

# Demographics, pollination syndrome and conservation status of *Macrozamia platyrhachis* (Zamiaceae), a geographically restricted Queensland cycad

Irene Terry<sup>A,E</sup>, Paul I. Forster<sup>B</sup>, Chris J. Moore<sup>C</sup>, Robert B. Roemer<sup>D</sup> and Peter J. Machin<sup>B</sup>

<sup>A</sup>Department of Biology, University of Utah, Salt Lake City 84112, USA.

<sup>B</sup>Queensland Herbarium, Environmental Protection Agency, Brisbane Botanic Gardens, Mt Coot-tha Road, Toowong, Queensland 4066, Australia.

<sup>C</sup>Department of Primary Industries and Fisheries, Yeerongpilly, Queensland 4105, Australia.

<sup>D</sup>Department of Mechanical Engineering, University of Utah, Salt Lake City 84112, USA.

<sup>E</sup>Corresponding author: Email: terry@biology.utah.edu

**Abstract.** To assess the International Union for Conservation of Nature (IUCN) status of *Macrozamia platyrhachis* F.M.Bailey, we surveyed this central Queensland cycad for its population abundance and health and its pollinator type and pollination syndrome (thermogenesis and volatile emissions). Plants are locally abundant within the 11 discrete populations surveyed, with an estimated population of 611 315 adult plants. Plants are highly restricted to a small area of occupancy, seed dispersal is nearly non-existent and extreme fires appear to have destroyed almost all seeds and seedlings and decimated the pollinators. Of known *Macrozamia* pollinators, only the thrips, *Cycadothrips chadwicki* Mound, were found on cones, and these were found in very low numbers. The pollination syndrome for this cycad appears to be unique, based on two cone traits. For one, thermogenesis peaks in early evening, a contrast with daytime peaks of other *Cycadothrips*-pollinated *Macrozamia*, but matches that of the *Tranes* weevil-pollinated *Macrozamia machinii*. In addition, cone volatiles include both previously unreported compounds as well as those reported exclusively on either *Cycadothrips*- or *Tranes*-pollinated species. Based on its small, fragmented area of occupancy, projected population declines and the unique pollination syndrome, we recommend that *M. platyrhachis* retain its current status as ‘Endangered’. Habitat management plans should stipulate that controlled burns be avoided during cycad coning season and that wildfires be controlled to minimise damage to seedlings and pollinators.

## Introduction

Cycads (families Cycadaceae and Zamiaceae) are an ancient lineage of plants that originated in the Permian and are thought to have been most abundant during the Mesozoic (Norstog and Nicholls 1997; Schneider *et al.* 2002; Brenner *et al.* 2003). Currently there are ~300 named species of cycads found in sub-tropical and tropical parts of both the Old and New Worlds and in warm climates of some temperate zones (Jones 2002; Whitelock 2002; Hill *et al.* 2004). Australia is a major centre of diversity for extant cycads with ~81 endemic species in the genera, *Bowenia* (2 spp.), *Cycas* (36 spp.), *Lepidozamia* (2 spp.) and *Macrozamia* (41 spp.) (Hill 1998; Forster 2004a; Hill *et al.* 2004).

Cycads can be considered as ‘flagship’ species for conservation biology (Given 1994; Meffe and Carroll 1997) because more than 50% of species are threatened, most are restricted in distribution (Donaldson 2003, 2004) and they have unusual life histories (e.g. dioecy; gymnosperms with dependent pollination mutualisms with insects; thermogenic cones). They are also of much commercial interest for landscape horticulture and collectors (Whitelock 2002). There are many factors that have been attributed to causing their global

decline over geological time, including climate change and their inability to compete with angiosperms (Norstog and Nicholls 1997). In addition, many life history features continue to make them less competitive and more vulnerable to frequent perturbations (Donaldson 1995). For one, many species have a long juvenile stage, from 5 to 20 or more years, and thus cycads are generally absent from areas of high disturbance (Bond 1989). Second, pollination of these dioecious plants is mediated by insects involved in highly specialised mutualisms with their hosts (Schneider *et al.* 2002), which may be adversely affected by the many years between coning events that may occur at unpredictable intervals. Third, most species occur in disjunct populations with little evidence of genetic flow between populations resulting in incipient inbreeding (Sharma *et al.* 1998, 1999, 2004; van der Bank *et al.* 2001; Keppel *et al.* 2002; González-Astorga *et al.* 2003; Xiao *et al.* 2004; Jianguang *et al.* 2005; Xiao and Gong 2006). Fourth, seed dispersal is very localised (i.e. < 100 m) (Burbidge and Whelan 1982; Forster 2007; Snow and Walter 2007), and subsequent seedling establishment is usually very low (cf. Raimondo and Donaldson 2003) with seed death rate high as a result of

predation and fire. In addition, massive land clearing for development and agriculture and illegal collection of rare species likely interact synergistically with the above life history traits to cause further declines (Donaldson 2003). Together, these factors contribute to the modern species being restricted in their distribution, often to areas of aperiodic dryness and low soil fertility, similar to many conifers (Bond 1989).

Regarding *Macrozamia* species, little is known about their fecundity, dispersal ecology, pollination biology and ability to persist. Forster (2004b, 2007) identified several variables that may limit persistence and expansion of cycad populations in Queensland, especially fire frequency and severity, low recruitment and pollination failure. *Macrozamia* cycads have irregular coning events that appear to be stimulated by fire in the habitat two years beforehand (Baird 1977; PIF, PJM pers. obs.) that may result in a massive masting of seed cones. However, there is limited quantitative data concerning seed production resulting from masting events (Ballardie and Whelan 1986). Seed dispersal appears to be poor with population boundaries often being sharply defined, indicating that dispersal is limiting plant distribution (Primack and Miao 1992; Snow and Walter 2007). Most seeds of studied *Macrozamia* species are not

dispersed more than 1 or 2 m from the adults (Ballardie and Whelan 1986; Snow and Walter 2007; PIF, PJM pers. obs.), although up to 24 m has been recorded for *Macrozamia riedlei* (Burbidge and Whelan 1982); still a short dispersal distance (cf. Cain et al. 2000). Snow and Walter (2007) found that native rodents (*Rattus* sp.) were only seed predators of *Macrozamia lucida*, whereas brushtail possums (*Trichosurus vulpecular*) were seed dispersers as well as predators.

Of the *Macrozamia* species studied to date, pollination is undertaken by either obligate specialist beetles (*Tranes* sp. weevils) or thrips (*Cycadotherips* sp.), with the pollinator dependent on the cycad cones to complete their life cycles, and the cycads dependent on the insects for pollination (Table 1). These cycad–insect interactions are dependant mutualisms, as found in some angiosperm pollination systems, e.g. fig–fig wasp and yucca–yucca moth (Weiblen 2002; Pellmyr 2003). The cones of these cycads (particularly males) are thermogenic, as are most of the studied cycads (Tang 1987) with a daily periodicity that is associated with increased volatile emissions and insect movement between cones (Terry et al. 2004a, 2004b). *Tranes* weevils and *Cycadotherips* thrips have been documented from a range of *Macrozamia*

**Table 1. *Macrozamia* species and their known or putative pollinator**

Sections within *Macrozamia* species, M = *Macrozamia* and P = *Parazamia* (Forster 2004a). Species grouped by location (State) in Australia, designated by State abbreviation. Conservation status designated by T, threatened or Not T, not threatened (Hill and Stevenson 2000; Forster 2004b). Reference code: O90 (Ornduff 1990); O91 (Ornduff 1991); C93 (Chadwick 1993); CandL93 (Connell and Ladd 1993); F94 (Forster et al. 1994); M91 (Mound 1991); M01 (Mound and Terry 2001); M98 (Mound et al. 1998); J01 (Jones et al. 2001); T04 (Terry et al. 2004a); unpubl. unpublished voucher specimens

<i>Macrozamia</i> species (Section)	Location	Status	Pollinator or putative pollinator	Reference or species complex
<i>M. communis</i> (M)	NSW	Not T	<i>Cycadotherips</i> , <i>Tranes</i>	O90, M91, C93
<i>M. concinna</i> (P)	NSW	Not T	<i>Tranes</i>	unpubl.
<i>M. fawcettii</i> (P)	NSW	Not T	<i>Tranes</i>	F94
<i>M. johnsonii</i> (M)	NSW	Not T	<i>Tranes</i>	F94
<i>M. montana</i> (M)	NSW	Not T	<i>Cycadotherips</i> , <i>Tranes</i>	unpubl.
<i>M. cardiacensis</i> (M)	Qld	T	<i>Cycadotherips</i> , <i>Tranes</i>	J01
<i>M. conferta</i> (P)	Qld	T	<i>Tranes</i>	F94
<i>M. crassifolia</i> (P)	Qld	T	<i>Tranes</i>	F94 <i>M. pauli-guilielmi</i> <sup>A</sup>
<i>M. douglasii</i> (M)	Qld	Not T	<i>Tranes</i>	F94, <i>M. miquelii</i> <sup>B</sup>
<i>M. lomandroides</i> (P)	Qld	T	<i>Tranes</i>	F94
<i>M. longispina</i> (M) <sup>C</sup>	Qld	Not T	<i>Cycadotherips</i>	F94, <i>M. miquelii</i> <sup>B</sup>
<i>M. lucida</i> (P)	Qld	Not T	<i>Cycadotherips</i>	F94
<i>M. machinii</i> (P) <sup>D</sup>	Qld	T	<i>Tranes</i>	F94
<i>M. miquelii</i> (M)	Qld	Not T	<i>Cycadotherips</i> , <i>Tranes</i>	F94, <i>M. miquelii</i> <sup>B</sup>
<i>M. moorei</i> (M)	Qld	Not T	<i>Ulomoides australis</i> <sup>E</sup>	T2004
<i>M. mountperriensis</i> (M)	Qld	Not T	<i>Cycadotherips</i>	F94, <i>M. miquelii</i> <sup>B</sup>
<i>M. parcifolia</i> (P)	Qld	T	<i>Tranes</i>	F94 <i>M. pauli-guilielmi</i> <sup>A</sup>
<i>M. pauli-guilielmi</i> (P)	Qld	T	<i>Tranes</i>	F94 <i>M. pauli-guilielmi</i> <sup>A</sup>
<i>M. serpentina</i> (M)	Qld	T	<i>Cycadotherips</i>	F94, J01
<i>M. macdonnellii</i> (M)	NT	Not T	<i>Cycadotherips</i>	M01
<i>M. riedlei</i> (M)	WA	Not T	<i>Cycadotherips</i> , <i>Tranes</i> , <i>Paracucujis rostratus</i> <sup>E</sup> <i>Xenocryptus tenebroides</i> <sup>E</sup>	O91, C93, M98, CandL93

<sup>A</sup>*M. pauli-guilielmi* species complex (Jones and Forster 1994); *M. crassifolia* (cs sp. aff. *pauli-guilielmi* No. 1 in Forster et al. 1994); *M. parcifolia* (cs sp. aff. *pauli-guilielmi* No. 2 in Forster et al. 1994) (Jones and Forster 1994).

<sup>B</sup>*M. miquelii* species complex (Jones et al. 2001).

<sup>C</sup>cs sp. aff. *mountperriensis* in Forster et al. 1994 (Jones et al. 2001).

<sup>D</sup>cs sp. aff. *plurinervia* in Forster et al. 1994; *M. machinii* is in the *M. plurinervia* complex (Jones and Forster 1994).

<sup>E</sup>Putative pollinators, those insects not tested rigorously as pollinators on any *Macrozamia* species: *Ulomoides australis* (Tenebrionidae); *Paracucujis rostratus* (Coleoptera: Boganiidae) and *Xenocryptus tenebroides* (Coleoptera: Languriidae) from Ornduff 1991; Connell and Ladd 1993. *Tranes* sp. and *Cycadotherips* sp. have been tested as pollinators on some but not all of the species on which they have been found.

species, and a few species of *Macrozamia* have a dual weevil–thrips pollination mutualism (Table 1). Other putative pollinator species have been collected (Table 1) but have not been confirmed by rigorous testing.

*Macrozamia platyrhachis* F.M.Bailey is a small (<50 cm tall) cycad (Fig. 1A, B) in *M.* section *Parazamia* (Hill 1998; Forster 2004a) and is endemic to central Queensland with a distribution centred on the Blackdown Tableland in the Dawson Range (Fig. 2). It has been listed as ‘Endangered’ by the Australian Federal Government *Environment Protection and Biodiversity Conservation* (EPBC) ([www.deh.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=flora](http://www.deh.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=flora)) (effective 16 July 2000) and the Queensland State Government *Nature Conservation Act 1992* schedule (effective 1994 and current in the 2006 *Nature Conservation (Wildlife) Regulation*). This listing was based on limited knowledge of the species’ distribution and abundance and mainly relied on herbarium records and anecdotal information from cycad hobbyists. In contrast, other reports have suggested a less threatened status. Osborne (1995) proposed *M. platyrhachis* as ‘Vulnerable’ and presented a figure of 4000 plants in the wild.

More recently Osborne (2000) and Hill and Osborne (2001) considered that *M. platyrhachis* was ‘not considered to be at risk, this species is well conserved in Blackdown Tableland National Park (IUCN Red List category **LR**, lc; ROTAP risk code **2RCat**)’, and Hill (2003) suggested that *M. platyrhachis* was of ‘Least Concern’ with 2500–10 000 individuals in ~50 km<sup>2</sup>. However, those reports do not indicate how their figures were obtained and their suggestions have not been adopted into official listings.

To obtain data to examine the status of *M. platyrhachis* relative to IUCN (2001) criteria, we surveyed populations and documented its (1) geographical distribution, habitat, occupancy and abundance, (2) population health (coning, pollinator presence, recruitment, dispersal, predation) and (3) pollination biology (likely pollinator and pollination syndrome based on the specific cone traits of thermogenesis and volatile emissions). Following the approach of Schemske *et al.* (1994), we also address several demographic questions and identify the vulnerable life history stages. For any *Macrozamia* species, a significant vulnerability is its obligate pollination mutualism. Thus, identification of the associated pollinator is required for



**Fig. 1.** *Macrozamia platyrhachis* female (A) and male (B) cones in habitat showing the stature of the plants and (C) a plant showing the top of the burned caudex in one habitat (D) that has been severely burned ~two years prior, with surviving trees still showing the blackened burned trunks.

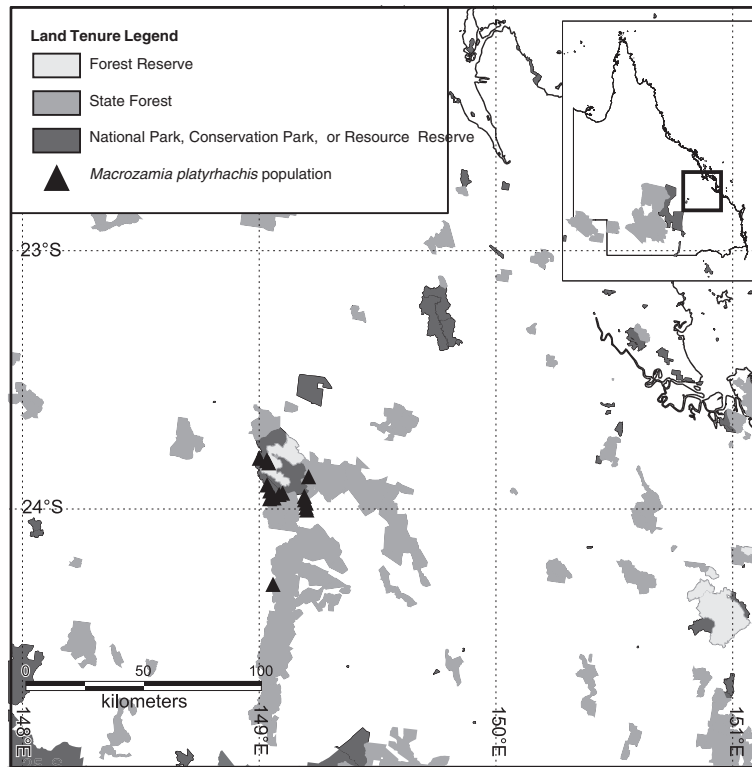


Fig. 2. Map of regional distribution of *Macrozamia platyrhachis* populations in central Queensland.

developing management options for conservation of the pollinator as well as its host. We surveyed cones for pollinators and measured the associated cone traits to determine whether the *M. platyrhachis* pollination mutualism is unique. Unique obligate pollination mutualisms are especially worthy of conservation and study (Bond 1994; Kearns *et al.* 1998), not only for their scientific value but also to understand the role and needs of pollinators. Specifically, we wanted to determine whether this system fits one of the three major pollination syndromes for *Macrozamia* identified to date (Mound and Terry 2001; Terry 2001; Terry *et al.* 2004a, 2004b, 2005) viz.: (1) species pollinated only by *Cycadotherips* sp. that move between cones during the daytime associated with daytime cone thermogenesis and release of specific volatiles, (2) species pollinated only by *Tranes* sp. weevils that move between cones around sunset and early evening in association with cone thermogenesis or emission of specific volatiles, (3) species pollinated by both *Cycadotherips* sp. and *Tranes* sp. that move between cones at midday and dusk respectively.

### Materials and methods

We conducted our surveys during November 2003 and 2004 (November is the coning season for many other *Macrozamia* in *M.* section *Parazamia*). In 1999, 2000 and 2002, uncontrolled and intense wildfires affected different parts of Blackdown Tableland National Park and adjacent areas (see Fig. 1C, D), affecting almost the entire area occupied by *M. platyrhachis* (D. Samson, Queensland Parks and Wildlife

Service, pers. comm.). These fires were sufficiently intense as to kill mature canopy individuals of a range of eucalypt species. Because *Macrozamia* cycads will often mast cone approximately two years after such events (Baird 1977), we considered 2003 and 2004 to be propitious to observe coning and pollinator activity. Also, seed set was evaluated at one site in March 2005, when seeds were unravelling from cones, four months after a mast coning event.

### Geographical distribution, habitat, occupancy and abundance

*Macrozamia platyrhachis* has been previously recorded from the Blackdown Tableland (National Park, State Forests), the adjacent pastoral properties on Grazing Homestead Perpetual Leases (GHPL) and the Planet Downs station area of the Dawson Range (Fig. 2). There were few prior herbarium collections of this species (eight vouchers from four identifiable localities) and few or no data on population abundance, apart from terse collectors' notes on herbarium labels. Based on local knowledge from EPA staff, we surveyed 11 disjunct (by >2 km) populations in the Dawson Range (Table 2) to establish their area of occupancy (IUCN 2001). Vouchers of all 11 populations were deposited in the Queensland Herbarium (BRI). The total area of occupancy of each population was determined by summing its measured square and rectangular sub-areas, as determined by GPS measurements of their outer edges. To estimate the number of individuals in each population, we counted adults in one representative rectangular 50 × 8 m plot (0.04 ha) and extrapolated to the entire population size.

**Table 2. Population statistics for 11 populations of *Macrozamia platyrhachis* in November 2003**

NP = National Park; SF = State forest; GHPL = Grazing homestead perpetual lease

Population number and voucher data [Tenure]	No. of plants in 50 × 8 m	Projected occupancy of population (ha)	Projected no. of adults in population	Number of adults per hectare	Seedlings present	Evidence of coning	Evidence of pollinators
1. PIF29617 [GHPL]	68	25	42 500	1700	None	2003	Yes
2. R.Healy 205007 [GHPL]	53	36	47 700	1325	None	?2001	No
3. R.Healy 205009 [GHPL]	55	144	198 000	375	None	None	No
4. R.Healy 205008 [GHPL]	154	9	34 650	3850	None	?2001	No
5. PIF29634 [NP]	183	9	41 175	4575	4/0.04 ha <sup>2</sup>	2003	Yes
6. PIF29637 [NP]	82	16	32 800	2050	None	2003	Yes
7. PIF29638 [NP]	80	9	24 790	2750	None	2003	Yes
8. PIF29644A and B [NP]	110	49	122 500	2500	None	2003	Yes
9. PIF29647 [NP]	56	16	22 400	1400	None	2003	Yes
10. PIF29648 [NP]	28	36	25 200	700	None	2003	Yes
11. PIF29649 [SF]	49	16	19 600	1225	None	2003	Yes

*Population health (coning, pollinator presence, recruitment, evidence of seed dispersal, predation and poaching)*

In the same plot, we also counted the following and estimated their totals per population as for adult plants: the presence and number of seedlings (small individuals with leaves less than 10 cm long); evidence of coning (current and past seasons); evidence of pollinators (either *in situ*, or inferred from existence of pollinated female cones); evidence of seed; evidence of seeds dispersed more than 2 m away from adult plants (indicating beyond gravitational movement); evidence of invertebrate predators such as the lycanid butterfly *Theclinestes onycha* (Hewitson) and the chrysomelid beetle *Lilioceris nigripes* (Fabricius) (Forster and Machin 1994); and evidence of poaching (i.e. holes in the ground, discarded leaves, damaged plants).

*Pollination biology*

To identify potential pollinators and determine whether or not the pollination mutualism fits previously described pollination syndromes, we collected temperature and volatile data from several cones and sampled cones for insects during 2003 (13–15 November) and 2004 (5–7 November). Results were compared with traits and pollinators of previously studied *Macrozamia* species (Seymour *et al.* 2004; Terry *et al.* 2004a, 2004b; Roemer *et al.* 2005).

Insects were sampled on dehiscent male cones by either removing a few sporophylls or by destructively sampling an entire cone. Female cones were non-destructively sampled by observing female cones for insect presence and by trapping insects arriving at cones. In 2003, only a few plants with cones were present, with most plants past or nearly past their dehiscence phase. Three populations were studied: Population 1 had three male cones (45, 90 and 95% dehiscence stages); population five had five male cones (one pre-dehiscent and all others >90% dehiscent); and Population 8 had twenty male cones, nine of which (all >85% dehiscent) were sampled. In 2004, Populations 5 and 8 were re-surveyed. At Population 5, a mast coning event was in progress and almost

all male cones were <10% dehiscent. Fifteen male cones were sampled entirely, and six to eight sporophylls from each of thirty other male cones were inspected. Sticky traps (collars with Tack trap (Tanglefoot, Grand Rapids, MI, USA), 3 cm wide × 7 cm diameter) were placed around twenty five receptive female cones (i.e. odours detected and small gaps observed between sporophylls.) for 48 h. At Population 8, ten male cones were destructively sampled.

Cone volatiles were collected to compare quantitative and qualitative changes at mid-day, late afternoon and evening. Sample times were 120 min (except one of 100 min). Previously described protocols were used (Terry *et al.* 2004b). In brief, air and volatiles were withdrawn (100 mL min<sup>-1</sup>) from a polyester bag-covered cone through a glass Pasteur pipette containing Porapak Q. Pipettes were wrapped in aluminium foil and stored at ~15–20°C. Volatiles were desorbed from the Porapak Q (Waters, Milford, MA, USA) within three days of collection with 1 mL dichloromethane and the resulting samples concentrated to 0.5 mL. Chemical components were identified by GC/GC-MS methods (Terry *et al.* 2004a, 2004b). In addition, solid phase micro-extraction (SPME) techniques were used to determine volatile components of an excised male cone in the laboratory. The cone was enclosed in a polyester bag and a SPME (carboxen-PDMS) fibre was exposed inside the bag between 1200 and 1300 hours. The SPME fibre was then placed in the injection chamber of the GC-MS for desorption and analysis.

To determine the diel timing of cone thermogenesis, temperatures of shaded cones (under awnings) were monitored continuously (2-min intervals) *in situ* by using protocols reported previously (Terry *et al.* 2004b). Concurrent ambient temperatures were measured close to cones under similarly shaded micro-climates. In 2003, four male and one female cones were sampled, and in 2004, seven males and three females were sampled. In addition, in 2003 six male and six female cones were measured with a hand-held thermocouple data logger (Fluke 54 II: Fluke Corporation, Everett, WA, USA) at ~30 min intervals from ~0930 to 2130 hours. Average *M. platyrhachis* male cone dimensions (min/max) were diameter 5.1 cm (4.5/6) and height 21 cm (16/27.5). Their

average dehiscence status was ~45% dehisced (range, 5–90%). The 10 monitored female cones had an average (min/max) diameter of 6.5 cm (5.5/7.5) and height of 12.2 cm (9.5/13.5). A mathematical modelling procedure that estimates the timing and magnitude of a cone's metabolic rate from measured *Macrozamia* cone temperatures (Roemer *et al.* 2005) was used to evaluate and compare the model results of *M. platyrhachis* cones to those of *Macrozamia machinii* and *M. lucida*.

## Results

### *Geographical distribution, habitat, occupancy and abundance*

On the basis of our survey and interpretation of the herbarium record at BRI, there are 12 known major populations for *M. platyrhachis* (Table 2). Only 47% of the plants occur on National Park or State Forest land where land management conservation recommendations can be put into practice. We surveyed all but one of these (*Brushe JB1598*, 28 March 1998, from Planet Downs Station), where the plants were recorded as 'abundant'. This population is less than 20 km distant to those that we surveyed and appears to be of a similar density and occupancy (J. Brushe pers. comm. 2004). All sites were at altitudes between 300 and 780 m in eucalypt dominated woodland or open forest on soils derived from sandstone, with sandstone rocks and outcrops being predominant in the landscape. Dominant canopy species in these communities included *Angophora leiocarpa*, *Corymbia bunites*, *C. citriodora* subsp. *citriodora*, *C. hendersonii*, *C. watsoniana*, *Eucalyptus baileyana*, *E. cloeziana*, *E. crebra*, *E. melanoleuca*, *E. suffulgens*, *Lophostemon suaveolens* and *Lysicarpus angustifolius*. The mid- and under-storeys of the vegetation may be quite dense, depending on fire history.

We estimated a total area of occupancy of 365 ha for the 11 populations, with individual populations occupying from 9 to 144 ha (average 33.2 ha) (Table 2). Adult numbers in the 50 × 8 m (0.04 ha) plots, varied from 28 to 183 (average 84) plants, with the projected numbers per ha ranging from 700 to 4575 (average 2086), and per population ranging from 19 600 to 198 000 (average 55 574) plants. On the basis of these numbers, we estimate as many as 611 315 adult plants of *M. platyrhachis* in habitat.

### *Population health (coning, pollinator presence, recruitment, dispersal, predation and poaching)*

#### *Coning*

In 2003, cones were abundant in 6 of the 11 populations studied, and absent or very rare in the other 5 (Table 2). In 2004, two of those five sites were resurveyed and were found to have mast coning. Most sites had mast coning events following fires two to three years prior, which corroborates observations on other species (Baird 1977; PIF, PJM, pers. obs.). Interestingly, at Population 8 there are two subpopulations, separated by a firebreak road, and each responded differently to fires that swept through both sides of the road (October 1999 and January 2002, D. Samson, QPWS, pers. comm.). One subpopulation, 8b, had no cones in 2003, but cones were found on 89% of its plants in 2004. In contrast, at 8a most plants had cones in 2003 but no cones were found in 2004.

In terms of the timing of cone appearance and the pollination period, we found that of 1203 plants counted in the November 2004 survey at Population 5, 79 male and 29 female plants, or 9% of all plants, had cones. A later count at this same site during March 2005 revealed that 302, or 47.3%, of 639 plants surveyed had cones; 158 males and 144 females revealing that early November was at the beginning of the population's coning process in 2004.

#### *Pollinator Presence*

All coning populations had evidence of insect pollinators (Table 2), determined by finding either insects *in situ* or pollinated female cones with expanding ovules.

#### *Recruitment*

Only four seedlings were seen, all in one population (Table 2). It is assumed that all other seedlings had been killed in the fires as it takes several years for the underground caudex to develop to the stage when the contractile roots and stems can pull it below the level of high temperature penetration (Fig. 1C) (Stevenson 1980; Norstog and Nicholls 1997). The fires had been sufficiently severe to kill all the foliage on adult cycads, with the existing foliage having been produced since the fires (Fig. 1C, D).

#### *Dispersal*

Although there were thousands of old seeds lying immediately adjacent to the adult females, these had all been killed by fires based on the seeds either being burnt through or shown to be unviable (seeds floated in water). There was no evidence of dispersal away from the adult females.

#### *Predation*

Adult butterflies (females) of *T. onycha* were abundant in all populations, except for Population 1, and this represents a new host plant record for that butterfly (Forster and Machin 1994). Females were observed laying eggs on young expanding fronds of the cycad and larvae were present in most populations. No other invertebrate predators were observed.

#### *Poaching*

There was no evidence of recent poaching of adult plants of *M. platyrhachis*, although only Populations 5 and 6 are in an area with public access. The presence of mature plants of *M. platyrhachis* in private collections in Australia and several botanic gardens overseas (Osborne 1995) indicates that poaching or removal of seeds from National Parks and State Forests has occurred in the past. If these plants were taken as seed or seedlings, they must be at least 20 years old, based on age at reproductive maturity for this species (pers. comm. S. Walkley).

### *Pollination biology (insect sampling, pollination, cone thermogenesis and volatile emissions)*

#### *Insect sampling*

During the 2003 survey, insects were sampled from male cones at Populations 1, 5 and 8. The only insects found were adults and larvae of thrips and moths. In male cones that

were destructively sampled, the numbers of thrips per cone were very low (from 0 to 12 adult thrips and 0 to 12 larvae, with an average 3.7 adults per cone). No thrips were found in cones that were  $\geq 100\%$  dehisced. Moth larvae and adults were found mostly in the older spent cones, up to 30 larvae in one cone. No insects were observed near female cones. Voucher insect samples were sent to CSIRO Entomology (Australian National Insect Collection), and their identities were confirmed as *Cycadothrips chadwicki* Mound for the thrips and *Conobrosis* sp. aff. *haplochroma* Common for the moth.

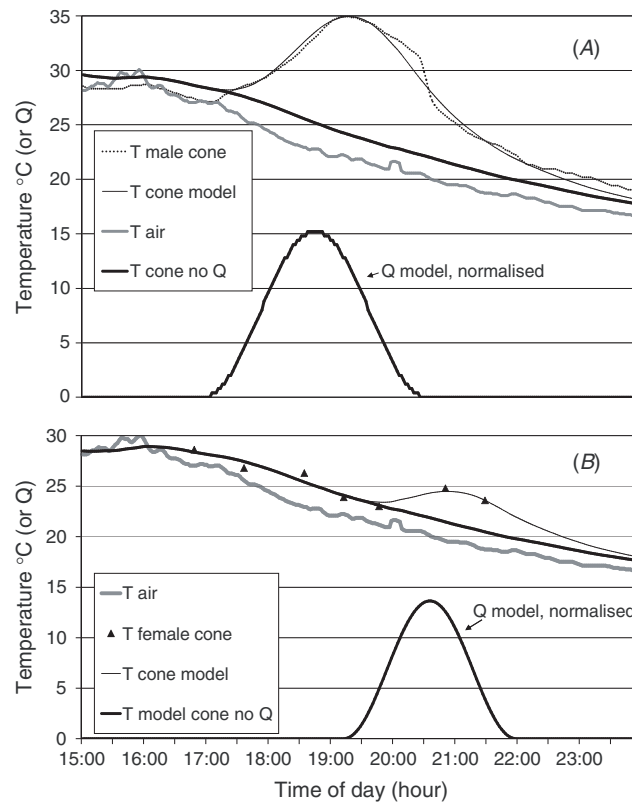
During the November 2004 survey, no insects were found inside male cones at Populations 5 or 8, and only termites were trapped (during a nearby mass emergence of winged termites) around female cones at Population 5. Cones were at the initial stages of their pollination phase (see Materials and methods).

*Seed set*

Despite the lack of potential pollinators at Population 5 in November 2004, substantial seed set was observed at this site in March 2005. Of 56 female cones examined, all had at least one viable (pollinated and fertilised) seed, with an average of 54% ( $\pm 4$  S.E., range 2–98%) seed set per cone (range of 29–254 ovules per cone). Because a higher percentage of coning plants was found in March 2005 (47%, see previous section on coning) compared with early November 2004 (9%), many more cones emerged after the early November survey. If pollinators tended to emerge later and/or are more concentrated later in the coning season, this would explain the lack of detection of pollinators during early November 2004.

*Cone thermogenesis*

Male cones are thermogenic only during sunset/early evening (Fig. 3A, Table 3). Sunset occurs around 1820 hours during November at this site, with civil twilight (sun  $6^\circ$  below horizon) about 1850 hours. Nine of the eleven males measured at 2 min intervals and five of the six males measured manually were thermogenic, with similar temperature peak magnitudes (avg. =  $30.4^\circ\text{C}$  and  $32.4^\circ\text{C}$ , respectively) and peak times (1924 and 1914 hours, respectively). The peak cone temperatures were on average  $8.3^\circ\text{C}$  and  $9.1^\circ\text{C}$ , respectively, above concurrent ambient temperatures. Only two of the ten female cones sampled, both sampled manually, showed evidence of thermogenic



**Fig. 3.** The ambient and cone temperatures of a thermogenic male (A) and female (B) *Macrozamia platyrhachis* measured on 15 November 2003, and the results of modelled cone temperatures by using the basic heat transfer model equations developed by Roemer *et al.* (2005) to estimate metabolism required to produce the thermogenic temperatures. Only data from the modelling period are shown, but data were recorded from ~0930 hours 15 November through ~2130 hours for the female cone and through 0730 hours on 16 November for the continuously measured male cone. T air is the local ambient temperature; T cone is the measured cone temperature; T cone model is the simulated cone temperature; Q is the normalised simulated metabolism (W); T cone no Q is the expected (modelled) cone temperature if the cone were not thermogenic.

metabolism (Fig. 3B), with peak temperature increases of  $3.3^\circ\text{C}$  above the concurrent ambient occurring at 1942 and 2050 hours. A few others showed weak thermogenesis, evidenced from cone temperature decay patterns that were

**Table 3.** Average ( $\pm 1$  s.d.) model results for *Macrozamia platyrhachis* and *Macrozamia machinii* male cone metabolic and thermogenic traits

T = temperature,  $^\circ\text{C}$ ; t = time in hr:min; Q = metabolism (W);  $T_{pk}$ , cone thermogenic temperature peak; Error, average absolute temperature error (modelled cone T - actual cone T) over the complete time period simulated;  $t_{Qi}$ ,  $t_{Qf}$ , the time of day when metabolism (Q) starts, i (initial) and ends, f (final), respectively;  $t_{pQ}$ ,  $t_{pT}$ , the time of day when metabolism and cone temperatures peak, respectively;  $\tau$ , the time constant of the cone,  $\tau = Mc/UA$ , where U is the overall heat transfer coefficient in  $\text{Wm}^{-1}\text{ }^\circ\text{C}^{-1}$  and A is the cone area, M is cone mass (kg) and c is the mass specific heat,  $\text{Jkg}^{-1}\text{ }^\circ\text{C}^{-1}$ ;  $Q_{max}/Mc$ , the metabolism amplitude ( $10^{-3}\text{ }^\circ\text{C s}^{-1}$ ) parameter

Species	$T_{pk}$ $^\circ\text{C}$	Error $^\circ\text{C}$	$t_{Qi}$ hr:min	$t_{Qf}$ hr:min	$t_{pQ}$ hr:min	$t_{pT}$ hr:min	$\tau$ hr:min	$Q_{max}/Mc \times 10^{-3}\text{ }^\circ\text{C s}^{-1}$
<i>M. platyrhachis</i> n = 10 events	30.5 (1.8)	0.29 (0.15)	16:55 (0:24)	20:34 (0:29)	18:45 (0:08)	19:24 (0:12)	1:57 (0:43)	1.59 (0.9)
<i>M. machinii</i> <sup>A</sup> n = 20 events	33.5 (2.3)	0.37 (0.13)	16:45 (0:35)	21:07 (0:42)	18:54 (0:26)	19:14 (0:34)	0:56 (0:28)	3.48 (1.6)

<sup>A</sup>*M. machinii* cones' average dimensions (cm) (n = 6) were: height  $\times$  diameter,  $22.6 \times 6.9$  (Roemer *et al.* 2005).

elevated above the decaying ambient more than would be accounted for by the cones' time constant alone.

#### Volatile emissions

A total of 11 cone volatile samples were taken from four different male cones and a single female cone. Male and female cones are similar in both major components and their relative ratios (Table 4). The major cone component is octanol, which represents more than half of the total volatile output (Table 4, Fig. 4). Other major components include methyl salicylate,  $\beta$ -myrcene,  $\beta$ -caryophyllene, ocimene isomers ((Z)- $\beta$ , (E)- $\beta$ - and allo-), and other monoterpenes. Some of these components were also detected in small amounts in the leaf background sample (Table 4).

There was no clear difference in emission rates between samples taken during thermogenic and non-thermogenic periods. For example, of three comparable male cones all at ~40–60% dehisced, one had its highest emissions during the 1215–1415 hours sample (with a peak cone temperature of 37.8°C and peak ambient temperature of 38.8°C) with values approximately 2-fold higher than either its 1400–1600 hours or 1730–1930 hours sample (when the cone was thermogenic with a peak cone temperature of 30.3°C and concurrent ambient of 25.6°C). This was true of the total volatile output and for most of the individual components. In contrast, two other

cones had 1.5 times higher emissions during the evening compared with mid-day samples. (The mid-day maximum ambient temperature and concurrent cone temperatures in these cones reached ~31.5°C and 30°C, respectively, whereas the thermogenic temperatures reached their peaks of 30.3°C and 35.3°C at 1858 and 1910 hours when the concurrent ambient temperature was 22.3°C.) Ambient temperatures may have played a role in the different patterns observed, such that the cone on the hotter day had a higher mid-day volatile release.

#### Discussion

*Macrozamia platyrhachis* is locally abundant in habitat with an estimated 611 315 adult plants in the 11 populations surveyed, with more plants not included from the population not sampled. Notwithstanding this encouraging number of adult plants, there are several factors that affect the long-term viability of this species, as identified in four critical questions outlined in a 'top-down' approach (Schemske *et al.* 1994).

**Question 1. Biological Status of the Species** – are individuals and populations of the species increasing, decreasing or stable? This is largely unknown; however, the recent fire events have undoubtedly decreased the numbers of individuals, especially juveniles.

**Table 4. Components identified from *Macrozamia platyrhachis* cone volatiles**  
RT = GCMS retention time. Calculations of  $\mu\text{g}$  per sample is based on comparison with internal standard

Component	RT (min)	Avg. $\mu\text{g}/\text{sample}$	s.e. $\mu\text{g}$	Male cone, $n=9$		Total area %	Female cone, $n=1$	
				min	max		$\mu\text{g}/\text{sample}$	Total area %
Internal standard	5.28	20	–	–	–	–	–	–
Monoterpene <sup>A</sup>	7.78	2.44	0.79	0.05	7.28	6.7	0.01	0.38
Unknown	7.90	0.46	0.10	0.02	1.50	1.3	0.01	0.24
Unknown	8.67	0.59	0.14	0.01	1.79	1.6	ND <sup>B</sup>	ND <sup>B</sup>
$\beta$ -myrcene <sup>A,C,D</sup>	8.98	4.21	1.73	0.07	18.30	8.7	0.52	18.79
Octanal <sup>A</sup>	9.22	0.35	0.05	0.11	0.73	1.1	0.01	0.36
Unknown	9.47	0.98	0.19	0.01	2.64	2.6	ND <sup>B</sup>	ND <sup>B</sup>
$p$ -cymene <sup>C</sup>	9.64	0.95	0.23	0.36	3.15	4.9	0.04	1.53
Limonene <sup>C</sup>	9.70	0.27	0.05	0.11	0.68	0.8	ND <sup>B</sup>	ND <sup>B</sup>
(Z)- $\beta$ -ocimene <sup>C,D</sup>	9.82	0.42	0.16	0.05	1.69	0.9	0.04	1.60
(E)- $\beta$ -ocimene <sup>D</sup>	10.02	0.44	0.17	0.03	2.02	0.9	0.06	2.07
Unknown <sup>A</sup>	10.22	0.25	0.04	0.04	0.60	0.7	ND <sup>B</sup>	ND <sup>B</sup>
Octanol <sup>A</sup>	10.43	19.16	2.69	4.84	36.39	58.4	1.63	58.40
Linalool <sup>C</sup>	11.02	0.18	0.03	0.06	0.42	0.7	0.05	1.91
Unknown <sup>A</sup>	11.05	0.15	0.02	0.07	0.28	0.6	0.03	0.91
Allo-ocimene <sup>D</sup>	11.43	0.10	0.02	0.03	0.21	0.4	ND <sup>B</sup>	ND <sup>B</sup>
Unknown <sup>A</sup>	12.22	0.04	0.01	0.01	0.12	0.1	ND <sup>B</sup>	ND <sup>B</sup>
Methyl salicylate <sup>A</sup>	12.57	0.86	0.14	0.09	2.24	2.4	0.01	0.41
Decanal <sup>A</sup>	12.75	0.12	0.02	0.04	0.21	0.4	0.01	0.42
Decanol	13.49	0.36	0.07	0.13	0.75	1.1	0.05	1.87
Unknown	13.62	0.25	0.03	0.11	0.37	0.9	0.02	0.79
Unknown <sup>A</sup>	13.70	0.70	0.11	0.21	1.19	2.2	0.14	5.17
$\beta$ -caryophyllene	16.07	1.64	0.53	0.16	6.51	3.5	0.14	4.86
$\alpha$ -caryophyllene	16.57	0.11	0.03	0.01	0.44	0.2	0.01	0.28

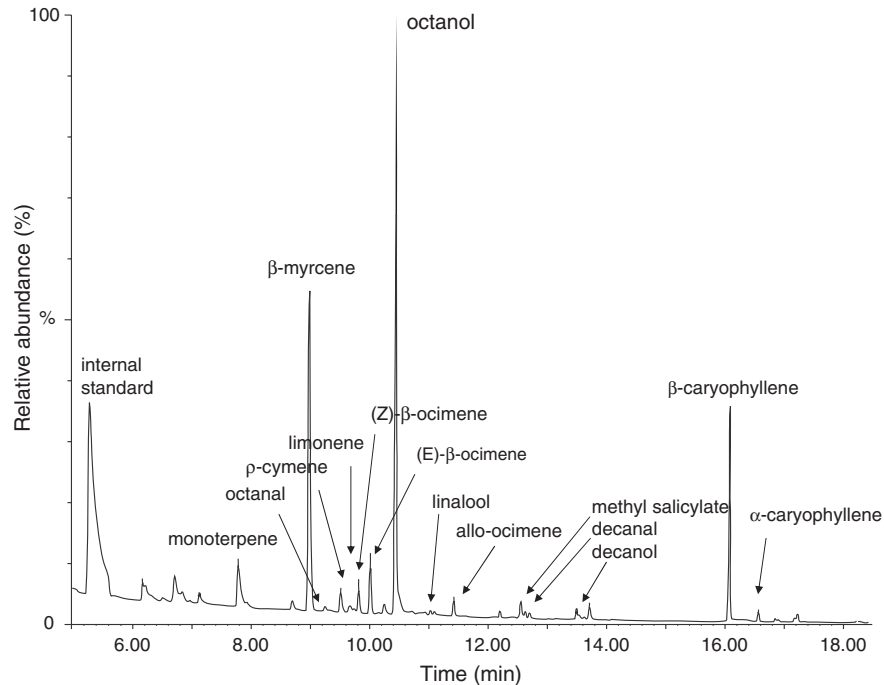
<sup>A</sup>Component was also detected in sample of volatiles from leaflets; level of each component in leaf sample was between 0.013 to 0.03  $\mu\text{g}$ , except for decanal, with a calculated level of 0.11  $\mu\text{g}$ , and the unknown component at RT of 13.7, which was calculated to be 0.47  $\mu\text{g}$ .

<sup>B</sup>ND, not detected.

<sup>C</sup>Component has been reported from other *Macrozamia* species pollinated by *Tranes* sp. (Terry *et al.* 2004a, 2004b, 2005).

<sup>D</sup>Component has been reported from other *Macrozamia* species pollinated by *Cycadotrips* sp. (Terry *et al.* 2004a, 2004b, 2007b).





**Fig. 4.** Chromatogram from a gas chromatography-mass spectral (GC-MS) analysis of volatiles of a male *Macrozamia platyrhachis* cone sampled 1700–1900 hours, 15 November 2003, during a thermogenic period, by using a dynamic head space technique. Time is the retention time from the time the sample was injected into the GC.

**Question 2. Life History** – what stages are limiting population growth and species persistence? (a) Lack of seed dispersal, (b) Poor recruitment as exhibited by extremely low current seed or seedling survival and (c) Adult plant dependence on a specific insect pollination mutualism for reproduction make this species highly sensitive to disturbances.

**Question 3. Biological Causes of Variation in Life History** – what causes have the most demographic impact? (a) Lack of dispersal agents result in short (<100 m) or no seed dispersal. This limits range expansion and also results in inbreeding depression due to recruitment of siblings. (b) Intense fires, but also predation by butterflies, may result in poor recruitment of seeds and seedlings. (c) Intense fires occurring during the coning season are especially harmful to pollinators. (d) Finally, the long generation time (probably 20–25 years, 60–80 years for 3 generations) and the highly unpredictable nature of coning events likely contribute to variability in pollinator populations, fertilisation and population recruitment.

**Question 4: Geographical and physical constraints** – is there room to move? The species is endemic and restricted to an area of unique geology and topology in central Queensland and is not likely to colonise outside of this area. There are large areas that appear to be suitable habitat within the known area of occurrence, but lack of seed dispersal appears to limit expansion outside the population boundaries.

#### Pollination survey

Because *Macrozamia* pollination systems involve obligate mutualisms with one or two specialist insects, it is necessary

to study the pollination process of any threatened species. In our survey, the only known *Macrozamia* pollinator found was the thysanopteran, *C. chadwicki*, which has been reported from numerous *Macrozamia* species (Table 1). *Conobrosis* moths have not been considered pollinators because they have only been trapped on male cones (Common 1994; Terry 2001; PIF, PJM, pers. obs.) during pollination, although Snow and Walter (2007) found larvae on maturing *M. lucida* seeds, several months past the pollination stage.

Many cone traits of this species appear to be unique and do not match those of other *Cycadothrips*-pollinated *Macrozamia* species (Terry *et al.* 2004a, 2004b) such as *M. lucida*, whose male and female cones are both thermogenic at mid-day. In contrast, the male *M. platyrhachis* cones clearly match the metabolic attributes and evening thermogenesis (Fig. 3) of male *M. machinii* (Seymour *et al.* 2004; Terry *et al.* 2004a; Roemer *et al.* 2005), a species pollinated solely by *Tranes* sp. (Terry *et al.* 2005). However, in contrast to *M. machinii*, whose females exhibit no significant thermogenesis (Seymour *et al.* 2004; Roemer *et al.* 2005), there is some evidence of significant thermogenesis in female *M. platyrhachis* cones. In terms of volatile emissions, *M. platyrhachis* cones show no dramatic increase during thermogenesis, as has been observed in both *M. lucida* and *M. machinii* (Terry *et al.* 2004b). Further, male and female cones of *M. platyrhachis* produce key volatile elements found exclusively either in species pollinated by *Tranes* sp. only (linalool to which *Tranes* respond) or by *Cycadothrips*-only ((*E*)- $\beta$ - and allo-ocimene to which *Cycadothrips* respond) or those found in both groups ( $\beta$ -myrcene to which both pollinators respond) (Terry *et al.* 2004a, 2004b, 2007a, 2007b) In addition, the major

component, octanol, and several other minor components (methyl salicylate, decanal, decanol,  $\alpha$ - and  $\beta$ -caryophyllene) have not been reported to date from other studied *Macrozamia* species. In sum, this system may represent a unique pollinator syndrome that is worthy of conservation in itself (cf. Bond 1994; Kearns *et al.* 1998).

These cone traits suggest that *M. platyrhachis* could be pollinated by either *Cycadotherips* or *Tranes* sp. (Terry *et al.* 2007a, 2007b). The lack of detection of any *Tranes* sp. weevils could be the result of extremely low numbers of pollinators present, with those low numbers possibly a result of the hot fires in previous seasons. The fires in at least two of the areas occurred when pollinators may have been actively involved with cones. Alternatively, if *M. platyrhachis* was pollinated by both *Tranes* and *Cycadotherips* in the past, and then lost *Tranes*, it may still produce the chemical cues associated with *Tranes*. Regarding thrips, the low numbers detected in cones contrasts with the thousands of insects detected in male cones of other species (Mound and Terry 2001; Terry *et al.* 2005), although very few pollinators are required per cone for effective pollination (Terry *et al.* 2005). Further surveys are needed throughout the pollination period to determine whether this species is pollinated only by *Cycadotherips*, by both thrips and *Tranes*, or by a pollinator species not yet reported.

#### *Species IUCN status and management recommendations*

*Macrozamia platyrhachis* appears to be healthy in terms of the total number of adults estimated (611 315 individuals is much higher than 2500 or 10 000 individuals used as limits for either the 'Endangered' or 'Vulnerable' status) and a viable pollination mutualism based on the number of seeds found at most sites. On the other hand, the small area of occupancy and almost complete lack of juveniles indicates that not all is well in this particular cycad paradise. In addition, the low numbers of pollinators found suggest that pollinator numbers may be in decline, if not under threat. Finally, it is impossible to assess some of the criteria used by the IUCN (2001) (e.g. decline over 10 years or 3 generations whichever is the longer; decline in area of occupancy, number of locations or number of mature individuals) given the long time period for these cycads to reach maturity (~20 years to maturity for reproduction, pers. comm. S. Walkley) and the lack of historical baseline data. All species have an origin, expansion and eventual demise (Levin 2000) and it is probable that *M. platyrhachis* is past the expansion phase and is likely moving towards the last category, with certain populations more on the edge of the extinction vortex than others. The species is already fragmented into disjunct populations and it is likely that inbreeding depression may be occurring (cf. Soulé 1987).

On balance, based on the available data, we propose that the conservation status of *M. platyrhachis* be retained as 'Endangered' because it meets the IUCN (2001) criteria of B.2,b.i,ii,iii,iv,v concerning, respectively: (B.2) the area of occupancy is less than 500 km<sup>2</sup> (current study indicates 365 ha, or 3.65 km<sup>2</sup>) and there is a continuing decline observed, inferred or projected (current study indicates essentially no recruitment is occurring because of fire

severity); (b.i) the extent of occurrence (distribution is already highly fragmented); (b.ii) the area of occupancy (the populations have sharp boundaries indicating a seed dispersal-limited distribution); (b.iii) the area, extent and/or quality of habitat (recurrent severe fires are preventing recruitment); (b.iv) the number of locations or subpopulations (area now reasonably well surveyed and dioecious nature of the plant makes establishment of new populations doubly hard); and (b.v) the number of mature individuals (with no evidence of recruitment, attrition over time will result in adult population decline).

Regardless of the classification of threat level, several management issues are critical to the long-term persistence of this cycad in habitat, especially controlling intense fires during coning season when the insect pollinators are most susceptible and during the period of seed ripening. If it is possible to manage fire in the habitat, which is unlikely given the high flammability of the vegetation, then individual populations of *M. platyrhachis* should be burnt in a mosaic pattern, probably at a minimum of five years. This timing interval may enable establishment of seedlings beyond the stage where the subterranean caudex is killed by above ground fires. Cycad species take up to two years to develop their contractile roots, which pull the stem of seedlings well below the soil surface where they are protected (Stevenson 1980; Norstog and Nicholls 1997). In addition, this controlled fire interval may prevent the occurrence of the very intense and damaging wild fires that also drastically change the overstorey vegetative structure.

The research presented here adds information about the diversity of cone traits among *Macrozamia* species, such as the unique cone volatiles not reported previously. However, surveys of other *M. platyrhachis* coning populations throughout the pollination season are needed to determine whether other pollinators are involved that may have been destroyed by the extreme fires in our study populations. Protecting these cycads in their natural habitat must include conserving their specialist pollinators as well as their host plant. Model simulations suggest that plant species of large pollination networks appear to be relatively tolerant of pollinator loss (Memmott *et al.* 2004) where there is redundancy in pollinators; however, the potential extinction of individual plant species due to fragmentation or other perturbations, especially with specialist pollinators whose hosts serve as nurseries, is high (Fabienne Harris and Johnson 2004). Therefore, additional measures to protect these particular insects over and above those protecting the plants may be required.

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