival.

Rainfall was significantly different between study sites (one-factor ANOVA: $F_{3,40} = 4.61$, $P = 0.01$) (Table 6.3). SNK tests revealed that rainfall for RNP and WNP was similar and significantly greater than CTI, but less than MB. There was a high correlation between mean annual rainfall and seedling density (correlation: $r^2 = 0.85$, n = 4), but the sample size of study sites was too small to have any confidence in this result. It is possible that seedling density was influenced more by the disturbance history of each site than by mean annual rainfall.

6.3.2 Relative frequency of trunked palms

Size structure at the four study sites was compared (Figure 6.2). CTI and MB lacked palms above 13 m. The difference in maximum palm height between the four sites reflected the overall height of the surrounding forest canopy with the eucalypt forest at WNP and RNP being taller than the rainforest canopies of CTI and MB. The variation between the soils of each site was not considered to be a factor in the structural differences between these palm populations although this was not tested. In general the influence of exposure due to topography, associated vegetation and the level of precipitation has a more dominant influence on *L. australis* populations (Rodd 1998). The evaluation of trunk height frequency between sites is constrained by limited sample size in each size class. At MB the relative frequency of the size classes of trunked palms above 1 m was similar. It is assumed that this population structure is a consequence of low disturbance at the site for greater than 100 years (see Chapter 2). The relative frequency of trunked palms at WNP over the same size classes showed a similar structure to MB. A small proportion of this

Table 6.3: Mean annual rainfall (mm) at four study sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); Royal National Park (RNP). Student-Newman-Keuls (SNK) results are also shown.

	CTI	MB	WNP	RNP
Mean	924.2	1422.1	1155.2	1125.3
S.E.	75.6	166.1	96.3	52.1
Range	600 - 1349	924 - 2075	784 - 1464	631 - 1669
n	11	11	8	17
SNK	c	a	b	b

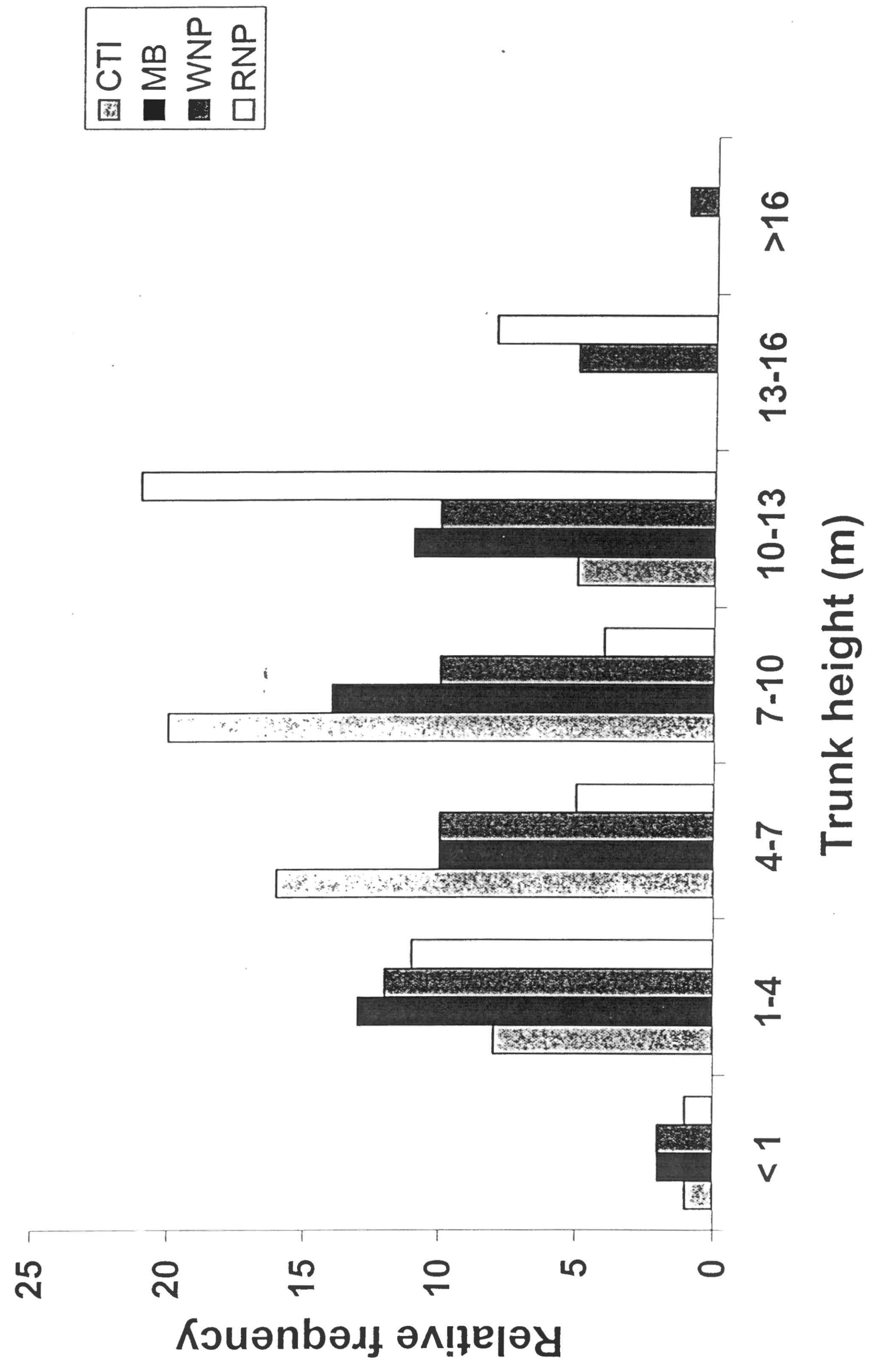

Figure 6.2: The relative frequency of 50 trunked *Livistona australis* in each of seven height classes at four sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP).

population was taller than palms at MB (12%). This reflected the sheltered characteristics of this forest site, providing opportunity for some individuals not overtopped by the dominant Eucalypt canopy to obtain greater height. These higher size classes were less frequent when compared to the lower classes. At RNP the relative frequency of trunked palms contrasted with both MB and WNP. There was relatively few palms between 4.0 - 10.0 m. Palms above 10.0 m were the most common at this site (56%). This structure is the result of a complex disturbance history in which the intervals between fire frequency may be only one part. A comparison of CTI and MB showed that there was a correlation between palm heights ($r^2 = 0.861$) and there was no significant difference between heights at these sites ($t_{(2)49} = 0.153$).

6.4 Discussion

The population structure at each site was different, presumably reflecting differing environmental factors and histories of disturbance. Each population is considered separately.

6.4.1 Mungo Brush (MB)

Compared to all other sites MB had the highest density of seedlings (0.7 per. m^2, Table 6.1) and in all size classes except single-leaf seedlings (Figure 6.1). Low survival rates had been recorded at this site for seedlings aged between12 and 30 months old (Chapter 4). The low number of single leafed seedlings may have resulted from competition for resources between these and the more established seedlings. It may also have been indicative of a population that was stable. It was estimated that in stable populations of the Cabbage Palm, *Sabal palmetto,* only 3% of all seedlings developed an above-ground trunk (McPherson & Williams 1996). The Fijian understorey palm *Balaka microcarpa* suffered seedling age class mortality of 99.8 to 99.9% in undisturbed rainforest over a 15-year period (Ash 1988). MB had the highest density of seedlings with $\geq$ 6 leaves compared to all other sites (Table 6.2). This seedling class included individuals with emerging trunks (up to 35 years of age; Section 5.4.3) and indicates this population was showing the greatest potential to replace adult palms. The overall population structure at MB suggests a stable palm forest that has the ability to recruit future reproductive palms from a large pool of established seedlings.

6.4.2 Wyrrabolong National Park (WNP)

Overall seedling density at WNP was high and similar to that at MB. The relatively low occurrence of older seedlings with ≥ 6 leaves when compared to MB however, is cause for concern if MB represents a stable population capable of recruitment should the opportunity arise. At WNP this low occurrence of older seedlings, those with ≥ 6 leaves, may reflect repeated disturbance by fire in the recent past. The palm forest at WNP shows a high prevalence of vine tangles and invasion by Bracken Fern, *Pteridium esculentum,* indicating disturbance of this site by fire (Duncan & Isaac 1986). The time elapsed since the regular encroachment of fire into the rainforest until the early 1980s (Lyons 1984) is of sufficient length to currently not have reduced general seedling density (Table 6.1) which is similar to that of the undisturbed site at MB.

The structure of trunked palms at WNP was similar to that at the undisturbed site at MB and indicates that there has, as yet, been no measurable effect on trunked palms from the known history of disturbance at WNP. The palm population at WNP appears viable in the long-term provided that the invasive Bitou Bush, *Chrysanthemoides monilifera,* continues to be controlled within the rainforest to reduce it's ability to smother any regeneration.

6.4.3 Cabbage Tree Island (CTI)

The seedling density of *L. australis* was lowest on CTI (Table 6.1). This is a consequence of rabbits grazing on palm seedlings (Priddel *et al.* 2000, Chapter 4). Seedlings that were not caged from the effects of rabbit grazing had a survival rate less than half that of protected seedlings at 30 months since germination. The absence of seedlings with more than 4 leaves indicate that seedlings surviving since rabbits were eradicated (1997) have not yet grown to this size. Plants of more than 4 leaves are estimated to be older than 4 years (Chapter 4). Clearly, the process of regeneration of the vegetation on CTI has only recently commenced and will take many years to complete.

Rabbits may have also affected the age structure of trunked palms. Rabbits were present on CTI for 90 years (Priddel & Carlile 1997) and substantially reduced seedling survival and recruitment. From the known rates of growth at this site, the lower seed density would eventually have an impact on recruitment. This would be evident in the number of seedlings with more than 4 leaves (see Chapter 4), trunked palms < 1 m and trunked palms 1.0 – 4.0 m (see Chapter 5). In the random sample of trunked palms chosen for this study the frequency of size classes did not show an increasing dominance towards the taller palms (Figure 6.2). It maybe that the estimated age of small palms on this island (Chapter 5) is an underestimate and such differences are yet to become apparent.

The absence of palms greater than 13 m in height indicates the influence of topography. Exposure to high winds prevents the vegetation at this site reaching the height attained in more sheltered sites (e.g. RNP). On CTI, palms taller than 13 m grow only among associated vegetation on the deeper soils, where they generally do not dominate.

When seedling density was measured in 2000 it showed one seedling for every 20 square metres. While not measured again in 2001 it was observed that seedling density, though patchy, appeared to have increased substantially. The lower rainfall at CTI, when compared to the other three sites, may have some influence on seedling density by reducing survival, however, this is far from clear. In the period of this study, germination (see Chapter 3) and seedling survival (see Chapter 4) has been favourable. Further research is necessary to clarify this. It would seem that the recovery of this palm population from such a sustained period of disturbance may well be possible providing any new disturbance, such as fire, can be excluded for many decades.

In light of these and other results (Chapter 5), the specific case of the palm population on CTI raises a number of points. The reduction in recruitment of palms due to rabbit browsing over the 90 years prior to 1997 had the potential to substantially affected the survival of the population. It is likely that short-lived species have been eliminated from the floral composition of this site due to the effects of rabbits (Werren & Clough 1991). If it had been found that palms were short-lived, the 90-year hiatus in their regeneration may have been sufficient to create a significant gap in regeneration. This loss in potential recruitment of a major forest component may have been detrimental to the survival of the rainforest, as the current canopy would eventually begin to break-up through a process of senescence and storm damage. Now that it has been established that palms are long-lived, the probability of significant decline to the rainforest itself is reduced. The recent seedling recruitment will take up to 200 years before individuals reach reproductive age. Palms currently within the lower height classes of the reproductive population, however, may well continue to reproduce until the more recent recruits are able to replace them, ensuring unbroken recruitment into the population.

6.4.4 *Royal National Park (RNP)*

Seedling density at RNP was low when compared to the other two mainland sites. The lower occurrence of seedlings with ≥ 6 leaves relative to MB may reflect repeated disturbance by fire over recent years, from which few individuals have survived. The prevalence of grass dominated cover within this wet forest indicates that repeated fires have altered the structure and floristics of the ground stratum. Density of palm seedlings can be strongly influenced by competition for light from ground covers. The fire-induced dominance of the fern *Calochlaena dubia* at a site in Victoria was considered to have contributed to the dearth of palm seedlings there (Orscheg & Parsons 1996b). Palm seedling density can be reduced by grassy ground covers when compared to that within undisturbed palm forest (Bonilla & Feil 1995). Palm seedlings being displaced by grasses may have caused the low seedling density at RNP (Table 6.1). There was some anecdotal evidence to suggest that the introduced Rusa

Deer, *Cervus timorensis*, grazed seedlings. It is not known to what extent these mammals have influenced seedling density.

The structure of populations of trunked palms at RNP possessed few individuals within the 1.0 – 10.0 m height classes and a concentration of trunked palms in the 10.0 – 13.0 m height class. This indicated a complex history of disturbance beyond known records. A major site disturbance such as logging may have produced an even age population in the past and the cohort is now at canopy height. It is not known what frequency or intensity of fire is needed to bring about structural change within palm dominated vegetation. The recent fire history of two fires in the last 13 years may be too frequent for seedling survival, while favouring grasses. For long-term population stability at RNP, fire frequency may need to be moderated in some way to allow sustained recruitment. This is particularly relevant when other disturbance factors, such as an introduced mammal species, may be further reducing seedling survival.

7. Flowering and fruiting ecology of the Cabbage Tree Palm, *Livistona australis*

Abstract

This study aimed to better understand the reproductive functioning of *Livistona australis* by looking at four disjunct populations of varying latitude. For the first time details of the reproductive ecology of *L. australis* were measured at the four sites over four years. Frequency of flowering was variable between years, with a mean of 32% of mature plants flowering annually but appears consistent between sites within years. The frequency of flowering did not vary in relation to trunk height. The species is moderately to strongly monoecious (< 4% hermaphroditic) and males produce fewer inflorescences than females. Frequency of flowering, rates of growth and leaf production were not influenced by the gender of the palm. Over a six-year period the mean time between flowering was approximately once every two years (1.84 years) although 25% of palms flowered in consecutive years. During the study, 10% of all adults of reproductive age sampled failed to reproduce. *L. australis* flowers and fruits extensively all within a period of 12 months but the period of fruit fall may last a further six months. Frequency of fruiting was highly variable between sites with an annual mean of 21% over three successful seasons. Production of fruit did not vary in relation to trunk height among adult palms. One in seven palms suffered some fruit loss due to insect and fungal attack but the losses were rarely severe. Widespread failure of flowering in 1999 and therefore fruiting in 2000 affected a substantial proportion of all *L. australis* palms in central and southern New South Wales, the causes of which were unknown. This reproductive failure was followed by a season of above-average flowering and fruiting that indicated a tendency for masting within local populations. The reproductive synchrony recorded within populations may have been supported by the accumulation of starch and assimilates necessary to produce a mast crop, during the years of non-flowering. The crowns of adult palms contain leaves amassed over 5 years of growth but juveniles may take as long as 50 years to replace all leaves in their crowns. Leaf production was correlated

positively with trunk height and steadily increased after development of the basal bulge until reproductive age was reached. Fire may increase leaf production immediately following the event but long-term effects of this disturbance are unknown. The recognition and identification of flowering scars on the trunks of adult palms provided insight into the reproductive history of populations. Palms had a mean height at first flowering of 6.1 m. The interval of time between first flowering and any subsequent flowering was 11 years and may represent a reproductive strategy to increase the chance of successful replacement. *L. australis* has the ability to reproduce for over 160 years but periods of up to 24 years without flowering may occur. The species undergoes years of low flowering but these do not appear to be related to changes in the Southern Oscillation Index as an indicator of El-Nino Southern Oscillation events (ENSO).

7.1 Introduction

Little is known about the flowering and fruiting ecology of *Livistona australis*. It is assumed that the species flowers every second year (Orscheg & Parsons 1996b) but supportive data are lacking (Rodd 1998). No long-term study has been carried out to look at flowering frequency or any other aspect of the reproductive ecology of this palm. For the appropriate management of this, or any other species, it is beneficial to have a working understanding of the species' reproductive strategy and functions.

Basic details regarding the timing of reproductive events for *L. australis* have been recorded. The species flowers from August to October (Floyd 1989; Orscheg & Parsons 1996b; Rodd 1998) and fruit falls from March to June (Floyd 1989). Flowers occur intrafoliar (Rodd 1998) within the leaves of the crown and below the newest leaves produced in the year of flowering (this study). From casual observations *L. australis* appears to be monoecious (Rodd 1998) with individuals consistently producing inflorescences of either male or female flowers. This observation, however, has yet to be quantitatively tested. Sexual differentiation of inflorescences is made possible by the presence or absence of thickening of fruit stalks on the rachillae (Rodd 1998). Observations have been made that suggest flower buds remain in the canopy for a period of two years (Jakobasch 1981) and the cycle from emergence of flowers to production of ripe fruit takes 18 months (Orscheg & Parsons 1996b). It is not known whether the sex of the individual affects the number of inflorescences produced or if fruit production in an individual plant differs from one flowering to the next.

This study aimed to better understand the reproductive functioning of *L. australis.* The study examined several aspects of phenology including: frequency of flowering; the number and sex of inflorescences; height of palms at first flowering; and the relationship between plant height, reproduction and leaf production. The time sequence of flower and fruit, the time period between sequential flowerings and the quantity of fruit produced were also investigated. Four disjunct populations of varying latitude were studied (see Chapter *2*).

To understand the demography of *L. australis* it is important to know the age (or height, if height is a useful surrogate of age) at which a palm becomes reproductive. These, and other elements of the reproductive biology, are currently unknown. The patterning or scarring on palm trunks produced by aging, drooping and abscission of leaves has been used previously to estimate growth rates of *Livistona* (Hnatiuk 1977; Orscheg & Parsons 1996b). This study makes use of an additional feature of the trunk — an inflorescence scar — created by each flowering event, that appears as a bulge in the palm trunk. The history of each plant's flowering can be determined from the frequency of these inflorescence scars and the distance between them. These features only form once a palm reaches a considerable height, whence it is reproductive. The absence of these scars on the lower trunk has probably precluded any previous examination of their presence or regularity. Considering that these features record the total reproductive history of an individual specimen over many decades, if not centuries, they represent an extremely informative depiction of the reproductive history of the individual. For this information to be useful, two features of flowering and growth needed to be clarified. It was unknown whether inflorescence scars are produced at every flowering event or only those that result in fruit production. It was also not known how many years these scars take to emerge from beneath the palm crown. One of the aims of this study was to address these questions and to provide a detailed account of the occurrence of these inflorescence scars. An examination of the frequency of these inflorescence scars was also undertaken. By using the distance between each bulge to date each flowering event, it was possible to estimate the timing and frequency of flowering that has occurred over much of the last century.

Populations of *L. australis* have been shown to occasionally fail to produce fruit (Waterhouse 2001). The occurrence of any reproductive failure occurring within the study sites and the extent of this event beyond the study area and over the wider distribution of the southern range of the species was investigated.

7.2 Methods

A sample of 50 *L. australis* palms with above ground trunks was randomly selected in each of the four main study sites — Cabbage Tree Island (CTI), Mungo Brush (MB), Wyrrabolong National Park (WNP) and Royal National Park (RNP) (see Chapter 5). These samples were principally to serve for a study of trunk growth rates and so encompassed the full range of heights present at each site. Consequently, each sample included a number of non-reproductive (immature) specimens which were excluded for this study. A palm was considered to be a reproductive adult if it showed scarring from a least one flowering. The sample size of reproductive adults in each population at the beginning of the study was as follows: CTI $n = 28$, MB $n = 28$, WNP $n = 22$ and RNP $n = 24$. As additional palms flowered for the first time during the study the sample sizes for some sites increased during the course of the study. To accommodate all aspects of the research being carried out at the four study sites logistical constraints prevented use of a larger sample size of reproductive palms.

To assist in determining whether the height of a palm influenced flowering and fruiting the sampled individuals were categorised into seven height classes based on trunk heights: < 1 m, 1.0–4.0 m, 4.0–7.0 m; 7.0–10.0 m, 10.0–13.0 m, 13.0–16.0 m, and > 16 m as used in another study on *L. australis* (Orscheg & Parsons 1996b). The lowest two height classes included all palms yet to reach reproductive height. Trunk height was defined as the distance from ground level to the base of the lowest photosynthetic leaf. Crown height was defined as the distance from ground level to the top of the highest leaf or emergent spike within the palm crown. Crown depth was the difference between these two measurements. All height measurements were determined by trigonometric calculations involving the distance from the palm, measured by a 30 m fibreglass tape, and the angle of elevation, measured with a clinometer.

Palms were climbed annually from 1998 to 2001 in the cooler months during early autumn and winter (March to August). Flowers are produced in the winter months of any given year and the female inflorescences go on to develop fruit during the summer months. Fruit fall begins from autumn into the following winter (this study). This observed sequence provides for flowering in one calendar year and fruiting in the following year. The timing of climbing activities was selected to enable recording of fruit production prior to the commencement of fruit fall. At this time it was also possible to determine palms that had flowered but not produced fruit. This was inferred from the remains of recently emerged inflorescences. The sequence of data collection from climbing activities is illustrated in Table 7.1.

The period of this study encompassed information collected on the potential fruit production in 1998 to 2001, which was the result of flowering in 1997 to 2000. The remains of flowering in 1996 was also inferred from the relatively fresh inflorescences still observed within palm crowns in the first year of this study, 1998. These structures were still close to the center of the crown but were readily distinguishable from earlier flowering as they still retained the strong yellow colouration of the rachis. Inflorescences older than these were positioned further from the crown centre and were brown and desiccated. The sex of these older inflorescence remains was not determined. The potential flowering levels within the study palms for 2001 was also inferred from observations of emerging inflorescence buds within the palm crowns during final data collection at each of the sites in late winter of that year. The sex of these

Table 7.1: The sequence of climbing activities for *Livistona australis* from 1998 to 2001, and the potential data available for collection on flowering and fruiting. c = collected; i = inferred.

	Year					
	1996	1997	1998	1999	2000	2001
Flowering	i	i	c	c	c	i
Fruiting			c	c	c	c

developing inflorescence could not be determined.

7.2.1 Description of inflorescence scarring

Each palm was sampled by ascending the trunk using a technique known as prussiking (a description of the technique is given in Chapter 5). The number of inflorescence scars and distance between them was recorded. A palm was considered to be a reproductive adult if it showed scarring from at least one flowering event.

7.2.2 Scarring parameters

The inflorescences produced from the 1997 flowering at MB and RNP were monitored from 1998 until 2001. The progression of these infloresences through the growing crown was easily identified and monitored, as the majority of the palms in which they were produced did not contain the remains of previous inflorescences from any recent flowerings. Through the process of leaf shedding at the base of the crown, the remains of the inflorescences eventually become exposed below the crown. When this occurred the date was noted and the presence or absence of an inflorescence scar was also recorded. The data collected provided evidence of whether all inflorescences (both male and female palms) produce scars or only those that subsequently developed fruits (female palms only). It also indicated the time taken between the formation of an inflorescence and the appearance of the subsequent scar under the palm crown. Both these observations influenced subsequent interpretation of previous flowering events based on the frequency and position of these scars.

7.2.3 The number and sex of inflorescences

Flowering of palms was recorded over a period of six years, 1996 to 2001 (Table 7.1). The reproductive status of the palm was determined by the presence or absence of recently emerged inflorescences. Inflorescences produced during a reproductive cycle are readily identifiable as they encircled the most recent expanded leaves in the crown of the palm. The number of these new inflorescences was counted. On palms with inflorescences not bearing fruit, the sex of the flowering was determined by the presence or absence of thickening in the flower stalk on the rachillae. Flower stems without fruit but with thickened stalks indicated female flowers that had aborted fruit and those without thickening were assumed to be the result of male flowers (Rodd 1998).

7.2.4 Frequency of flowering

Flowering frequency for palms was established over a period of six years, 1996 to 2001 (Table 7.1). Following a successful flowering within an individual palm, the number of years between this and subsequent flowering events was recorded. From this data the time period between flowering events could be determined.

7.2.5 The time sequence of flower and fruit

Palms were sampled during the period March to August each year between 1998 and 2001. Sampling was timed to occur before fruit fall, which varied with latitude (this study). Indications of impending flowering were evident from the eruption of rachis sheathes between the upper leaf petioles. While no specific data were recorded, the reproductive status of the population at each site was noted during each climbing trip.

7.2.6 Quantity of fruit produced

The number of fruits produced, if any, was estimated for each palm each season from 1998 to 2001 (Table 7.1). Fruit production was assessed by counting the number of fruits on each inflorescence. A sub-sample of 100 fruits on an inflorescence was first counted, then the remaining fruit estimated by extrapolating the volume of this initial count over the remainder. The number of palms fruiting within any one year represented a sub-sample of the total number of reproductive adults as not all palms flowered in a year. The timing of fruit assessment was, with few exceptions, before any ripe fruit was lost from the canopy.

7.2.7 Widespread failure in fruit production

In some years fruiting may not occur. In the years when all of the sampled palms failed to fruit, additional palms were examined to gauge how widespread this phenomenon was. Initially the populations local to each study area were assessed. Where sites where too expansive to allow the entire population to be surveyed, a total of 250 reproductive palms were sampled. In years when there was widespread fruiting failure within the locale of each study site other populations were visited covering the most southerly distribution of the species (see Chapter 2). To assess the total area of *L. australis* was logistically impossible as it covers almost the entire eastern seaboard of Australia. In targeting the southern portion of the range of the species, the sole Victorian population and 60% of the NSW population range was assessed. A sample of the reproductive adults in each palm population was checked to determine whether fruit set had occurred.

7.2.8 Leaf production

The number of open leaves, together with the number of unexpanded leaf spikes in the crown of each palm, were counted annually. An estimation of annual leaf production was not made, as palms appeared to produce leaves continuously throughout the year (this study).

7.2.9 Flowering history

The entire sequence or linear arrangement of inflorescence scars was determined for each individual palm sampled, and mapped relative to their position along the trunk. Recording was carried out in strict order beginning with the first scar to appear closest to the base of the palm, which was produced from the palm's first flowering event, then proceeding up the trunk to the most recent scar to emerge from the crown. The distance between the top of each scar to the top of the scar immediately above it was recorded as the amount of growth between subsequent flowering events. The distance between the highest scar on the palm trunk and the lowest photosynthetic leaf in the palm crown was recorded. Distance from ground level to the first scar was also measured (see Chapter 5). The data collected provided details of height at first flowering and the number of, and distance between, flowering events during the life of the palm.

Using aging techniques outlined in Chapter 5, the data pertaining to flowering scars was analysed in conjunction with known rates of growth from trunks of different heights at each of the study sites. These rates of growth give an indication of the relative increase each year in the height of a trunk throughout the life of a palm. This distance was then compared to the distance between each flowering scar recorded at a known height. Calculating backward from 1998, when the measurements were taken, an approximate date could be calculated for each flowering scar on all reproductive palms.

7.2.10 Analysis

It was assumed that the palms sampled within each study site reflected the height range of palms present in each population. Analysis of fruiting data relied on sub-samples within each of the four locations and these were pooled across the study area to increase the sample size. Homogeneity of variances was checked prior to analysis using Cochran's C-test. Flowering frequency was analysed using an unreplicated two-factor (site and proportion of flowering) AVOVA, as frequency was determined as a single figure for each site. Chi-square was used to analyse the relationship between sex ratio of inflorescences with year and site, and the sex of inflorescences was *t*-tested against inflorescence numbers. The number of flowering events was pooled across all sites and analysed by *t*-test and linear regression. Fruit production was analysed using linear regression and replicated three-factor ANOVA in which height classes and sites were considered fixed factors and years a random factor (as not all years were sampled). A repeated measures ANOVA is inappropriate as in almost all cases an individual was not sampled in consecutive years. Leaf production was similarly analysed using replicated two-factor ANOVA and linear regression. Height of first flowering and time period between each inflorescence scar was analysed using a one-factor ANOVA. A *t*-test was applied to the mean interval between first and second flowering and the sex of the palm as well as to the mean flowering period between observed and inferred data sets. Finally, linear regression analysis was used to determine any relationship between years of low flowering and the Southern Oscillation Index as an indicator of ENSO (El Nino Southern Oscillation) events. Student-Newman-Keuls (SNK) was applied in multiple comparison tests at 95% confidence. All statistical tests performed were two-sided unless stated otherwise. Where means are presented, standard errors are included.

7.3 Results

7.3.1 A description of inflorescence scarring

The surface of a palm trunk is covered predominantly with petiole scars that are arranged in a phyllotactic spiral. Additionally, as a result of the production of inflorescences, the trunk is left with a distinctive bulge or ridge as an uneven ring after each flowering event. When an individual plant produces an inflorescence the petiole butt may persist as part of this distinctive bulge for several years after flowering and fruiting have been completed. The scar is typically 20–30 mm wide and extends out from the palm trunk 10–20 mm. On the tallest palms, evidence of the earliest flower events — being the lowest on the palm trunk — persists only as a faint raised scar.

The vertical distance between scarring is determined by the amount a palm grows between flowering events, and can be as little as 40 mm. There was a substantial gap between the first scar, at the lowest point on the palm trunk, and any subsequent scars. On taller palms the frequency of scarring increased toward the crown (Figure 7.1) and the remnants of rachis stems became more pronounced, creating a bulkier appearance. The mean frequency of scars per metre varied from site to site. CTI had the highest frequency at 10 scars per

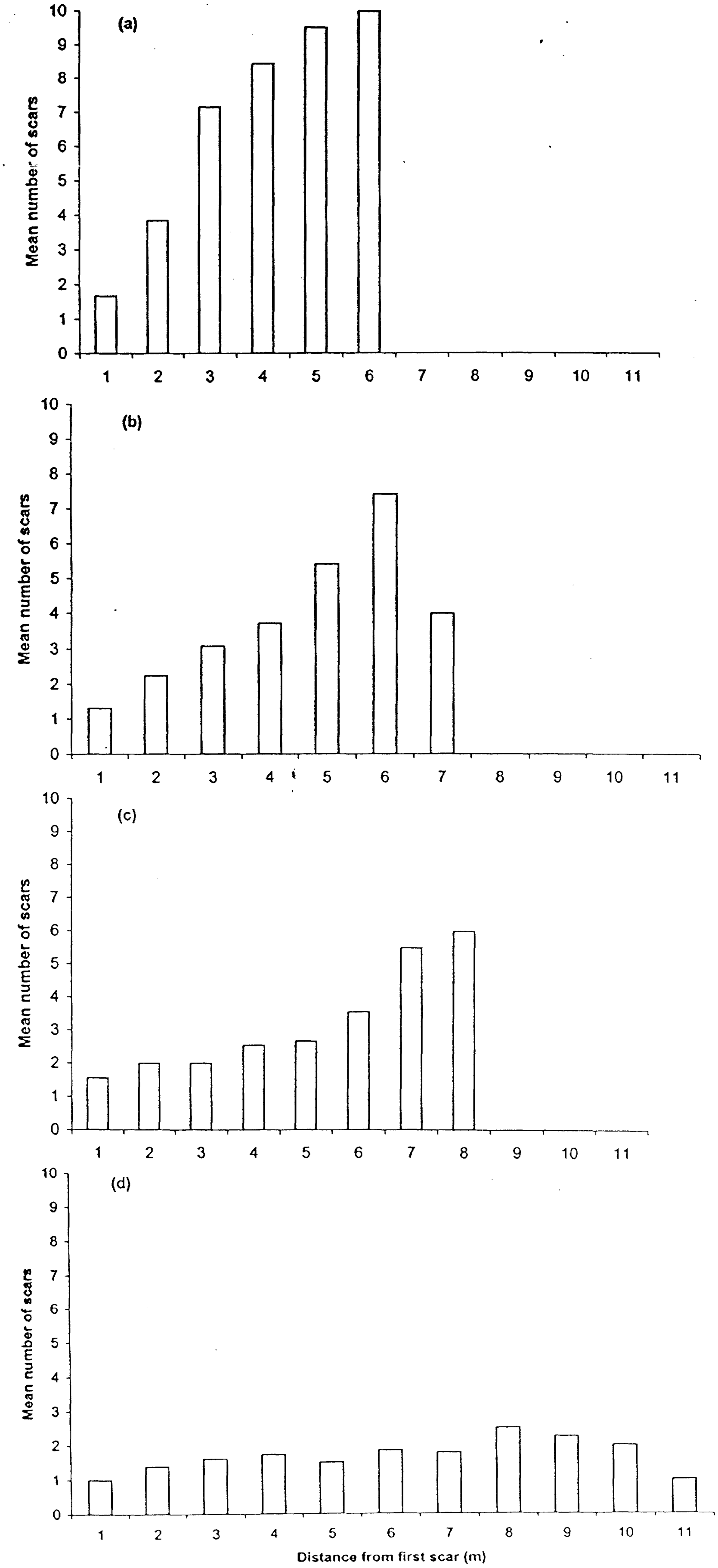

Figure 7.1: Mean frequency of inflorescence scars with increasing distance from the lowest scar on trunks of *Livistona australis* at Cabbage Tree Island, CTI (a), Mungo Brush, MB (b), Wyrrabolong National Park, WNP (c) and Royal National Park, RNP (d).

metre and the RNP the lowest at 1 scar per metre.

7.3.2 Emergence of inflorescence scarring

Two *L. australis* populations (MB and RNP) were monitored for scar emergence under the crown of the adult palm (Table 7.2). All female flowering proceeded to fruiting. All scar emergence observed was recorded four years following the production of either male or female inflorescences and amounted to 71% of palms. At MB all inflorescence scarring from flowering in 1997 had been exposed below the palm crowns in 2001. From the same flowering event in 1997 in the RNP only 46% of palms had exposed inflorescence scars in 2001. The remaining unexposed scars were covered by less than three leaves and were therefore likely to appear within the following growing season.

From growth data (see Chapter 5) the crown depth of adult palms was significantly greater in RNP ($\bar{x}$ = 4.7 m, s.e. = 1.22) compared to those at MB ($\bar{x}$ = 3.4 m, s.e. = 0.73) ($t = 5.17$, d.f. = 25, $P < 0.01$). The crowns also contained significantly greater numbers of leaves in the RNP ($\bar{x}$ = 69.3, s.e. = 15.9) compared to those at MB ($\bar{x}$ = 56.7, s.e. = 10.6) ($t = 3.72$, d.f. = 25, $P < 0.01$). The greater crown depth and higher number of leaves in RNP may affect the time it takes for inflorescence scars to be exposed below the palm crown.

7.3.3 Assessing the sex of plants from inflorescences

Data on the sex ratio of flowering palms are presented as a ratio of male to female flowering (Table 7.3). The sex of inflorescences was not determined for 1996 or 2001. The 1996 inflorescences were examined in 1998 (see Table 7.1) while still retained within the palm crowns. These inflorescences were viewed from a distance of greater than 2 metres and had undergone some desiccation since flowering and sex of the flowering could not be confidently determined. The 2001 inflorescences were not fully expanded at the time of the observations and therefore the sex was unable to be determined. In 1999 no female inflorescences were produced within the study sites and therefore a sex ratio could not be calculated, although a small number of male inflorescences were

Table 7.2: Inflorescence scar emergence under the crowns of *Livistona australis* four years after flowering or fruiting at two sites, Mungo Brush (MB) and the Royal National Park (RNP).

	MB		RNP		
Inflorescence sex	**M**	**F**	**M**	**F**	**Total**
Flowering in 1997	4	7	2	11	24
Exposed in 2001	4	7	1	5	17
% Emergence	100	100	50	46	71

Table 7.3: The sex ratio (male:female) in reproductive adults of *Livistona australis* between 1997 and 2000 at four sites: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP). Female sample size in parentheses.

Year of flowering	CTI	MB	WNP	RNP	Yr. Mean
1997	0.75 (4)	0.57 (7)	1.6 (3)	0.18(11)	0.77
1998	0.71 (7)	0.09 (11)	0.33 (3)	0.50 (2)	0.41
1999	— (0)	— (0)	— (0)	— (0)	—
2000	0.14 (7)	0.44 (9)	— (0)	1.60 (5)	0.54
Site Mean	0.40	0.27	0.42	0.57	

produced at CTI ($n = 2$) and MB ($n = 1$). In the remaining years it was found that there was no relationship between year or site in the sex ratio of inflorescences (chi-square test, $X^2 = 0.52$, d.f. = 12, $P > 0.99$), with the sex ratio being highly variable (Table 7.3). *L. australis* is moderately to strongly monoecious, with individual palms generally producing only male or only female inflorescences. Less than 4% of all reproductive palms ($n = 107$) were hermaphroditic, producing either male or female inflorescences on the same tree but in different years.

Trees that produced only male flowers had the same flowering interval ($\bar{x} = 2.7$ years, s.e. = 0.22) as trees that produce only female flowers ($\bar{x} = 2.5$ years, s.e. = 0.19) ($t = 0.61$, d.f. = 27, $P = 0.55$). There was a significant difference between the number of male inflorescences produced per palm if they were female or male flowers ($t = 4.42$, d.f. = 35, $P < 0.01$). Palms that produced only female flowers had more inflorescences ($\bar{x} = 8.1$, s.e. = 0.49, $n = 72$) than male flowering palms ($\bar{x} = 5.3$, s.e. = 0.30, $n = 36$).

7.3.4 Frequency of flowering

The proportions of reproductive adults at each site that flowered each year between 1996 and 2001 are presented in Table 7.4. Included in this table is the mean percentage of palms flowering each year, pooled across all study sites. In 1998, for three of the four populations monitored, 1996 season flowerings were identified. These data were not collected from CTI, the first site assessed, as at the time it was not known that it was possible to differentiate between 1997 inflorescences and those of earlier years. Logistical constraints prevented returning to CTI to collect this additional data. The increase in sample size over the study period for RNP reflects the addition of palms into the reproductive population as they flowered for the first time.

There was no significant difference in the proportion of flowering between sites (unreplicated two factor ANOVA, $F_{3,99} = 0.30$, $P = 0.82$). Conversely, there was a significant difference in the proportion of flowering between years ($F_{5,97} = 7.95$, $P < 0.01$). An SNK test indicated that the proportion of flowers in 2001

Table 7.4: The proportion of reproductive *Livistona australis* palms that flowered each year between 1996 and 2001 at each study site: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP). Student-Newman-Keuls test (SNK) results are also shown. Sample size in parentheses.

	STUDY SITES					
	CTI	MB	WNP	RNP		
YEAR					$\bar{x}$	*SNK*
1996	–	0.25 (28)	0.14 (22)	0.25 (24)	0.21	b
1997	0.25 (28)	0.39 (28)	0.36 (22)	0.46 (28)	0.36	b
1998	0.43 (28)	0.43 (28)	0.18 (22)	0.11 (28)	0.29	b
1999	0.07 (28)	0.04 (28)	0.00 (22)	0.00 (28)	0.03	c
2000	0.29 (28)	0.46 (28)	0.00 (22)	0.45 (28)	0.30	b
2001	0.64 (28)	0.57 (28)	1.00 (22)	0.59 (29)	0.70	a
Mean	0.34	0.36	0.28	0.31	0.32	

was significantly greater than in all other years and in 1999 was lower than in all other years. Flowering from 1996 to 1998 and in 2000 was similar.

7.3.5 *Time period between flowering*

A total of 198 flowering events from 107 reproductive *L. australis* were recorded between 1996 and 2001. The number of flowering events observed in individual palms over the six years of the study were categorised into four groups: palms that never flowered during the study; palms that flowered once; twice; or three times (Table 7.5). Eleven palms (10%) from the original number of reproductive adults in 1997 (*n* = 102, Table 7.4) which showed previous inflorescence scarring, failed to reproduce in the six years covered by this study. The difference between the total sample size in 1997 and that given in Table 7.5 is the result of increasing sample size over the six years following the inclusion of palms flowering for the first time. Of the 26 palms that flowered once in the six years, five of these (5% of all reproductive adults) were individuals that were flowering for the first time, all from RNP. From the 28 palms that flowered three times between 1996 and 2001, 26 had consecutive years of flowering for two of the three flowering events. No palm flowered three years consecutively. The mean time between flowering was approximately once every two years (1.84 years).

A comparison was made of frequency of flowering in this study and trunk height for palms that flowered at different intervals between 1997 and 2001, pooled across sites (Table 7.6). The mean height of palms from all flowering events was between 9.8 and 10.6 m. There was no significant difference between the height of the adult palm and the number of flowering events (t = 4.65, d.f. = 2, P = 0.55). Linear regression analysis showed that height was a poor predictor of flowering frequency (r^2 = 0.02, P = 0.17).

7.3.6 *Flowering and fruiting phenology*

L. australis produce flowers and develop these into fruits all within a 12 to 18

Table 7.5: Pooled data from four study sites of flowering attempts of *Livistona australis* between 1996 and 2001.

Flowering attempts	(n)	%
Failed	11	10
1	26	24
2	42	39
3	28	27
Total	107	100

Table 7.6: Comparison of number of flowering attempts to trunk height in *Livistona australis* between 1996 and 2001. Sample size in parentheses.

Flowering attempts	Mean height (m)	S.E.
0	10.29 (23)	0.55
1	10.60 (26)	0.52
2	10.40 (42)	0.66
3	9.75 (28)	0.25

month period (Figure 7.2). Palms at WNP fruited only twice in the four years that fruit production was monitored (1998 to 2001), precluding any detailed assessment of their timing of flowering and fruiting. Generally flowers begin to emerge in July each year (Figure 7.2). Following flowering, fruit development continues through summer. Fruit fall varies between palms within sites, between sites and from year to year. At CTI and MB all fruit falls between March and June, within the 12-month period following flowering (Figure 7.2). This provides minimal overlap between flowering and fruiting. At the most southern site in the RNP fruit fall can begin as late as August and continue through to December, some 18 months after flowering began. The extended period of fruit fall at RNP does not exclude palms from initiating flowering during this period, though it was rare to have a palm flowering as the same time as fruit was held in the canopy.

7.3.7 Quantity of fruit produced

The magnitude of fruiting was assessed between 1998 and 2001. The percentage of adult palms fruiting as a proportion of total reproductive adults from all sites for 1998, 1999 and 2001 were 24%, 21% and 19% respectively. There was no fruiting at any site in 2000. The mean fruit production per annum was compared between four height classes: 4.0 – 7.0 m; 7.0 – 10.0 m; 10.0 – 13.0 m; 13.0 – 16.0 m (Table 7.7). Sample sizes in the highest and lowest height classes were small as the majority of reproductive palms were between 7 m and 13 m tall. (Table 7.7). Dropping of ripe fruit from individual palms occurred occasionally prior to data collection. This occurrence was particularly noticeable when individual palms were climbed. In the action of climbing, agitation of the crown would release fruit onto the climber, indicating that fruit fall had commenced prior to data collection. After data had been collected from individuals where fruit fall had already commenced the ground immediately below the palm was assessed for an estimation of fallen fruits. The total fruit fall was then divided by the number of inflorescences within the individual palm canopy and the total for each individual inflorescence increased accordingly. In unusual circumstances fruit production could not be estimated if all fruit had fallen prior to the time of data collection. In 1998 four additional palms had

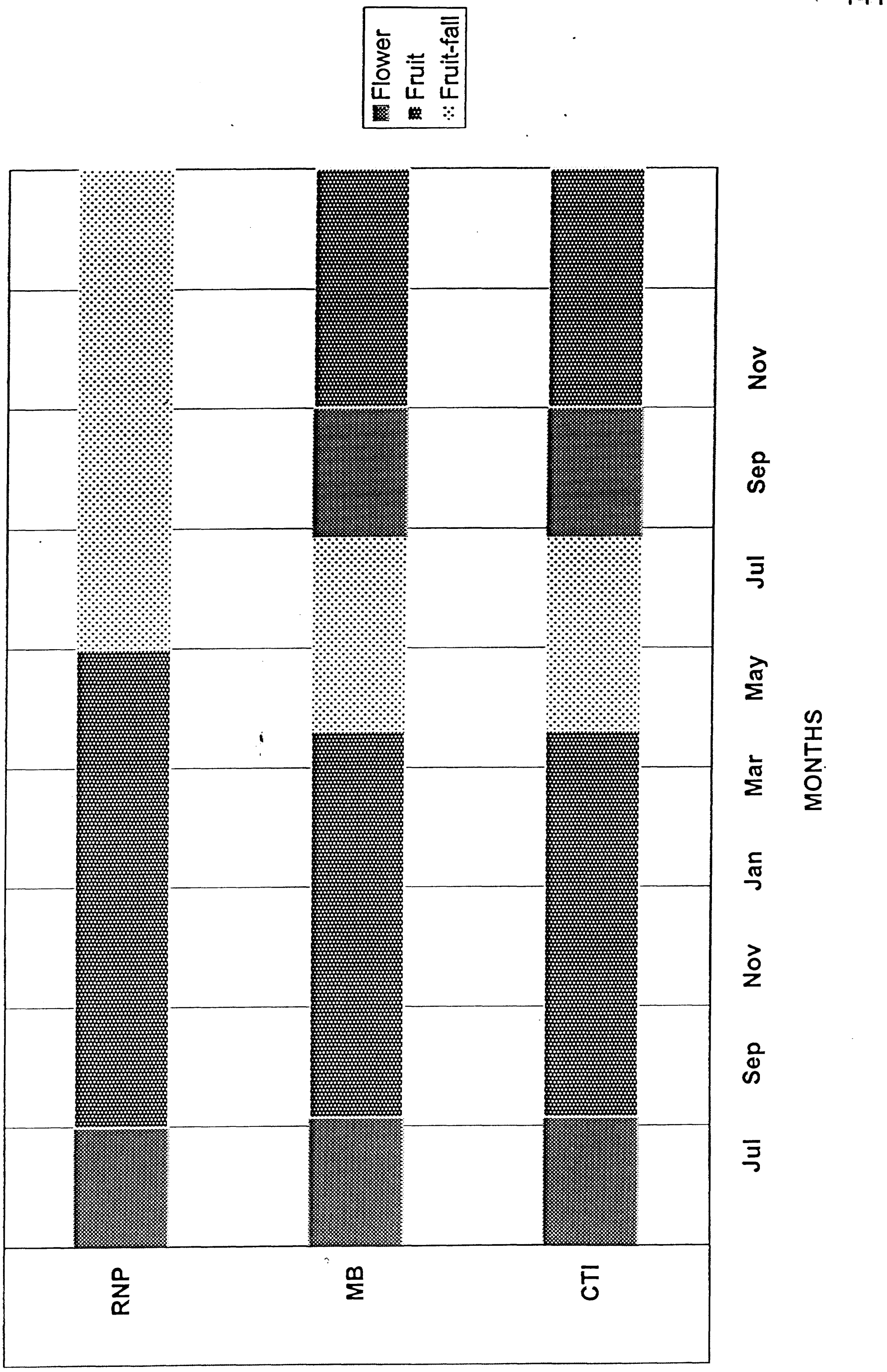

Figure 7.2: Time sequence of flowering, fruit development and fruit fall observed for *Livistona australis* at three sites Cabbage Tree Island (CTI), Mungo Brush (MB) and Royal National Park (RNP).

Table 7.7: The mean number of fruits produced by *Livistona australis* within four height classes (HC) between 1998 and 2001. Sample size in parentheses. Standard errors in italics for samples greater than two. No fruiting occurred in 2000.

	Year			
HC (m)	**1998**	**1999**	**2001**	**Mean (all years)**
4.0 - 7.0	—	1538 (2)	1220 (1)	1432 (3)
		806.5	—	*477.6*
7.0 - 10.0	3550 (5)	3482 (8)	3651 (9)	3567 (22)
	1936.5	*1618.8*	*1183.5*	*835.8*
10.0 - 13.0	8594 (11)	6096 (5)	5832 (10)	7051 (26)
	2514.7	*2289.7*	*1201.8*	*1225.4*
13.0 - 16.0	10850 (2)	24200 (1)	11250 (1)	14287 (4)
	10150.0	—	—	*5300.6*
Year Mean	7443 (18)	5851 (16)	4935 (21)	5877 (55)
	1887.5	*1668.2*	*855.5*	*847.4*

dropped all fruit before the data was collected, two from the 7.0 – 10.0 m class and two from the 10.0 – 13.0 m class. In 1999 nine additional palms had dropped all fruit before the data was collected, five from the 7.0 – 10.0 m class and four from the 10.0 – 13.0 m class. In 1998 no reproductive palm within the 4.0 – 7.0 m class produced fruits.

For analysis purposes the number of height classes was reduced to include only those with a sufficient representative sample in each site to allow a comparison of significance. Height classes 4.0 – 7.0 m and 13.0 – 16.0 m were excluded. There was no significant difference in fruit production between palms with trunks 7 to 13.0 metres in height (replicated two factor AVOVA: $F_{1,47} = 3.92$, $P = 0.06$). Analysis by linear regression showed that palm height was not a good indicator of quantity of fruit produced ($r^2 = 0.29$, $P < 0.01$). While the relationship between the two factors was strongly positive only 29% of the sample was accounted for by the regression indicating the relationship is not linear. No significant difference was found in fruit production between years ($F_{2,53} = 0.28$, $P = 0.76$) and a regression of all years pooled showed that the year was not a good predictor of fruit production ($r^2 = 0.03$, $P = 0.24$). There was no interaction of fruit production in height classes and years ($F_{2,53} = 0.30$, $P = 0.74$).

A total of 68 fruiting events were observed over the four years of this study. Ten of these events showed some sign of abortion of fruit due to either insect attack of the developing fruit or a fungus associated with such activities. Only one palm was found to have its crop totally destroyed by insect or fungal attack, and it was excluded from the tabulated data.

7.3.8 Widespread failure in fruit production

In 1999, flowering at all study sites was dramatically reduced and in 2000 fruiting was non-existent in this study. When the sample palms at each of the four study sites failed to fruit, an additional sample was undertaken from each local population to assess fruiting success (Table 7.8). At CTI and RNP all palms within the immediate discrete population were examined for flowering,

Table 7.8: Local populations of *Livistona australis* palms surveyed for fruiting success in 2000 in four study areas: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP).

Study sites	n	Fruiting palms	Approx. total population
CTI	500	0	500
MB	250	1	1500
WNP	250	0	1000
RNP	200	0	200

with samples of the total population examined at MB and WNP. From the four sites only a single palm of 9 m trunk height was found successfully fruiting. This palm was located at MB and held approximately 450 - 500 fruit. This is only 10% of the mean fruit production for this height class in other years of the study (Table 7.7).

Populations of *L. australis* north and south of the immediate study area were investigated for fruiting following the failure within the study areas (Table 7.9 and see Chapter 2). In the most southern part of the *L. australis* range at Cabbage Tree Creek, Victoria, Gulaga National Park NSW and Tilba NSW, fruiting was observed within these small populations. Further north at the southern end of the Illawara Escarpment at Fox Ground, NSW and also at the northern end of the escarpment at Stanwell Park, no fruiting was observed. At Booti Booti National Park, 30 km north of MB on the NSW mid-north coast, no fruiting was observed.

7.3.9 Leaf production

Data were collected annually on the mean number of leaves contained within the palm crowns for seven height classes (Table 7.10). The lack of data for height classes above 13.0 m at CTI and MB and above 16.0 m at RNP reflects the lower overall canopy height for these palm populations compared to WNP. The lowest leaf counts corresponded to the smallest height class at all sites. Linear regression analysis using data from all sites pooled showed that palm height was not a good predictor of number of leaves within the crown ($r^2 = 0.60$; $P < 0.01$), similarly at each site (CTI: $r^2 = 0.27$; MB: $r^2 = 0.73$; WNP: $r^2 = 0.64$; RNP: $r^2 = 0.65$; all $P < 0.01$). The regression analysis showed that while the relationship between palm height and annual leaf production was strongly positive, the variance between the two factors accounted for between 27% and 73% of all data.

For analysis purposes the number of height classes was reduced to include only those with sufficient representative samples in each site to allow a comparison of significance. There was no interaction in the mean leaves

Table 7.9: Populations of *Livistona australis* palms of reproductive size surveyed for fruiting success in 2000 at six locations: Cabbage Tree Creek, Orbost, Victoria (CTC); Gulaga National Park, Bega Valley, NSW (GNP); Tilba Tilba, Bega Valley, NSW (TT); Fox Ground, southern Illawarra, NSW (FG); Stanwell Park, northern Illawarra, NSW (SP); and Booti Booti National Park, mid-north coast, NSW (BBNP). Site location in latitude and longitude.

Locations	n	Number Fruiting	Est. Total Pop.	Site Location
CTC	20	8	48	37°47' 148°28'
GNP	9	6	9	36°24' 150°00'
TT	25	9	25	36°24' 150°02'
FG	30	0[1]	100	34°43' 150°45'
SP	16	0[2]	45	34°14' 150°59'
BBNP	600	0[3]	1000	32°18' 152°31'

Sources:[1] Richard Scarborough pers. comm.[2] Judy Scott pers. comm.[3] David Turner pers. comm.

Table 7.10: The mean annual number of leaves contained within the crowns of *Livistona australis* for seven height classes (HC) in four study areas: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP). Student-Newman-Keuls test (SNK) results are also shown. Standard errors in italics. Sample size in parentheses.

(HC)	CTI	MB	WNP	RNP	Mean
< 1.0 m	13.5 (1)	14.4 (2)	9.9 (2)	32.7 (1)	19.0
	—	*4.75*	*1.12*	—	*4.02*
1.0 – 4.0 m	34.3 (8)	21.1 (13)	26.5 (12)	44.4 (11)	30.8
	3.27	*1.91*	*4.74*	*2.94*	*2.14*
4.0 – 7.0 m	40.6 (16)	48.4 (10)	31.8 (10)	54.8 (5)	42.1
	2.51	*4.00*	*2.13*	*2.22*	*1.87*
7.0 – 10.0 m	43.3 (20)	61.4 (14)	42.4 (10)	76.6 (4)	51.1
	1.56	*1.62*	*3.81*	*4.22*	*1.99*
10.0 – 13.0 m	44.1 (5)	62.4 (11)	50.1 (10)	68.0 (21)	61.9
	2.43	*2.10*	*3.30*	*1.92*	*1.94*
13.0 – 16.0 m	—	—	62.3 (5)	66.3 (8)	69.5
			6.29	*3.79*	*3.61*
16.0 – 19.0 m	—	—	71.5 (1)	—	71.5
			—		—
Mean	35.2	43.4	42.1	61.4	
SNK	c	b	b	a	

produced when trunk height (between 1 to 13.0 metres) and site were analysed ($F_{3,177} = 1.69$, $P = 0.18$). Similarly there was no significant difference in the mean leaves produced when compared to trunk height ($F_{1,179} = 1.99$, $P = 0.16$). There was, however, a significant difference in the mean leaves produced between sites ($F_{3,177} = 17.37$, $P < 0.01$). An SNK test indicated that the mean number of leaves at RNP was significantly greater than at all other sites. Annual leaf production was not assessed during this study because at no time during any one year was there a definite cessation in emerging leaves.

From pooling data on all palms that produced fruit it was found that the number of leaves a palm produces does not predict levels of fruiting ($r^2 < 0.01$; $P = 0.97$). Trunk growth rate (from Table 4.2) was not predictive of the number of fruits produced (Table 7.7) ($r^2 = 0.16$; $P = 0.01$). There was no significant difference in the growth rate of palms that produced fruit compared to non-fruiting adult palms (two-sample *t*-test: $t = -0.70$, d.f. = 39, $P = 0.49$). When all sites were pooled it was found that the rate of trunk growth was not a predictor of the number of leaves a palm will produce ($r^2 = 0.23$; $P < 0.01$).

7.3.10 Flowering history

The height of the estimated initial flowering of palms was determined within the study sites (Table 7.11) using inflorescence scars. An increase in the standard error and range of this height, from north to south highlights greater variability in the more southerly populations. There was a significant difference between the height of first flowering between the four sites ($F_{3,100} = 7.79$, $P < 0.01$). An SNK test indicated that the mean height at first flowering was significantly lower at CTI and MB compared to the other sites and was similar between these sites. Mean height of first flowering was similar between WNP and RNP.

A total of 1505 previous flowering events were identified from inflorescence scarring on 102 adult palms across all four study sites. Greater distances between inflorescence scarring was presumed to indicate a longer period of time between flowering. Using known rates of trunk growth obtained from each study site (see Table 5.2) the time period between each flowering event could

Table 7.11: The height of the estimated first flowering event of *Livistona australis* from four populations: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP). Student-Newman-Keuls test (SNK) results are also shown. Sample size in parentheses.

Ht (m)	**CTI**	**MB**	**WNP**	**RNP**	**$\bar{x}$ all sites**
$\bar{x}$	5.2 (28)	5.5 (28)	6.8 (22)	7.0 (25)	6.1 (103)
S.E.	0.19	0.28	0.35	0.44	0.31
Range	3.4 – 7.3	3.3 – 9.2	3.7 – 10.4	3.9 – 11.7	3.3 – 11.7
SNK	b	b	a	a	

be calculated in years (Figure 7.3).

The time period between inflorescence scars beginning at the lowest (and therefore oldest) was compared (where n > or = 30) using one-way ANOVA (Table 7.12). There was a significant difference in the number of years between all flowering events tested. The SNK results indicate that the initial three intervals in the scarring are significantly greater than subsequent intervals on the palm trunks (Table 7.12). The first interval is almost 100% greater than the third interval and 25% greater than the second interval (Figure 7.3). There was no significant difference between the sexes in the mean interval of years from the first and second flowering events (two-sample t-test: $t = 1.01$, d.f. = 24, $P = 0.32$). The longest time interval between first and second flowering was approximately 65 years and the longest flowering interval once regular flowering had commenced was estimated at 24 years.

The largest number of scars on an individual palm was 53. This individual on CTI had a trunk height of 12.2 m and a crown height of 14.9 m. The earliest flowering event was estimated to be in 1840 and the longest gap between flowerings was 9 years. The individual was estimated to be approximately 352 to 392 years old (see Chapter 5).

A comparison of inflorescence scars across some of the palms with a comparable trunk height from the four sites can be made (Table 7.13). The 10.0 – 13.0 m height class was chosen because it contains the largest number of individuals across the four sites (Table 7.10).

The difference in the rate of trunk growth at each site (see Chapter 5) has strongly influenced the differences apparent in Table 7.13 (e.g. earliest scar date; mean palm age). Palms in the RNP grow faster than at other sites. Faster growth results in individuals being taller when they first flower, flowering fewer times for their height and having a lower estimated age, than those at other sites. The difference in the age of the earliest scars between CTI and MB was because the individual palm with the earliest scar at MB began flowering at a much lower height than the equivalent CTI palm.

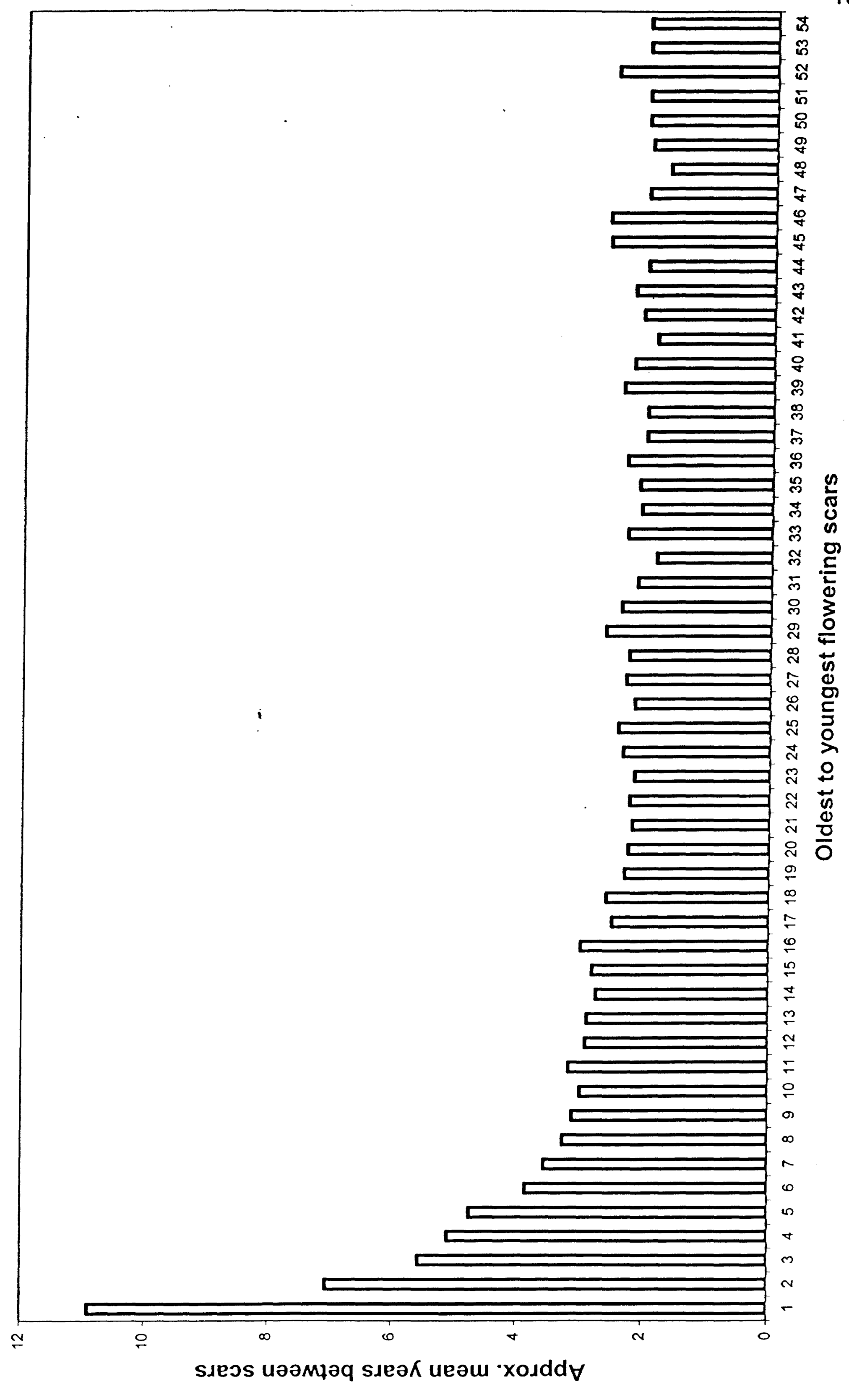

Figure 7.3: The mean time, in years, between each subsequent flowering scar of a sample of *Livistona australis* beginning at the lowest (and oldest scar) where n = 30 or more. Standard error bars shown.

Table 7.12: The results of a one-way ANOVA comparing time between the production of the first inflorescence scar and each subsequent scar on the trunks of 30 *Livistona australis* pooled from four sites. Site specific rates of trunk growth were used to determine time intervals. Degrees of freedom = 1. Student-Newman-Keuls test (SNK) results are also shown.

Scar gap	SS	F	P	SNK
1st to 2nd	3608.03	98.44	<0.01	a
2nd to 3rd	1293.63	92.55	<0.01	b
3rd to 4th	885.63	99.03	<0.01	c
4th to 5th	750.00	76.05	<0.01	c, d
5th to 6th	598.53	236.26	<0.01	d, e
6th to 7th	422.53	142.51	<0.01	f
7th to 8th	348.15	123.72	<0.01	f, g
8th to 9th	279.89	172.56	<0.01	f, g, h
9th to 10th	326.70	87.48	<0.01	f, g, h, i
10th to 11th	252.80	158.07	<0.01	g, h, i, j
11th to 12th	297.79	108.78	<0.01	g, h, i, j, k
12th to 13th	264.03	163.03	<0.01	g, h, i, j, k
13th to 14th	268.15	191.03	<0.01	g, h, i, j, k, l
14th to 15th	263.26	117.04	<0.01	h, i, j, k, l
15th to 16th	242.98	261.75	<0.01	h, i, j, k, l
16th to 17th	297.86	76.84	<0.01	h, i, j, k, l
17th to 18th	192.53	100.66	<0.01	h, i, j, k, l
18th to 19th	188.23	127.89	<0.01	l
19th to 20th	158.38	170.01	<0.01	l

Table 7.13: A comparison of inflorescence scars from *Livistona australis* of the same trunk height from four populations: Cabbage Tree Island (CTI); Mungo Brush (MB); Wyrrabolong National Park (WNP); and Royal National Park (RNP). Height in metres. Dates in calendar years. Age in years.

	Study Site			
	CTI	**MB**	**WNP**	**RNP**
Trunk height	10.2	10.0	10.0	10.1
Palm height	12.6	13.0	14.0	15.4
Inflorescence scars	25	26	13	2
Earliest scar date	1891	1868	1960	1979
Earliest scar height	6.8	3.5	5.0	8.7
Most recent scar date	1993	1991	1992	1993
Most recent scar height	10.15	9.75	9.75	10.1
Mean palm age	205	172	140	102

The technique of aging inflorescence scars using rates of trunk growth can provide information on the most recent flowering events up until 1993. From the 1998 inflorescence scarring data, the most recent flowering event exposed below the crown was from 1993 (based on Table 7.2 results), as more recent scars where still hidden within the crown. All inflorescence scars below the most recently emerged scar are dated backward from 1993. Using the observed flowering intervals from 1996 to 2001 (Table 7.5) a comparison can be made of two recent six year periods using the two techniques (Table 7.14). Over the six years of this study the mean proportion of adult palms flowering was 0.32 (s.e. = 0.09, range = 0.03 – 0.68). For the six-year period between 1988 and 1993 the mean proportion was estimated to be 0.29 (s.e. = 0.05, range = 0.16 – 0.50). The mean flowering between these two time periods was not significantly different ($t = 0.66$, d.f. = 3, $P = 0.56$). Mean flowering occurred approximately once every two years (2.40 years).

The proportion of palms flowering in every year from 1922 to 1993 was calculated using the inflorescence scar technique and pooled into 6-year periods to be comparable to data collected between 1996 to 2001 as part of this study (Figure 7.4). Data before 1922 is not included as the sample size of the population falls below 30 individuals. Data was pooled into six year periods rather than shown as individual years as the ability to accurately date each year becomes more speculative with time before the present (Discussion Chapter 5). The mean proportion of flowering between 1922 and 1993 was once every two to three years (2.62 years). When years of low flowering were compared against the occurrence of low rainfall years, represented by the Southern Oscillation Index associated with extreme ENSO phases, no association was evident ($r^2 = 0.04$; $P = 0.10$). A similar result was obtained with recent Index figures (Bureau of Meteorology Australia 2002) ($r^2 = 0.16$; $P = 0.43$). Adjusting the periods of low flowering periods to take into account that they may have been in response to ENSO events from a few years previous (a lag time) provided no better association between the events.

Table 7.14: A comparison of the flowering attempts in *Livistona australis* from two recent six-year periods. Observed attempts were recorded between 1996 and 2001 and inferred flowering attempts were determined from inflorescence scarring dated between 1988 and 1993. Percentages in parentheses.

Flowering attempts	Observed	Inferred
Failed	20 (10%)	3 (2%)
1	48 (24%)	38 (23%)
2	77 (39%)	43 (26%)
3	53 (27%)	80 (49%)
n	198	164

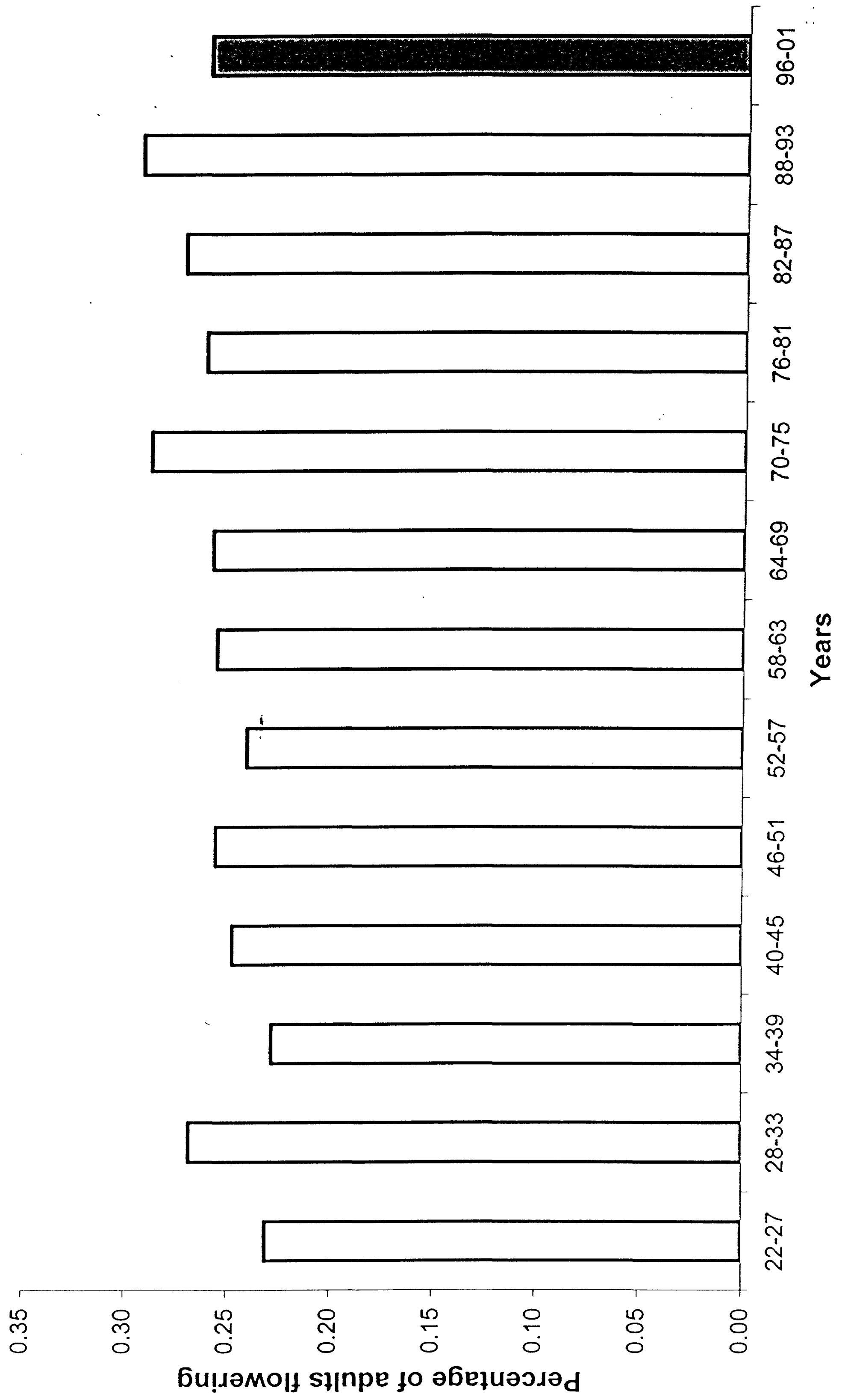

Figure 7.4: The proportion of *Livistona australis* flowering in every year between 1922 and 1993 pooled into 6-year periods. The same data collected during this study for 1996 to 2001 is shown as the final (dark-grey) bar on the graph.

Discussion

7.4.1 A description of inflorescence scarring

Inflorescence scarring on the trunks of *L. australis* forms the most striking feature of the trunk. The recognition and use of such scarring allows for a better understanding of the history of flowering within a population. This study highlights the usefulness of this feature when combined with other data such as rates of growth. It facilitates the determination of the height and age of first flowering, intervals between subsequent flowerings, flowering frequency and the relative proportion of palms flowering in recent years.

The amount of scarring evident on palm trunks differs between populations (Figure 7.1 a to d). Lower scars on very tall (and older) palms become obscured as they erode with age (personal observation). The mean height of the initial scarring at 6.1 metres (Table 7.11) may have deterred the examination of this feature by casual observers or in more detailed studies (e.g. Hnatiuk 1977). In the revision of *Livistona* in Australia (Rodd 1998) a general reference to the presence of inflorescence scars is made but their significance is not explored. In the absence of a more widespread recognition of this feature the scars may continue to be misidentified as features relating to 'growth rings' (e.g. Morici 1999).

7.4.2 Emergence of inflorescence scarring

Once the inflorescence scars have been identified it is necessary to establish whether their formation is the result of fruiting or the product of every flowering attempt. From the two sites monitored in this study, most adults that produced either male or female inflorescences in 1997 had the resultant scarring on their trunk exposed by 2001 or 2002 (Table 7.2). This establishes that four to five years is required to expose the inflorescence scars following flowering by either sex.

The difference in the rate of emergence of inflorescence scars on the trunks between MB and RNP may be the result of the deeper crowns in RNP compared to MB. Data from this study showed that not only were the crowns deeper at RNP but the larger number of leaves pre crown in RNP may affect the time it takes for inflorescence scars to be exposed below the crown. These data suggest that, if the rate of leaf production is similar between the sites, a greater number of years of leaf production are held within the crowns at RNP compared to MB.

7.4.3 Assessing the sex of plants from inflorescences

Identification of the sex of individual palms has not been systematically investigated, so any relationship between sex and flowering frequency and production of inflorescences has not been elucidated. It has been shown here that *L. australis* is moderately to strongly monoecious with some occurrence of hermaphroditic individuals. In general, *Livistona* have been described as 'hermaphroditic (rarely dioecious)' (Uhl & Dransfield 1987). Examinations of flowering in an accessible species, *L. humilis*, using fallen inflorescences showed dimorphism of inflorescence structure providing evidence that the species is monoecious (Rodd 1998). A similar observation of fallen inflorescences under individual *L. australis* pointed to the same conclusion. These reported observations are useful in discounting the possibility of dioecious flowering in individuals but could not discount hermaphroditic flowering. Over the four years where the sex of inflorescences was monitored in this study the extent of this dual sex in individual palms was found to be small (3.7%). The low percentage of hermaphroditic palms recorded would have been difficult to determine without the close yearly examinations undertaken over a number of seasons. A more long-term study of the sex of individuals may find that more plants exhibit hermaphroditic tendencies. Of the palms monitored, 34% either had failed to flower or flowered only once during this study (Table 7.14) therefore the sex designated to those palms that did flower only once can only be tentative as a change of sex in the inflorescences could not be ruled out.

For those palms that were monoecious there was no variation in flowering intervals regardless of whether the individuals produced seed crops or male-only flowers. This was despite the number of inflorescences on female palms being greater than on male palms. From this it can be concluded that the energy required for producing higher numbers of female inflorescences and their subsequent fruit crop does not impair an individual's ability to flower as often as palms that produce male-only flowers.

Jakobasch (1981) suggested that *L. australis* produced flower buds in one season that then lay dormant. The flower buds that were produced in the following flowering season, along with the dormant buds, then develop into inflorescences in the second year, consisting of two cohorts of bud production. From this study it can be concluded that this is likely to be an erroneous observation.

7.4.4 Frequency of flowering

The frequency and amount of flowering in *L. australis* has not previously been established. From this study the percent of flowering was found to be consistent across the four sites but differed between years, with an overall mean of 32%. In years of significant flowering (e.g. 2001) the inclusion of palms that flower less often contributed greatly to the high proportion of palms flowering in these years. This increase in the incidence of flowering in a population may indicate that more favorable conditions led up to the emergence of flowers in 2001. Such flowering synchrony has been recorded for the cycad *Macrozamia communis* within this same region, and is considered to be a consequence of as yet undetermined factors within local populations (Ballardie & Whelan 1986). Irregularity in the flowering of *L. australis* either between or within populations has been recorded elsewhere. A broader study found that while no palms were flowering in 1995 at two sites within the RNP, 61% of adult palms were flowering at the most southerly population (Orscheg & Parsons 1996b). During a five-year study of the interaction of Topknot Pigeons, *Lopholaimus antarcticus,* with *L. australis* (Waterhouse 2001), it was noted that flowering of individual palms was irregular (Waterhouse, pers.comm.).

Alternatively, the increase in flowering recorded in 2001 may have been in response to the poor flowering of recent seasons, giving a greater tendency to mast flower (and fruit). At WNP the population failed to flower in 1999 and 2000, then in 2001 all adult palms within the study site flowered (n = 22). Masting is the synchronous production of seed crops at long intervals by a population of plants (Janzen 1976) and is a common feature of many tree species (Harper 1977). Masting by trees has long been seen as a defensive strategy whereby seed predators are satiated in mast years and starved in the intervening periods (Silvertown 1980). In a review of the ecology of mast seeding this hypotheses is 'still the most widely known explanation for reproductive synchrony' (Kelly 1994). In some species flowering synchrony due to heavy rain following a long drought, has been shown to help attract pollinators and assist in good seedling establishment while milder conditions prevail (Augspurger 1983). This explanation is more relevant to plants that produce fruit and seed quickly with little dormancy before germination. Seed masting can be caused principally by either weather cues affecting adult members of a population, or selective mortality of individuals by the removal of their seed and seedlings (Janzen 1976). The masting exhibited by *L. australis* was more than likely to be environmentally triggered as it affected adults of unequal ages, whereas selective mortality of seeds and seedlings that establish single age cohorts is more common in bamboo (Janzen 1976). In this study no close association could be found between masting and edaphic, climatic or physical features of the local environment, through casual investigation. The synchrony of the WNP population may well have been assisted by the accumulation of starch and assimilates necessary to produce a mast crop, during the years of non-flowering. This is considered a key factor in determining the inter-mast period (Silvertown 1980) and has been proposed as a further reason for masting because of high accessory costs of reproduction (Kelly 1994). The increase in flowering frequency recorded over all the study sites in 2001, two years after the almost total failure of flowering, may indicate that resource accumulation from periods of non-flowering could support several years of high reproduction following a poor season.

In general the flowering frequency of *L. australis* is irregular and more long-term sampling is needed before an insight can be gained into the environmental factors that influence it.

The known fires at both WNP prior to 1981 and in RNP in 1988 appear to have had no effect on the flowering frequency of adult palms during these periods (Figure 7.2 c & d), based on inflorescence scarring. At WNP inferred flowering events show no change in flowering frequency when compared to MB or CTI, which have not been recently disturbed by fire ($t = 1.70$, d.f. = 6, $P = 0.15$). The frequency of inflorescence scarring recorded at RNP is different from all other sites ($t = -12.87$, d.f. = 10, $P < 0.01$) and may be more influenced by different growth conditions at this site than by the effects of two recent fires. This concurs with observations by others that fire does not increase the frequency of flowering in *L. australis* (Orscheg & Parsons 1996b).

7.4.5 Time period between flowering

Palm populations may have variable proportions of flowering plants over time but examination of the extent of flowering frequency of individual palms over time shows some regularity. Approximately 40% ($n = 107$) of palms flowered twice during the study making this the most common flowering interval. Of the palms that flowered three times (27%) the majority did so with two of those flowerings in consecutive years. Previously it had been suggested that this species required at least two years between successive flowerings (Orscheg & Parsons 1996b). Clearly this is not always the case. While no palms were recorded flowering three years consecutively the failure of flowering in 1999, at the mid-point of 6 years of flowering data, may have contributed to this observation. If resources within palms limit flowering ability, there is an indication from this study that they can be accumulated for use in more favourable years. Following two years without flowering at the WNP study site (1999 and 2000) all reproductive adults produced flowers in 2001. Failure of flowers to initiate fruit has been linked to lack of resources, genetic incompatibilities, or ecological constraints on pollination (Cunningham 1995). Further studies into what restricts the availability of resources to facilitate flowering in palms would be enlightening. Of the 107 reproductive palms monitored 10% failed to flower between 1996 and 2001, indicating that the time intervals between flowering within populations may be large. A period between flowering of 24 years was recorded in this study (Section 7.3.10). The interval between flower events was not related to the height of the palm. From this it can be concluded that increasing height of an individual does not increase its ability to flower more frequently.

7.4.6 Flowering and fruiting phenology

The timing of flowering and fruiting in *L. australis* has not been systematically studied until now. From this study, the reproductive cycle of flowering to fruit ripening is generally completed within 12 months, July to June. It is unclear why at the most southern site of RNP, fruit fall appears to extend for up to a further six months following the development of fully ripened fruit in the canopy, well beyond the other sites and that described by others (Floyd 1989). Previously, *L. australis* had been described as needing 18 months to progress from flowering to ripe fruit (Orscheg & Parsons 1996b). Not recognising the difference between when fruit ripen to when they actually fall may have contributed to this inaccuracy. This observation was made at the most southerly population of *L. australis*, in Victoria (37°47' 148°28'), and it appears that the tendency of fruit to remain in the canopy after ripening may be a feature of the higher latitudes. During a study of the interaction of Topknot Pigeons, *Lopholaimus antarcticus,* and *L. australis* (Waterhouse 2001) it was noted that, in the Illawarra Escarpment (34°25' 150°57'), ripe fruit could hang in the palm canopy from July to December (Waterhouse, pers. comm.). This observation concurs with that observed in the RNP (34°22' 151°01'). It is possible that synchrony of flowering between all sites is influenced by a common factor such as day-length, which would not vary much over the area in question, where fruit fall may be influenced by other, more latitudinally variable factors such as temperature. The loss of some fruit production data (Table 7.7) is indicative of the variability in the timing of fruit fall between years. Following the loss of four samples from 1998, adjustment was made to bring forward the timing of data collecting in 1999. The adjustment was insufficient to prevent a second loss of fruiting data because it too had varied from the timing of the first years collection. More detailed research is needed regarding the variation in fruit fall between sites to identify the key factors controlling this.

7.4.7 Quantity of fruit produced

Prior to this study the fecundity of *L. australis* had not been examined in detail. From the three seasons of fruiting recorded between 1998 and 2001 the mean proportion of adults producing fruit was 21%. This is similar to that reported for Cabbage Tree Creek in Victoria where fruit production recorded in 1995 was 22% or 24% (both figures given) (Orscheg & Parsons 1996b). The same study also recorded 10% and 5% fruiting of adults at two sites in RNP and 5% at an intermediate location between the RNP and Victorian site. High variation in fruiting between sites in the one year was also documented in the current study. During 2001 at MB 32% of palms produced female inflorescences (Table 7.3) and fruited subsequently, while no flowering or fruiting occurred at WNP that year.

In the years when fruiting did occur there was no difference in the magnitude of fruiting, in contrast to yearly flowering patterns. This discrepancy stems from the flower sampling being over 6 years where fruiting was only from three out of four years. The first and last years of flowering included the highest and second lowest flowerings from the study and contributed to the significant result. The height of the palms did not influence the level of fruiting recorded, nor did trunk height influence flowering during the study. From this it can be concluded that the increasing height of a palm trunk does not influence its reproductive potential; however, small sample sizes in the fruiting analysis would make this a preliminary result only, requiring further testing.

Fruit damage and fruit abortion as a result of the presence of sucking insects was observed in 16% of all fruiting events recorded between 1998 - 2001. It was observed that infestation of individual palms did not always include all inflorescences present in any one crown. There was evidence of blackening of the palm trunk or the ground in the immediate vicinity of palms from the fecal deposits of these insects, indicating that infestation had occurred some time before fruit had fully ripened. In only one individual did this cause a total loss of fruit. Sucking insects (Coreidae) have been recorded damaging juvenile fruits of *Cocos nucifera* (Stephenson 1981) but this is the first record of their presence in natural populations of *L. australis*. While the insects were present in all populations sampled, the damage to total fruit production was negligible.

A range of factors can influence the success of fruit and seed production including: limitations on pollen; resource limitations on nutrient and photosynthate availability; predators and disease; and damage from the physical environment (Stephenson 1981). From the results in this study it is more likely that the failure to successfully produce fruit within any one season is brought about by the more typical influence of resource limitation (Lee 1989; Stephenson 1981). If resources are lacking, rather than wholesale abortion of flowers and fruits once they were produced, *L. australis* appears to respond by not initiating flowering at all in those years. This may result in greater resources being available in subsequent seasons.

The percentage of reproductive palms that flowered in 2001 was twice that in the previous seasons (Table 7.4). It is likely that this substantial increase would also be reflected in the subsequent levels of fruiting from these sites in 2002, the recording of which was outside the scope of this study. This predicted increase in fruit production is based on the results during this study that demonstrated that poor flowering is followed by low fruit production, therefore the high flowering of 2001 should result in high fruit production in 2002. If it does follow that a dramatic increase in fruiting resulted from the flowering in 2001, it may be an indication of the species' tendency for mast seeding as discussed earlier. Significant variation in the fruiting of the New Zealand Nikau Palm, *Rhopalostylis sapida*, was reported over a seven-year period ranging from 54% to 83% (Enright 1992). It was concluded that this might reflect fluctuations in weather or events of mast seeding. Reproduction by *L. australis* exhibits some of the characteristics of mast seeding, including drastic fluctuations in crop size, supra-annual synchrony and irregular fruiting intervals (Janzen 1978; Silvertown 1980; Norton & Kelly 1988; Sork *et al.* 1993).

7.4.8 Widespread failure in fruit production

Widespread failure of fruiting has not previously been recorded for *L. australis*. The documented fruiting failure in 2000 encompassed at least 30% of NSW. The extent of this failure may have been greater had lower latitude sites beyond the NSW mid-north coast been investigated. The range of sites examined (Table 7.9) was inadequate to determine precisely at what higher latitudes failure of fruiting for *L. australis* became predominant. The fragmentation of the species' distribution over a large area was a factor in failure to determine this boundary. Variations in reproduction for the species have also been indicated from a broader study that found no palms flowering in 1995 at two sites within the RNP while 61% of adult palms were flowering at the species' most southern population in Victoria (Orscheg & Parsons 1996b). Very low levels of flowering and fruiting in *L. australis* populations probably occur infrequently.

The event in 1999 that resulted in reduced flowering and fruit failure in 2000 was not linked to disturbance of the sites by factors such as fire. While such disturbance influences reproductive rates of many other plant species (Gill & Catling 2001), there is no evidence to suggest that burning increases or synchronises flowering and fruiting in *L. australis* (Orscheg & Parsons1996b). Further research is necessary to clarify the cause of such failures.

7.4.9 Leaf production

Understanding leaf production in palms provides insight into the mechanisms of growth and reproduction. This study provides, for the first time, an indication of the years of leaf production that are contained within the growing head of *L. australis*. It has been established that the intrafoliar flowers require a minimum of four years to become exposed under the palm's growing head (Table 7.2). This suggests a minimum of five years is required for the emergent leaves produced in any year to finally abscise and be lost from the crown. From this it can be assumed that the crown of reproductive *L. australis* palms contains photosynthetic leaves amassed over 5 or more years of growth. This is the minimum estimated for *L. rotundifolia*, a species that may take as long as 12 years from leaf emergence to abscission, as determined by a study monitoring individual leaves (O'Brien & Kinnaird 1990). Growth rates of palms increase with increasing height (Table 5.2) and the estimate of crowns amassing 5 years of leaves is based on reproductive individuals. Non-reproductive palms, either with developed trunks or at the stage of developing a basal bulge, may retain leaves produced from more than 5 years of leaf growth. An example of this is a small-trunked individual monitored on Cabbage Tree Island (CTI). This palm was found to produce only a single leaf in 4 years without loss of any of the 12 developed leaves it had already amassed prior to this study. If this rate of leaf production was uniform then this palm may have taken up to 50 years to amass its current crown, an order of magnitude larger than for reproductive palms.

The relationship between leaf production, reproduction and plant height has never been explored for *L. australis*. From the time of the emergence of a trunk above ground the number of leaves produced increased until reproductive height was reached at approximately 6 m (Table 7.10), although regression of pooled data showed that height was not a good predictor of leaf numbers. After reproduction commences in a palm, leaf production slows and does not differ significantly throughout the plant's reproductive life. Overall, the rate of growth of a palm was not found to significantly affect the number of leaves an individual produces. Small sample sizes with inadequate representation in the full range of height classes present, however, precludes any definitive conclusions in this regard.

From the locations examined there was a significant difference in leaf production in RNP when compared to CTI, MB or WNP. The frequency and intensity of fires at RNP over recent years may explain the increased leaf production. Following the most recent fire in RNP in 1994, 75% of palms smaller than 9 m at a nearby site had all of their pre-fire leaves killed without the death of any individuals (Orscheg & Parsons 1996b). This would be classified as a low-intensity burn (Gill & Moore 1997), and most previous fires at the site (including those in 1988) were probably of similar intensity due to the protected location and areas of deep shade (Gill & Catling 2001). Palms in general have the ability to increase the rate of leaf production to replace damaged or lost leaves in response to fire or herbivory (Dalrymple & Fisher 1994). The effects of fire on the study site at RNP from the 1994 event, and perhaps the 1988 fire as well, may have been sufficient to increase leaf production to levels significantly higher than at sites that have not been burnt. While fire may increase leaf production immediately following the burn, the long-term effect of this disturbance is unknown.

A finding, which goes counter intuitively, was that there was no significant relationship between fruit and leaf production. The test to examine this relationship was weakened by the need to pool data across all sites. Further research is needed to examine this relationship using samples large enough to take into account intra-site differences.

There was no significant relationship between a palm's growth rate and the fruit it produced, and fruiting palms were no slower-growing than other reproductive adults. This suggests that the production of fruit does not cause a reduction in the growth potential of a palm.

7.4.10 Flowering history

The interpretation of inflorescence scars on the trunks of palms provides evidence of past flowering events. Through the application of incremental growth information the intervals between these scars can be aged. This information provides a history of when flowering events occurred as well as when reproduction was not attempted. This approach to the study of palm demography has no precedent.

The level of accuracy achievable from the dating of inflorescence scars is likely to decrease with time from the present. The growth rates used in the dating procedure are from current rates measured between 1998 to 2001, and take no account of temporal changes in growth rates. It is impossible to assess the total variability in growth that can be expected over the life of a palm. Dates given for the total history of a palm's flowering based on inflorescence scars, therefore, are approximate rather than definitive.

The question as to when a palm becomes reproductive is significant to understanding the potential for recruitment in a population (see Chapter 5). From this study the mean height of the first flowering event for *L. australis* was 6.1 m (Table 7.11). The lowest recorded height of a flowering palm, based on crown height, was a specimen of 5 m at Durras in southern NSW (Orscheg & Parsons 1996b). Trunk height of this individual could be estimated at 4 m, placing it within the range of those studied at RNP (Table 7.11). There was a significant difference between the height of first flowering between the two northern sites (CTI and MB) and the two southern sites (WNP and RNP). The limited number of sites precludes interpreting this as an effect of latitude, but further research may resolve this question.

This study has shown that palms flowering for the first time have a mean interval of 11 years before the subsequent flowering attempt, regardless of the sex of the individual (Figure 7.4). The subsequent interval between flowering averages 25% less time compared to the first flowering, and those after this required half the time between flowering intervals. This mechanism of early reproduction followed by a period of sustained growth without reproduction provides an insight into the ecological strategy of the species. One interpretation could be that of a resource-based limitation. A palm might be reproducing as soon as it reaches a predetermined minimum height, providing at least one possible cohort of seeds for its replacement (either by producing the fruit itself or providing pollen to fertilize another palm). It then would desist from further reproductive activity (for up to 65 years) until conditions had been met where further flowering was adequately resourced by perhaps a more favorable position in the canopy for photosynthesis.

During this study it has been demonstrated that palms vary in their growth increments between sites. This variability was highlighted in the intervals between scar formations within the different locations (Table 7.13). The results indicate that height alone is not an accurate determinant of the age of a palm, its flowering potential or the time spent as a reproductive adult. CTI and RNP represent the overall slowest and fastest growing palms, respectively, of the four sites studied (see Chapter 5).

The potential of inflorescence scars to provide accurate records of historical flowering is dependent on the accuracy of the methods used to determine growth rates. The methods used in this study provide a guide to the aging of inflorescence scars, but for reasons discussed elsewhere (Chapter 5), accuracy reduces with distance from the present time. In aging recent flowering events the accuracy of using inflorescence scars to assess flowering frequency appears comparable to that recorded as part of this study. The results of the observed flowering intervals over the period of this study ($\bar{x}$ = 1.8) are similar to inferred flower intervals based on the inflorescence scars ($\bar{x}$ = 2.4) from the same population. A more long-term study would be able to verify this if the observed flowering intervals from this study were re-examined as inflorescence scars after they appear below the crown.

In reviewing the 70-year history of flowering, events of low flowering were not discernable (Figure 7.5) because of pooling of data into six-year periods. Attempting to analyse patterns of low flowering from this data would become more speculative if viewed as individual years. The robustness of the technique of using inflorescence scars as an indicator of past annual flowering could be established by re-assessing the observed flowering data from this study. The measuring of gaps in inflorescence scars that were produced from known flowering events during this study should be possible in the coming years. Further research would assist in addressing this issue.

Despite the speculative nature of the historical flowering data when viewed at an annual level, a comparison was made with years of low rainfall. The lack of association between low flowering years with extreme ENSO events may be correct; however, the possible inaccuracy of the techniques involved in determining the historical dates could be masking any such relationship. When the observed annual proportion of reproductive adults was compared to recent ENSO data no significant relationship was apparent.

8. General discussion and conclusion

8.1 Yearly cycles: Flowering to seed germination

This thesis has elucidated some of the broader aspects of the ecology of *Livistona australis.* The palms generally flowered once every two years and the factors that influence poor years of flowering impacted over much of the range of the species' distribution. The factors affecting this are not yet understood. Reproductive failure appears to be followed by seasons of above-average flowering and fruiting that indicated a tendency for masting within local populations. Frequency of flowering did not vary with palm height. Nor did the frequency of flowering, or any other biomass measurement, vary with the sex of the individual, though males consistently produced fewer inflorescences than females. Flowering and fruit ripening occurred within a period of 12 months. From this study it was determined that the crowns of adult palms contain leaves amassed over 5 years of growth but juveniles may take as long as 50 years to replace all leaves in their crowns. Leaf production was correlated positively with trunk height and steadily increased after development of the basal bulge until reproductive age was reached.

Seed was up to 94% viable with 91% germination in a greenhouse, but was reduced to 19% by invertebrate attack and infection from soil pathogens *in situ.* Germination took up to eleven months with temperature appearing to be a controlling factor. The absence of mesocarp increased germination rates only when tested on an island free of seed predators. There was some evidence to suggest that in the presence of predators, seed that remained on the surface with the mesocarp intact was more likely to successfully germinate than seed that had the mesocarp removed. The Bush Rat, *Rattus fuscipes,* was the sole predator of fallen seed, but did not prey on newly germinated seedlings. Seedlings survival was poor in the presence of the European Rabbit, *Oryctolagus cuniculus,* but was higher for seeds germinating after their eradication from Cabbage Tree Island. Seedlings had growth resources within the attached seed that assist establishment, but evidence from this study suggests that after 12 months sufficient light for photosynthesis was needed if survival was to continue. Under good light conditions *in situ* seedlings produced leaves at a measurable rate for up to six years following germination, but at sometime after this, leaf production slowed as a basal bulge was developed and the process of trunk formation began.

8.2 Growth rates, aging and population structures

Morphological measurements showed that the taller the palm the larger the crown and the overall size of adult palms was strongly influenced by the local environment. At more sheltered sites taller, larger crowned palms developed. Rates of growth between these favourable sites and other, more exposed populations, were highly variable. In general, growth was faster and more variable prior to palms reaching reproductive age, after which the rate of growth declined and stabilised. Fire appeared to stimulate growth of sub-adults. Prior to palms reaching reproductive age, the basal area of the trunk was shown to swell, probably to strengthen the trunk in order that it is capable of supporting the additional load caused by fruit hanging in the crown.

The recognition and identification of flowering scars on the trunks of adult palms provided insight into the reproductive history of populations. Palms had a mean height at first flowering of 6.1 m and based on measurements of rates of growth, reach maturity at an average of 170 years, with the ability to reproduce for a further 160 years or more. Observations of the process of senescence suggested that accident, by structural failure or breakage of the trunk, was the prime cause of death in natural palm populations.

The structure of palm populations within size classes spanning young seedling to juveniles prior to trunk development appeared to be influenced by disturbance from fire, competition for resources and mammal browsing. The structure of trunked palm populations showed marked effects of long-term disturbance. Within 80 years, continuous suppression of seedlings led to a dearth of advanced seedlings and young trunked palms on Cabbage Tree

Island and a concentration of trunked palms in the tall height classes. In contrast, a stable population in an undisturbed habitat at Mungo Brush showed a large number of seedlings and trunked palms from smaller size classes and a relatively even distribution of palms in taller height classes. Palm populations that have been subject to disturbance factors such as fire have a more complex size structure. This was because the frequency and intensity of the fires not only influence recruitment, rates of growth and survival of the palms, but also affect the associated vegetation. Species composition of associated vegetation can change with more fire tolerant species becoming dominant, including exotic weeds. The change in species composition, particularly of ground covers, may increase the frequency of browsing mammals in an area and this may impact on the successful recruitment of palms. The manner in which these disturbance factors impact on palm population structure was far from clear.

8.3 Conservation management of palm populations

In studying the demography of *L. australis* many of the vital statistics concerning seed production and germination, seedling establishment and survival, time taken to reach reproductive maturity and longevity of the species have been determined. This information can provide a basis from which to better manage populations of the species, particularly those at risk of decline due to isolation, harvesting of reproductive adults, frequent fires or other disturbance. Isolated stands have little input by way of seedling recruitment from other populations. Harvesting of reproductive adults may suppress potential recruitment of small populations for an extended period and combined with other disturbance factors will lead to increased risk of local extinction. For effective palm conservation in southern NSW particularly, an inventory of the status of current populations would be beneficial. Such an inventory could cover assessment of the population structure of each stand, the structure and species diversity of associated vegetation and evidence of disturbance such as grazing and fire frequency. Management actions may include the fencing of stands, protection of vulnerable stands from fire by appropriate control measures or manipulation of associated vegetation to assist in palm regeneration.

The close link between Gould's Petrel and *L. australis* on Cabbage Tree Island dictates that for the petrels' ongoing survival it is important that the palm population at this site be appropriately conserved and managed. The exclusion of fire will be beneficial to regeneration within the population, allowing current regeneration to continue unimpeded. It is also essential that no mammal species be introduced to the island, particularly rats, as palm recruitment would be severely hampered by such an event.

A further consideration for conservation of this palm species relates to the aesthetic nature of the plant. The demand for the use of mature *L. australis* in streetscapes and landscaping in major urban and tourist developments may place an unrealistic pressure on extant populations outside of National Parks and Nature Reserves. Their removal from populations in southern NSW may further exacerbate the fragmentation of this species over its southern range and in turn impact on species that rely on their fruits such as Topknot Pigeon. The individual populations would take a century or more to recover from this form of disturbance. It would seem prudent, if conservation of the species over its entire range were a goal, that any removal of adult *L. australis* be limited to the larger more numerous populations north of Sydney. While these sites could not sustain regular harvest, their size and the close proximity of additional seed sources may reduce the chances of local extinction. A system of licensing may need to be introduced to ensure that any removal of palms be done in a manner to further reduce the possibility of fragmentation of the species over its entire range.

8.4 Implications for further research

This study described a technique to determine the growth rates of palms by taking a repeated series of measurements immediately below the crown. While this technique provided repeatable measures of rates of growth, the method used to determine the time taken to produce a basal bulge was not entirely satisfactorily. If future research was to be attempted to elucidate the time taken for palm trunks to emerge, a more long-term approach may be necessary. Seedlings may need to be selected in a range of palm environments and their growth monitored over several decades to obtain a satisfactory answer.

An innovative approach, involving tracking inflorescence scars that appear as a series of bulges along the trunk of the palm, was used to determine flowering frequency. Once the growth rate of palm trunks was determined the approximate date of each flowering could be calculated. This provided an opportunity to look back at the patterns of flowering that have occurred over much of the last century. No cause could be assigned for the pattern of flowering observed. If future research was to increase the sample size of adults examined at a study site, the accuracy of the pattern of flowering observed in this study may be enhanced. This may allow a better understanding of any abiotic process that drives palm reproduction on a broader scale.

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