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REGENERATION STRATEGIES OF PALMS (ARECACEAE) IN RESPONSE TO CYCLONIC DISTURBANCES

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ABSTRACT
LATIFAH, D., CONGDON, R. A. & HOLTUM, J. A. 2016. Regeneration strategies of palms (Arecaceae) in response to cyclonic disturbances. *Reinwardtia* 15 (1): 43 − 59. — Tropical cyclones may act as important ecological drivers in northern Australia including north Queensland, as several cyclones impact this region each year between November and May. Extensive research has been conducted to investigate how regeneration of rainforest plant communities respond to frequent cyclonic disturbances. However, there have been few such studies on palms although they are important components of many rainforests. This research aimed to investigate the effects of canopy gaps following cyclonic disturbance (case study: Cyclone Larry) on regeneration of *Arenga australasica* (H. Wendl. & Drude) S. T. Blake *ex* H. E. Moore, *Calamus australis* Mart., *C. moti* F. M. Bailey, *Hydriastele wendlandiana* (F. Muell.) H. Wendl. & Drude and *Licuala ramsayi* var. *ramsayi* (F. Muell.) H. Wendl. & Drude. The field research was carried out at five sites in three areas located in northern Queensland: Tam O'Shanter/Djiru National Park, Clump Mountain National Park and Kurrimine Beach Conservation Park. Observations were made of recruitment, growth rate, leaf turnover and life history. We found that responses of palm regeneration following cyclonic disturbance varied among study sites; however, the recruitment of several species was favoured in gaps created by cyclones. The results also provide information on the various stages in the life cycle of the study palms.

Key words: disturbance, northern Australia, palms, regeneration.

ABSTRAK
LATIFAH, D., CONGDON, R. A. & HOLTUM, J. A. 2016. Strategi regenerasi palem (Arecaceae) sebagai respon terhadap kerusakan habitat akibat siklon. *Reinwardtia* 15 (1): 43 − 59. — Siklon tropis dapat memiliki peran ekologis Australia utara termasuk Queensland utara, karena beberapa siklon melanda kawasan ini setiap tahun pada bulan November - Mei. Penelitian yang ekstensif telah dilakukan berkenaan dengan respon regenerasi tumbuhan-tumbuhan hutan terhadap siklon. Namun demikian, studi serupa pada palem masih kurang; padahal palem adalah elemen penting di banyak hutan tropis. Penelitian ini bertujuan untuk mengetahui pengaruh bukaan-bukaan kanopi hutan akibat kerusakan oleh siklon (studi kasus: Siklon Larry) terhadap regenerasi palem *Arenga australasica*, *Calamus australis*, *Hydriastele wendlandiana* dan *Licuala ramsayi* var. *ramsayi* Studi ekologi dilakukan pada tiga lokasi yaitu Tam O'Shanter/Djiru National Park, Clump Mountain National Park dan Kurrimine Beach Conservation Park di utara Queensland. Pengamatan dilakukan terhadap rekrutmen, pertumbuhan anakan/semai, laju pergantian daun dan siklus hidup. Hasil penelitian menunjukkan bahwa regenerasi palem di kawasan yang dipengaruhi siklon bervariasi, namun demikian rekrutmen beberapa jenis palem banyak dijumpai di bukaan-bukaan kanopi yang rusak akibat siklon. Hasil lain adalah siklus hidup palem dan implikasi hasil studi ini untuk upaya restorasi hutan hujan tropis di kawasan yang dipengaruhi siklon.

Kata kunci: Australia, bencana siklon, palem, regenerasi.

INTRODUCTION

Tropical cyclones may act as important ecological drivers in northern Australia including north Queensland, as several cyclones impact this region each year between November and May. Therefore, the rainforests in the region may frequently be affected by cyclones and may become cyclone-dependent (Turton, 2008). Cyclonic disturbance creates canopy gaps of differing size, from minor stripping of foliage to large wind throws, and these gaps play important roles in stimulating plant regeneration in most plant communities (Bullock, 2000; Dupuy & Chazdon, 2008; Fenner & Thompson, 2005; Harper, 1977).

Extensive research has been conducted to investigate how regeneration of rainforest plant communities respond to frequent cyclonic disturbances. Webb (1958) observed that cyclones may alter the emergent trees and vine composition, resulting in a reduced and uneven canopy in tropical lowland rainforest in north Queensland. De Gouvenain and Silander Jr. (2003) found that the height of forest canopies of lowland tropical rainforests in Madagascar was low, and that reduction in height was significantly correlated with the impact of tropical cyclones. Moreover, tropical cyclones increased tree population densities of the lowland rain forests in Madagascar (de Gouvenain & Silander Jr., 2003) and Nicaragua (Vandermeer *et al.*, 1996). Lugo (2008) investigated responses of forests to four major cyclones between 1943 and 2005 in Puerto Rico, North America and found that species diversity and density first increased within at least 15 years following a hurricane but then decreased gradually as a result of competition for light and space. Johns (1986) reported that Cyclone Ioma (1940), Cyclone Hanna (1972), an unnamed cyclone in 1976 and small cyclonic winds had destroyed rainforests in New Guinea. However, despite the destruction, the cyclones created canopy gaps that led to the dominance of *Anisoptera thurifera* var. *polyandra*, *Castanopsis* sp. and *Tristania* sp. (Johns, 1986). Other studies have demonstrated positive effects of cyclonic disturbances combined with past land use where cyclones reduced the abundance of secondary forest species and increased the similarity in species composition between disturbed secondary forests and adjacent mature forests (Comita *et al.*, 2010; Ogle *et al.*, 2006; Zimmerman *et al.*, 1994).

However, there have been few such studies on palms although they are important components of many rainforests. For example, adult palms of several species flourish and their populations become dense following cyclones/hurricanes that create canopy gaps. This is evident from studies of *Calamus australis* (Webb, 1958), *Licuala ramsayi* (Gorman, 1996), *Prestoea montana* (Frangi & Lugo, 1998) and *Archontophoenix alexandrae* (Dowe, 2009). Dransfield (1979) and Manokaran (1985) suggested that seedlings of *C. manan* grow slowly in the understorey until a canopy gap is formed. Clearly, these studies show the importance of studying regeneration strategies with respect to the post-cyclonic changes found in rainforests including the creation of canopy gaps.

Plant regeneration strategies are related to plant reproductive phenology. Phenological processes, such as flowering and fruiting, can be affected by cyclonic disturbance (Hopkins & Graham, 1987). Such flowering and fruiting following cyclonic disturbance may lead to increased seed fall in gaps, causing increased germination and mass-recruitment, which in turn affects size-class distribution with distinct cohorts recruited (Hopkins & Graham, 1987; Webb, 1958). Hopkins and Graham (1987) and Gorman (1996) also found that *L. ramsayi* showed increased flowering and fruiting, as well as seedling recruitment, in response to cyclonic disturbance caused by Cyclone Winifred in north Queensland in 1986. Webb (1958) reported that *Archontophoenix alexandrae* flowered shortly after a major cyclone, Cyclone Agnes, in 1956 between Bowen and Cairns, north Queensland. Regeneration success is also related to seed dispersal and predation (Crawley, 2000).

The current research investigated the immediate impacts (up to 1.5 years) post cyclones. Palm regeneration was examined under different light intensities created in canopy gaps established by Cyclone Larry in 2006. Specifically, the aims of this research were to: (i) investigate the effects of canopy gaps following cyclonic disturbance (case: Cyclone Larry) on regeneration of *Arenga australasica*, *Hydriastele wendlandiana*, *Licuala ramsayi*, *Calamus australis* and *C. moti*; and (ii) study the influence of cyclone disturbance on reproductive phenology stages (flowering, fruiting, seed dispersal). Many previous studies have shown the importance of cassowaries as seed dispersal agents (Stocker & Irvine, 1983; Willson *et al.*, 1989). Given that the study areas are important cassowary habitats, our research also investigated palm dispersal and germination of seeds collected from cassowary droppings.

MATERIALS AND METHODS

Study species

This research focused on five species with varied taxonomic affinities and growth habits (Uhl & Dransfield, 1987): *A. australasica* (subfamily Arecoideae, tribe Caryoteae; clustering trees), *C. australis* and *C. moti* (subfamily Calamoideae, tribe Calameae; clumping or climbing plants), *H. wendlandiana* (subfamily Arecoideae; clustering trees or usually single-stemmed trees) and *L. ramsayi* var *ramsayi* (subfamily Coryphoideae, tribe Coryphae; solitary or rarely clustered trees).

Study site

The regeneration strategies of the palms were studied in three areas in north Queensland: Kurrimine Beach Conservation Park, Clump Mountain National Park and Tam O'Shanter/Djiru National Park located in Mission Beach and Kurrimine Beach (Fig. 1). Tam O'Shanter/Djiru National Park site is considered to have the highest diversity of palms (10 species) of any forest in Australia (Dowe, 2010). Tam O'Shanter forest was initially categorised as a mixed to complex mesophyll vine forest (MMV/CMVF), but this vegetation type was altered by frequent cyclones in the past, and gradually replaced by mesophyll fan palm vine forest or MFPVF (Tracey, 1982; Webb, 1958; Webb, 1978). *Lophostemon suaveolens* (swamp mahogany) and *L. confertus* (brush box) dominate the canopy at Bicton Hill, Clump Mountain National Park (EPA-QPWS, 2003). Kurrimine Beach Conservation Park was established to protect the rare lowland rainforest types of the wet coastal lowlands. It is categorized as endangered mesophyll vine forest on low nutrient, calcareous and siliceous beach sands of the coastal wet lowlands (EPA-QPWS, 2003). Kurrimine Beach Esplanade is a swampy area with mangroves. Rainfall regularly exceeds 3.5 m annually with high intensities between November and May; temperatures range from 23-32°C in summer and 16-26ºC in winter in Tam O'Shanter State Forest (EPA-QPWS, 2003).

Tropical cyclones with wind (sustained wind near the centre) speeds of more than 55 kmh^{-1} occur quite frequently in north Queensland (Webb, 1958; BOM, 2010a; BOM, 2010b). Mission Beach and Kurrimine Beach, part of the Wet Tropics World Heritage Area, were chosen for this study as they were disturbed by the destructive Cyclone Larry (Category 5) on 20 March 2006. This cyclone had sustained wind speeds of 290 kmh^{-1} .

The study species locations of the study sites are detailed in Table 1. There were four plots in each study site. Depending on species occurrence in individual plots, Site A was divided into A2 and A3 (A1 was used for population structure study and published elsewhere), on the basis of different areas to permit comparison between particular species at the sites in the statistical analysis, for instance *L. ramsayi* in site A2 was compared to site B with only two plots each which had adequate individuals for this study.

Study period

In a review of the literature, Everham III and Brokaw (1996) found that the delays in recording post-cyclonic impacts ranged from 10 days to 13 years after the storms. In the present study, the duration of regeneration monitoring, *i.e.* 1.5 to 2.5 years was consistent with Poorter and Boot (1998) who studied gap phase regeneration. The current research investigated the immediate impacts (up to 1.5 years) post cyclones (Cyclone Larry in 2006).

Survey methods

Due to time constraints in locating sites for *L. ramsayi* and *H. wendlandiana*, field observations 1-2 were undertaken at the times specified.

Field Observation 1: Study site characterisation

Comparison of disturbed versus undisturbed areas was not possible due to the broad impact of Cyclone Larry in the Mission Beach area, so the study sites were selected on the basis of the level of disturbance. The level of cyclonic disturbance was used to characterise the study sites in order to facilitate analyses of data collected on regeneration and reproductive phenology. The responses of five palm species were observed in different study sites reflecting different light intensities and damage categories.

In a review, Everham III and Brokaw (1996) pointed out that various methods have been used to quantify the extent of damage after storms.

Table 1. Location of study sites and plots.

Sites[1]	Species	Study Plots	Location
A2	*C. australis*	Plot c (S17°54'.734"E146°04'.189")	Tam O'Shanter National Park
	C. moti	Plot d (S17°54'.637"E146°04'.123")	
	H. wendlandiana		
	L. ramsayi		
A3	*C. australis*	Plot c (S17°54'.734"E146°04'.189")	Tam O'Shanter National Park
	C. moti	Plot d (S17°54'.637"E146°04'.123")	
	H. wendlandiana	Plot e (S17°54'.795"E146°04'.398")	
		Plot f (S17°54'.710"E146°04'.547")	
B	*L. ramsayi*	Plot e (S17°54'.795"E146°04'.398")	Tam O'Shanter National Park
		Plot f (S17°54'.710"E146°04'.547")	
C	*A. australasica*	Plot g (S17°50'.394"E146°05'.982")	Clump Mountain National Park
	C. australis	Plot h (S17°50'.348"E146°05'.902")	
	C. moti	Plot i (S17°50'.358"E146°05'.982")	
		Plot j (S17°50'.370"E146°05'.994")	
D	*A. australasica*	Plot k (S17°46'.858"E146°06'.042")	Kurrimine Beach National Park
	C. australis	Plot l (S17°46'.853"E146°06'.041")	
	C. moti	Plot m (S17°46'.878"E146°06'.026")	
		Plot n (S17°46'.872"E146°06'.025")	
E	*C. australis*	Plot o (S17°46'.996"E146°05'.521"	Kurrimine Beach National Park
	C. moti	Plot p (S17°46'.980"E146°05'.547")	
	H. wendlandiana	Plot q (S17°46'.974"E146°05'572")	
		Plot r (S17°46'.985"E146°05.520")	

[1] A1 was used for population structure study and published elsewhere

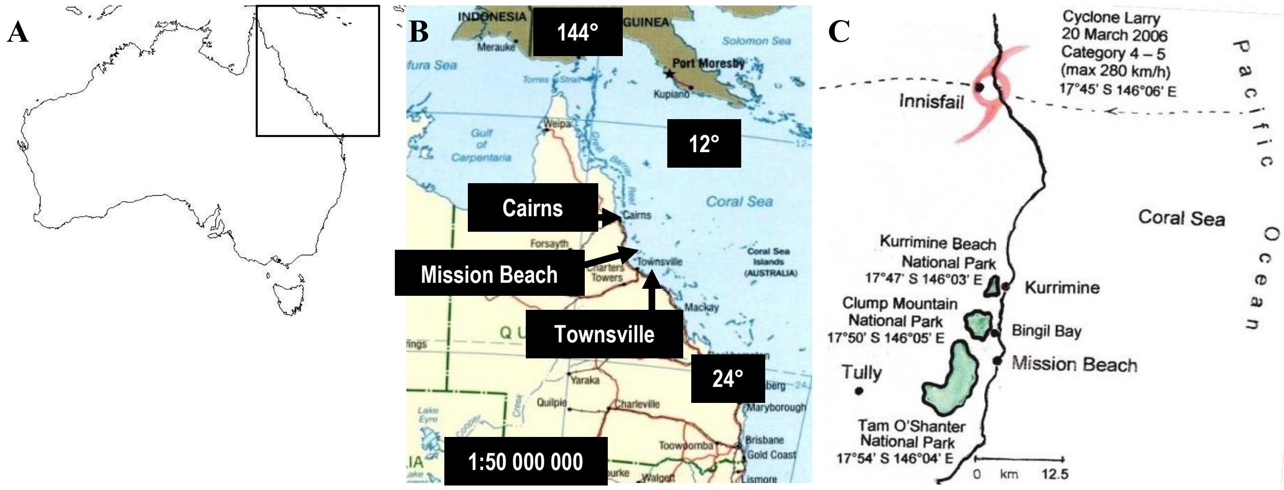


Fig. 1. A-B Maps of Australia showing the approximate location of Mission Beach between Cairns and Townsville (Source: maps-oceania.com) and C the path of Cyclone Larry (Source: BOM, 2010a).

Generally, six categories of damage are recognised: (1) stem damage, (2) branch damage, (3) canopy damage, (4) mortality, (5) volume or mass changes, and (6) extent of damage ranked on a scale from 'high' to 'low'. However, these authors proposed that there may be more than six categories of damage, including a combination of the six types listed above. Based on Unwin *et al.* (1988), Metcalfe *et al.* (2008) developed Bradford/ Unwin damage scales for plant communities affected by Tropical Cyclone Larry and the level of damage was ranked from 1 (severe and extensive disturbance) to 4.5 (minor disturbance) combining canopy, stem, branch and foliage disturbance with the magnitude of litter fall. In the current research, in order to compare sites, it was necessary to characterise the sites by assessing the level of cyclonic disturbance. This was achieved by investigating: (1) canopy openness (1A), and (2) damage categories modified from Dowe (2009) (1B).

Field Observation 1A: Canopy openness

Canopy openness was measured at the beginning of the first year of field research (October 2007 for Site A, C and D, May 2008 in Site E; September 2008 for Site B) and at the end of the field research period (December 2009; for all sites). Canopy openness was measured using hemispherical photographs/hemiphots (with wide-angled/fish-eye lens) based on the method described in Turton (1992) and ter Steege (1996). In the current research, the fish-eye lens specifications are 180 degree-wide angled, brand: Bower, 0.42x AF, 52–46 mm, without a lens converter, fitted to a Nikon D40 Digital Camera. In the field, the camera was mounted on a bubble-levelled tripod to stabilize the camera horizontally. The height of the tripod was maintained between 75–100 cm (ter Steege, 1996) depending on the varying topographical conditions of the plots. The camera (top of image) was directed to the north for analysis with Winphot 5.0. The hemispherical photographs were taken at 3-4 locations in each plot to capture the canopy openness and minimise overlap.

Field Observation 1B: Damage categories

Descriptions of both living and dead trees were used to document the nature and extent of the damage (Table 2). The damage categories were assessed based on the eight damage types during field observations. Each of the eight types was scored 0-3 based on whether damage was likely to cause palm mortality and disrupt the regeneration process (Table 2). The total of the scores for each plot represented the damage categories (Table 3). 'Tilting' means the trunk was leaning or curved but the roots were still in the ground.

Field Observation 2: Regeneration strategies and reproductive phenology

Field Observation 2A: Regeneration strategies: Recruitment, seedling growth and leaf turnover

Recruitment, survivorship and seedling growth were monitored using the 16 plots. In each plot, all seedlings were counted and individually tagged with long-lasting aluminium labels attached to pegs by wire, and placed within 5–10 cm of each seedling, to facilitate observation of seedling growth and survivorship. The seedlings were tagged when they first appeared. Net recruitment was determined as the number of surviving seedlings of each species in each plot on each subsequent field trip. The height of tagged seedlings and the number of leaves were recorded on each subsequent field trip: 2007 (July, October), 2008 (January, March, May, August, November) and 2009 (January, April, July, September and December). Height was determined by measuring the height above ground of the highest leaf tip when it was held upright. Clumps of seedlings were counted and assessed individually. Apparent reasons for mortality were recorded according to 12 categories (Table 4). The literature on the quantification of the causes of seedling mortality is limited. Hermann and Chilcote (1965) grouped the causes of seedling mortality into four categories: 'heat', 'animals', 'damp off' and 'others' in their field experiment. Sixty categories were recorded in the current study to cover various causes of seedling mortality in the field. However, to allow statistical comparison these were reduced to 12 categories by combining similar groups. The seedling counts were summed up and the proportion of surviving and died seedlings in each mortality category was analysed using chi-square test for independence.

Field Observation 2B: Reproductive phenology

This research involved detailed investigation of fruit production and seed dispersal. Reproductive phenology of mature plants in each plot was monitored. Field Observation 2B provided data on following live events/life history stages: (1) the number of mature palms producing fruit; for clumping palms *i.e. C. australis* and *C. moti* they were counted one per clump; for clustering palm *i.e. A. australasica* they were counted per stem, (2) the number of juveniles survived from previous cyclones, (3) the number of seedlings/recruits at the beginning of the first year of field research (October 2007 for Site A2, C and D; May 2008 for Site E and August 2008 for A2-*L. ramsayi*, A3 and Site B), (4) the number of flowering periods from July 2007 to December 2009, (5) the number of palms with unripe fruits, (6) the number of palms with ripe fruit, (7) the number of fruit dispersed/ predated (assumed as the number of absent fruit), (8) the results of the germination of the palm seeds found in a cassowary's dung which was conducted in the temperature-controlled room maintained at 30 ºC, (9) the germination period was observed

Table 2. Levels of damage assigned to individual stems of mature palms and associated non-palm trees observed in study plots following Cyclone Larry.

Descriptions of Damage Levels	Rank[1]	Score[1]
Trees survived without damage.	1	0
Fallen debris, e.g. large branches or stems.	2	1
Trees tilted but survived.	3	1
Trunk was partially snapped in the middle causing 'wounding' and 'tilting' but trees may survive and the growth may be abnormal.	4	2
Trunk was snapped at the apical meristem leaving abnormal shoot or crown growth but trees may survive and the growth may be abnormal.	5	2
Trees were partially uprooted causing trees to tilt or lie nearly horizontal but likely to survive and growth may be abnormal.	6	2
Trees did not survive as the trunks were partially snapped and the upper parts had fallen but the lower parts were not uprooted.	7	3
Trees did not survive as they were uprooted, lying horizontal or nearly so, with root ball out of ground; trees did not survive.	8	3

[1]Damage was ranked from 1 (the lowest) to 8 (the highest). The score of each damage type ranged from 0 (the lowest) to 3 (the highest): Score 0 = no damage, score 1 = fallen debris, score 2 = trees damaged but surviving, and score 3 = trees damaged and did not survive. Total scores were calculated to determine 'damage categories' for each study plot by counting the total number of the score of each damaged tree in each study plot (Table 3). The descriptions of damage levels were adapted from Dowe (2009). 'Wounding' and 'tilting' were found in palms only.

Table 3. The five damage categories for the study plots were determined as explained in Table 2 above.

Damage Categories	Total Scores of Damage
1 – Minor (D1)	0-10
2 – Minor to moderate (D2)	11-20
3 – Moderate (D3)	21-30
4 – Moderate to severe (D4)	31-40
5 – Severe (D5)	>40

from the radicle emergence until the opening of the first leaf/eophylls using the 3 seeds germinated each species from the author's original germination experiments that were conducted at the same study period and were published elsewhere in Latifah *et al*., 2014, (10) the size of seedling pool (number of surviving seedlings in December 2009 that were marked by label tags), and (11) size of the juvenile pool (number of surviving juveniles at the end of study).

A survey of cassowary dung was undertaken during every month in 2008-2009, except in February and April 2008 and June 2009. The survey areas were in Tam O'Shanter National Park and Clump Mountain National Park, along roads, loading ramps, walking tracks and study plots, including adjacent areas. This survey method was adopted from Stocker and Irvine (1983). The palm seeds found in the dung were collected and germinated in the 30°C constant-temperature room under continuous white light, to determine their germinability based on the number of seeds tested which germinated. Replicates were only possible when sufficient numbers of seeds were found.

Data analyses

Canopy openness was analysed as follows. Once the photographs were digitized, the degree of brightness indicating the percentage of sky visible at the study plots was determined using Winphot version 5.0 (ter Steege, 1996). The comparison between canopy openness of the first year and that of the second year was analysed with Paired-Samples T Tests. One-way ANOVA was used to compare the canopy openness (light intensities) among study sites. Site B was not included in the ANOVA since replication (number of plots) was insufficient. Damage categories were also analysed using one-way ANOVA to describe different damage levels of study sites based on the sum of the scores of the plot damage.

Regeneration strategies were described by analysing the recruitment, seedling growth and leaf turnover. The differences in recruitment over time among study sites were analysed using repeated measures ANOVA. To estimate recruitment and growth rate, regression analyses were used whenever the regressions were significant at the 95% confidence level or $p<0.05$ (Miles & Shevlin, 2001; Steel & Torrie, 1980). Differences in growth rate between study sites were not analysed due to limited number of seedling samples in each plot. Leaf turnover and causes of seedling mortality were analysed utilising one-way ANOVA.

When the ANOVA was significant for treatment effects, Tukey tests were performed to test for significant differences among treatment means for all parameters. All analyses were run utilizing SPSS for Windows version 17.0. The data collected on reproductive phenology were used to

Table 4. Categorization of risk factors contributing to seedling mortality[1].

Category	Principal Factor	Associated Factor
1	None of the following (2-12) applied; less shaded or open areas	No associated factors applied. This category is a common factor representing canopy removal after cyclonic disturbance
2	Predation	Diseases, no structural damage
3	Abnormal growth	No associated factors observed
4	Covered by fallen trees or logs	Fallen branches and debris
5	Covered by fallen dried *L. ramsayi* leaves	Fallen plant materials, *e.g.* rattan inflorescence stalks.
6	Predation	Diseases; abnormal growth; growing under fallen trees or logs, fallen dried *L. ramsayi* leaves, leaf litter and debris; covered by mud, growing in an aggregated cohort or shaded by other plants
7	Covered by debris or leaf litter	No associated factors observed
8	Growing in an aggregated cohort	Predation or diseases
9	Covered by mud	Debris; leaf litter
10	Shaded by other plants	Debris; leaf litter
11	Growing on degraded materials, *e.g.* debris, logs, roots from fallen trees	No associated factors observed
12	Early seedling stage (newly germinated/ sprouted seeds	No associated factors observed

[1]Observations were made in the field in July 2007-December 2009 at Tam O'Shanter/Djiru National Park, Clump Mountain National Park and Kurrimine Beach Conservation Park.

construct a descriptive life history for each study species in cyclone-prone rainforests.

RESULTS

The level of cyclone disturbances based on canopy openness and the level of damage varied between study sites (Table 5). Site E had the highest canopy openness (80%) and also showed the highest level of damage on the forest floor (severe). Site A (A2, A3) had a high level of canopy openness (52-62%) and moderate to moderate-to-severe damage. Site C had a medium level of canopy openness (31%); however, the level of damage was the lowest of all the sites (minor to moderate). Site D also exhibited a medium level of canopy openness (27%), but medium to high level of damage (moderate to severe). *L. ramsayi* was studied at Sites A2 and B. These sites were not statistically different; however, Site A2 had a 'higher canopy openness' compared with Site B. Overall, the study sites near Mission Beach and Kurrimine Beach had 49% canopy openness on average, and disturbance was categorised as 'moderate to severe' following Cyclone Larry.

Regeneration strategies

The total number of *A. australasica* surviving seedlings did not differ between sites C (31% canopy openness) and D (27% openness) (Fig. 2A). At site D (27% openness), no seedling was recruited until April 2009 (dry season) (Fig. 2A); however, the total number of seedlings began to decline afterwards giving 5 seedlings/100 m^2 recruited at the end of census date. At Bicton Hill (site C, 31% openness), the number of seedlings recorded in the plots decreased between the May and August census (dry season) then increased during the wet season between November 2008-April 2009 (Fig. 2A), giving net recruitment of 4 seedlings/100 m^2. However, there was a bigger increase in the number of seedlings in the study plots during the July to September 2009 period. *A. australasica* seedlings survived predation and disturbance (Fig. 3A). 'The early seedling stage' (C12) was most susceptible to disturbance and seedling death was highest in 'Less shaded or open areas' (C1) (Fig. 3A).

The total number of *C. australis* surviving seedlings differed between sites (Fig. 2A and C). Significantly more seedlings were found at the more open site (A2, 62%), than the less open site (D, 27%) (Fig. 2B). The net recruitment appears to be zero from July 2007 – March 2008 at site A2. The number of seedlings increased slowly at the beginning then rapidly from 6 to 26 seedlings/100 m^2 from March 2008 to January 2009 at the more open site (Fig. 2B), after which the recruitment rate goes back to zero, giving a net recruitment of 28 seedlings/100 m^2. On the other hand, the net recruitment at site D appeared to have held steady and close to zero overtime. There was only 4 seedlings/100 m^2 recruited at the less open site (D, 27%), and 3 seedlings/100 m^2 died, giving a total net recruitment of 1 seedling/100 m^2 (Fig. 2B). The difference in the number of seedlings between August 2008 and December 2009 was also significant between those seedlings in sites that were 62% and 27% open. The difference in seedling abundance between sites with 80% openness and 52% openness were not significant (Fig. 2B), due to the large variance of seedling numbers in site E (80%) where one plot had 24-32 seedlings and the other plots had 1-9 seedlings. More *C. australis* seedlings survived in microsites associated with cyclonic disturbance such as 'Less shaded or open areas' (C1) and 'Predation' (C2) (Fig. 3B). 'The early stage of seedling' (C12) was also most susceptible (Fig. 3B).

More seedlings of *C. moti* were recruited at sites with higher canopy openness (Fig. 2D). Between July 2007 and December 2009, more seedlings were recruited in plots at the sites with 62% openness (Fig. 2D), giving net recruitment of 22 seedlings/100 m^2, compared to site D with lower canopy openness (27%) with net recruitment of 1 seedling/100 m^2 (insufficient data for regression analysis). Moreover, the seedlings at site D were only recruited later, in July-December 2009. Three major mortality risk factors were 'Less shaded or open areas' (C1), 'Fallen dried *L. ramsayi* leaves' (C5) and 'The early stage of seedling' (C12) (Fig. 3C).

The net recruitment of *H. wendlandiana* seedlings was not significantly different between the sites with 52% and 80% canopy openness (Fig. 2E). There was considerable variation in the number of seedlings recruited, *i.e.* 2-15 seedlings in the plots at site A3 (52% openness), and 14-18 seedlings in one plot and 1-4 seedlings in the other plot at site E (80% openness) between August 2008 and December 2009. However, the net recruitment at the site with 80% canopy openness tended to be lower than that at the site with 52% openness. The number of seedlings in site A3 increased overtime (52% open; Fig. 2E). The seedlings of *H. wendlandiana* were resistant to many mortality risk factors related to cyclonic disturbance; no dead seedlings found caused by 'Less shaded or open areas' and only few seedlings did not survive. Although, 'The early seedling stage' (C12) was most susceptible to mortality (Fig. 3D).

The net recruitment of *L. ramsayi* seedlings in the more open site (52%) was lower than under a less open canopy (43%) (Fig. 2F); however, the difference was not significant. Between August 2008 and December 2009, the number of seedlings increased rapidly from 42 to 90 seedlings/100 m^2 between August 2008-January 2009 at site B (43%

Table 5. Canopy openness and level of damage of study sites[1].

Site	Canopy Openness (%)			Total Scores (Mean ± SEM)	Level of Damage	Number of Trees per plot (Mean ± SEM)
	2007/2008	2009	Mean ± SEM			
A3	52 ± 7	53 ± 7	52 ± 7^{a}	39 ± 4^{ab}	Moderate to severe	42 ± 3^{ade}
C	28 ± 2	33 ± 2	31 ± 2^{b}	15 ± 1^{c}	Minor to moderate	16 ± 2^{bc}
D	25 ± 3	28 ± 1	27 ± 2^{b}	34 ± 8^{b}	Moderate to severe	28 ± 6^{cde}
E	82 ± 6	77 ± 6	80 ± 6^{c}	50 ± 4^{b}	Severe	39 ± 4^{e}
Significance	t_{15}=0.35 p=0.73^{ns}		$F_{3,12}$=26.78 p=0.00*	$F_{3,12}$=9.69 p=0.00*		$F_{3,12}$=8.14 p=0.00*
***L. ramsayi*:**						
A2	62 ± 6	61 ± 12	62 ± 0.5	36 ± 4	Moderate to severe	40 ± 2
B	43 ± 5	44 ± 1	43 ± 3	43 ± 8	Severe	44 ± 6
Overall			49 ± 10	36 ± 6	Moderate to severe	31± 6

[1] The assessment was undertaken at the beginning of the first year of field research (October 2007 for Site A2, C and D; May 2008 for Site E and August 2008 for A2-*L. ramsayi*, A3 and Site B) and at the end of the field research period (December 2009). The canopy openness and level of damage in A2, A3, C, D, and E were used to characterise the sites. Asterisks (*) show significant differences at 0.05 level of confidence; ns = not significant; na = not available. Values in a column with the same superscript lower case letter are not significantly different (Tukey's test). Damage categories 'Minor' to 'Severe' were based on Table 3. A2 and B were not included in the statistical analysis because these sites only had two plots.

openness) (Fig. 2F) and 19 to 29 seedlings/100 m^2 at site A3 (52% openness). Seedlings were more abundant under conditions of 'Less shaded or open areas' (C1), up to 101 seedlings/400 m^2; although, most dead seedlings (seedlings/400 m^2) were in 'Less shaded or open areas' (Fig. 3E). 'Covering by fallen dried *L. ramsayi* leaves' (C5) was only a minor mortality risk factor.

The growth patterns of *A. australasica*, *C. australis, C. moti* and *H. wendlandiana* seedlings were sigmoidal, whereas that of *L. ramsayi* was sigmoidal only at one site (Fig. 4A-F); *L. ramsayi* seedling growth was logarithmic at the site with 62% openness. The height of *A. australasica* and *C. australis* between two sites was not different (Fig. 4A-C). There were a few seedlings of *C. moti* samples (insufficient data to calculate growth rate) at site C (31% openness) (Fig. 4D). The height of *H. wendlandiana* seedlings at the site with 52% canopy openness was higher than that at the 80% open site (Fig. 4E). The differences in growth rates of *L. ramsayi* between study sites could not be determined statistically due to the high variability of the data and limited number of seedling samples in each plot; however, the results suggested that the difference was not significant (Fig. 4F).

Leaf turnover of seedlings varied between 0-1.8 leaves/individual at the different sites during the study (Fig. 5; the data analysed were log-transformed). *A. australasica* under the more open canopy (31% openness) had a lower leaf turnover (0.3 ± 0.2 leaves/individual) than that under 27% openness. *C. australis,* under a more open canopy (62 and 80% openness) tended to have higher leaf turnover up to 0.8 ± 0.1 leaves/individual (Fig. 5B). The leaf turnover of *C. moti* seedlings was the lowest under the most open canopy (80% openness), but there was insufficient data to compare between different sites (Fig. 5C). *H. wendlandiana* did not show a significantly different pattern between sites A and E, and leaf turnover ranged between 0.5-0.6 leaves/individual (Fig. 5D). The leaf turnover of *L. ramsayi* seedlings was slightly lower under a more open canopy (52% openness); although, the difference was not significant (Fig. 5E). It varied from 0.5 ± 0.0 leaves/individual under 52% openness to 0.6 ± 0.1 leaves/individual under 43% openness.

Reproductive phenology

The life history of the five palm species varied (Table 6), for instance, their fruiting seasons differed. *C. australis* and *C. moti* were biennial fruit producers; while the other palms studied were annual. *A. australasica, C. australis, C. moti* and *H. wendlandiana* fruited between August-December 2008-2009 (the wet season including the cyclone season, *i.e*. between November-April); however, *H. wendlandiana* at upland sites and in the hill habitats in Clump Mountain National Park fruited between May-October 2008-2009 (dry season) while *L. ramsayi* fruited between March-August 2008-2009 (dry season). After the seeds were dispersed, they germinated in the following year; *A. australasica* and *H. wendlandiana* took *ca*. 7 months to complete germination from the radicle emergence until the opening of the eophylls (first leaf at seedling stage), while *C. australis* took *ca*. 6 months and *L. ramsayi ca*. 8 months (Fig. 6; Fig. 7). Germination of seeds obtained from cassowary droppings were: 60-80% in *C. australis*. Seedlings of *L. ramsayi* were found in droppings, but no seedlings of the other species were found in droppings.

Fruit production varied greatly between species, affecting seedling recruitment and the pool of juveniles. As shown in Table 6, *A. australasica* produced 865 fruit/100 m^2, resulting in 4 seedlings/100 m^2 and 4 juveniles/100 m^2 after two years. *C. australis* produced 295 fruit/100 m^2 over two years, yielding 15 seedlings/100 m^2 and 3

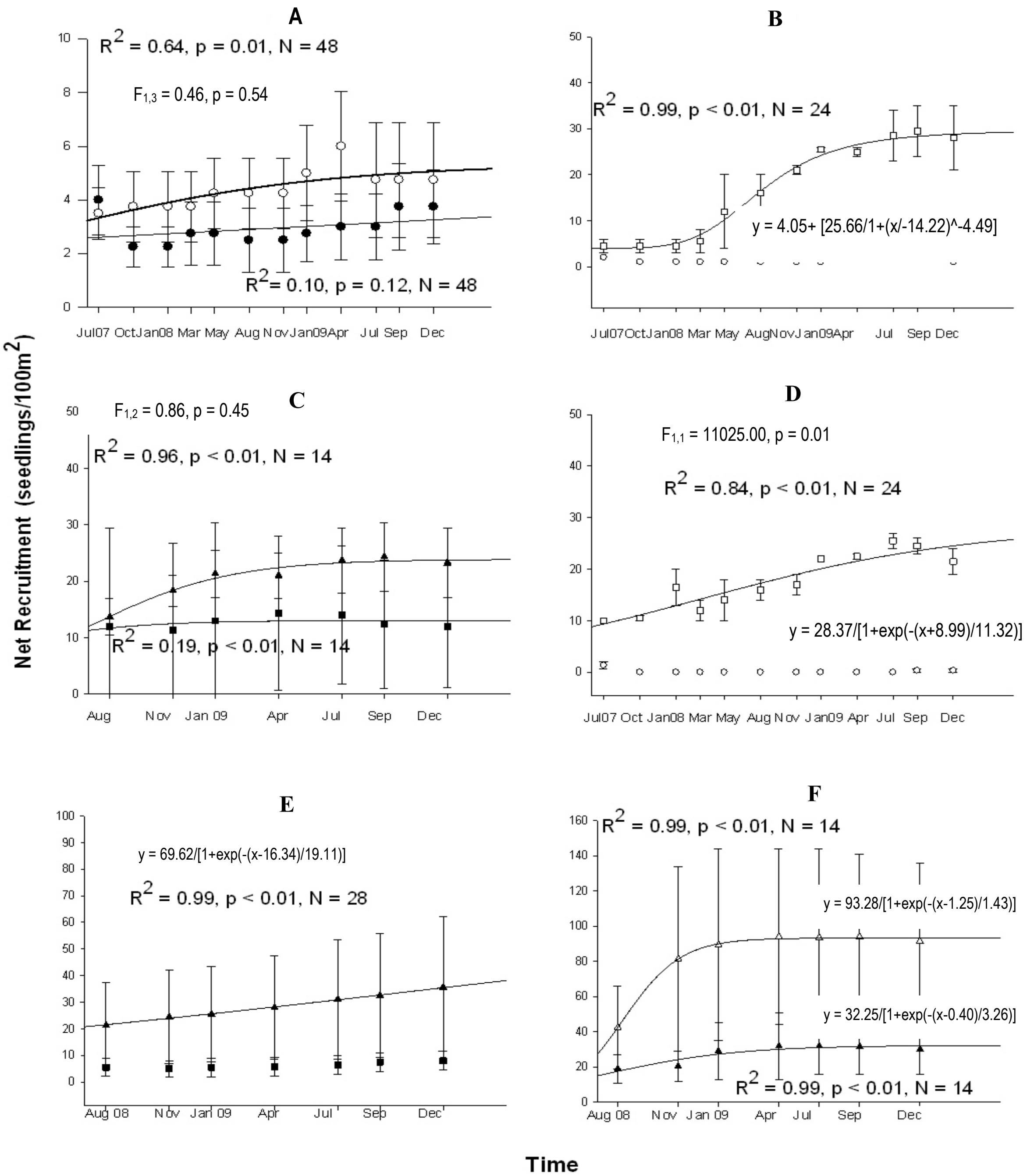


Fig. 2. Net recruitment of A. *A. australasica*, B-C. *C. australis*, D. *C. moti*, E. *H. wendlandiana* and F. *L. ramsayi* seedlings recruited in sites A2 - 62% sunlight (□), A3 - 52% (▲), B - 43% (△), C - 31% (●), D - 27% (○) and E - 80% (■).

juveniles/100 m². *C. moti* yielded 218 fruit/100 m² after two years, resulting in 8 seedlings/100 m² and 6 juveniles/100 m²; one seedling was recruited at site D (27% canopy openness) where mature individuals were absent. *H. wendlandiana* produced approximately 991 fruit/100 m² within two years, recruiting 47 seedlings/100 m² and establishing 7 juveniles/100 m². *L. ramsayi* yielded 23,488 fruit/100 m² with 47 seedlings/100 m² being recruited and 7 juveniles/100 m² being established after 2 years.

DISCUSSION

Canopy openness ranged from 27% to 80% within 1.5 to 3 years after Cyclone Larry struck in 2006 (but before Cyclone Yasi hit Mission Beach on February 2, 2011). This research showed that

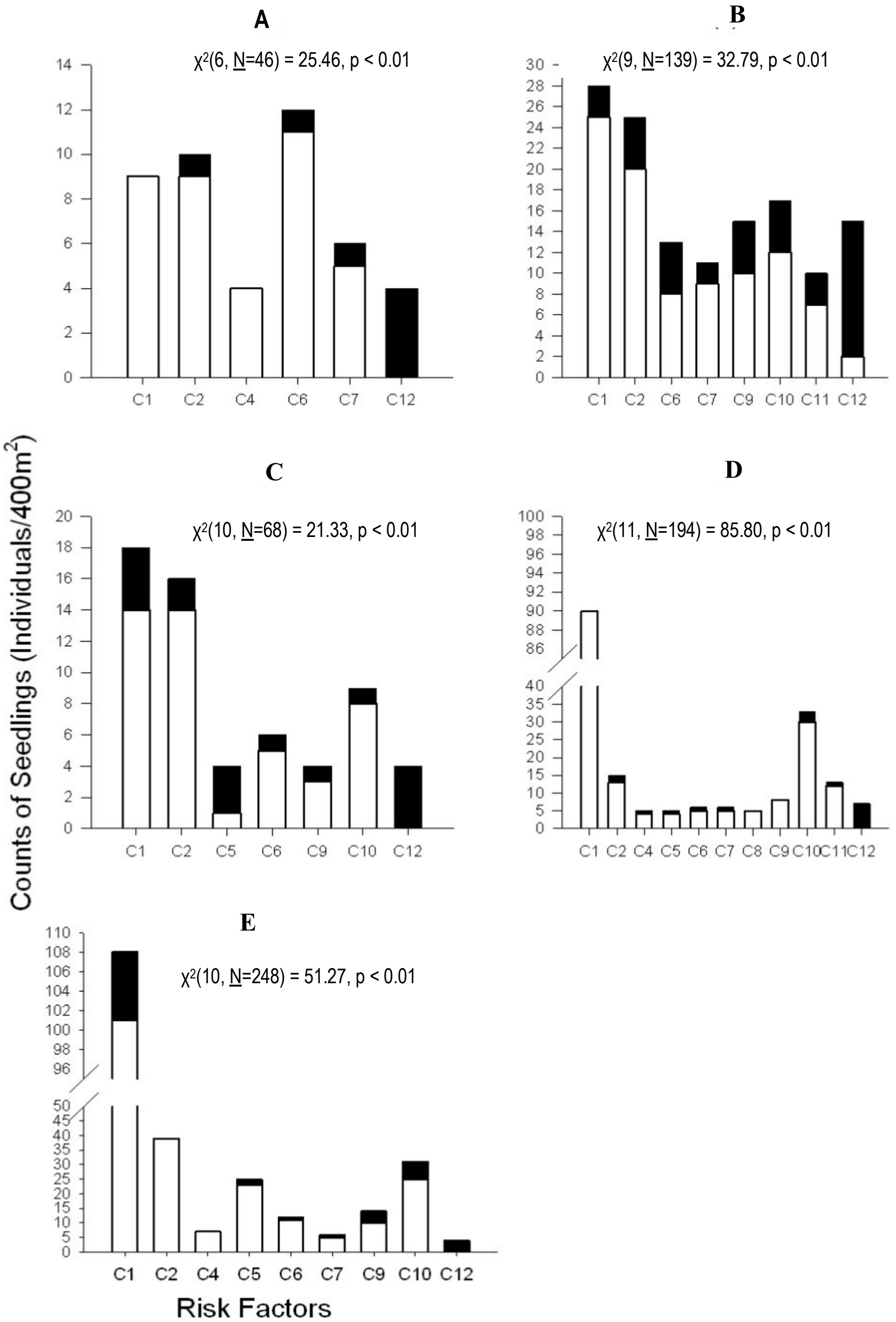


Fig. 3. Risk factors that might lead to seedling mortality of A. *A. australasica*, B. *C. australis*, C. *C. moti*, D. *H. wendlandiana* and E. *L. ramsayi* seedlings; 'surviving' (□) and those that 'did not survive' (■); C1-C12 were risk factors based on Table 4; only major risk factors were presented to simplify the figures and the others were left out.

rainforests at Mission Beach lack closed canopies and deeply shaded environments. This canopy openness range (15-80% openness, *i.e.* equals to 15-80% sunlight) also suggests that these rainforests cannot be considered closed forests (6-8% sunlight) according to Whitmore (1998), Gardiner and Hodges (1998) and Whitmore and Brown (1996) or 0-30% sunlight based on Specht and Specht (1999). The absence of a pre-Cyclone Larry census (or undisturbed control) means it is difficult to justify that they represent a post-Cyclone Larry mass recruitment. However, the cohort of seedlings censused in July 2006 was more likely to be post-Larry recruitment.

Mass recruitment in canopy gaps following Cyclone Larry was evident in *C. australis* and *C. moti*, as more seedlings survived at sites with higher canopy openness (Fig. 2). More seedlings

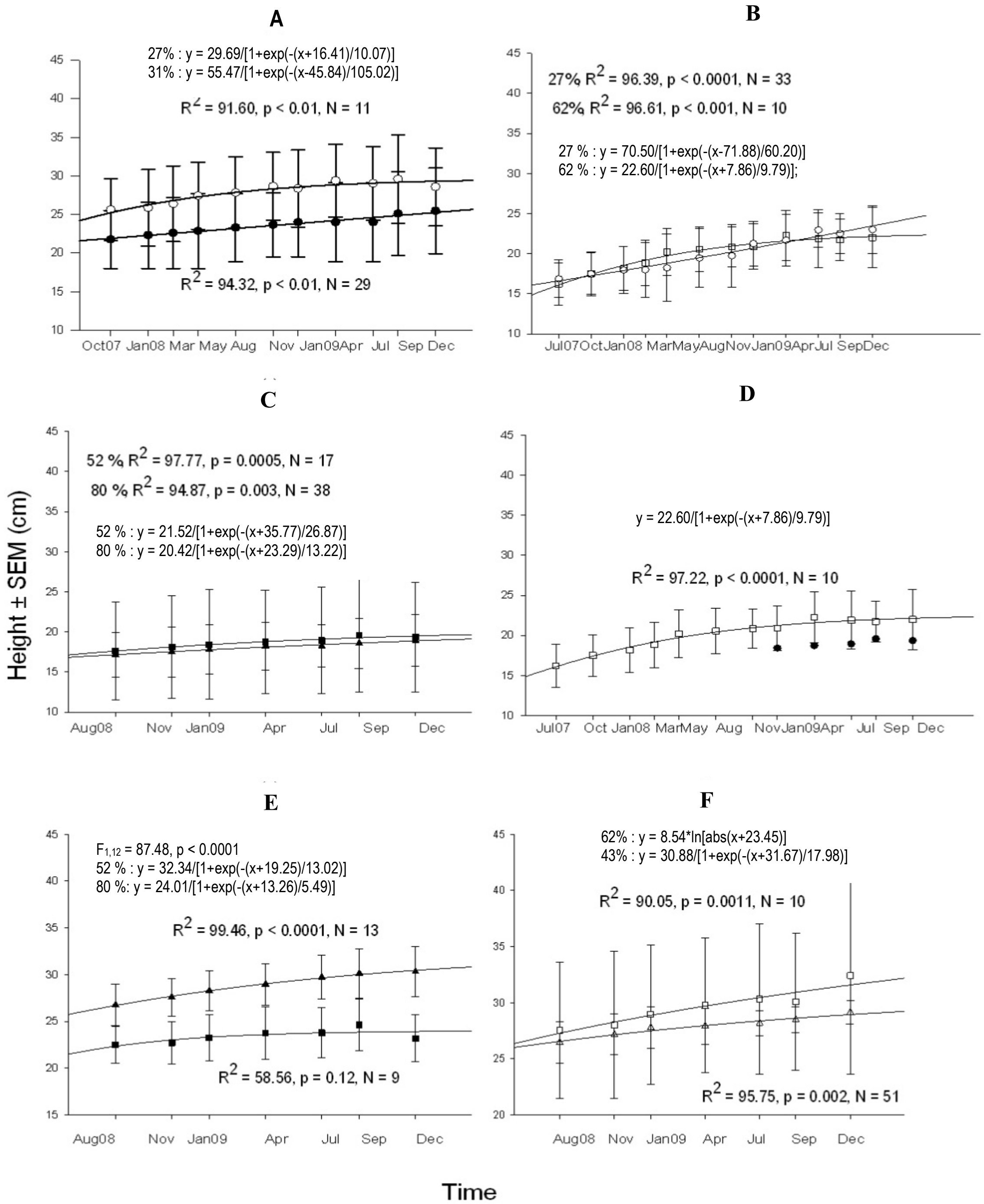


Fig. 4. Growth rate of A. *A. australasica*, B-C. *C. australis*, D. *C. moti*, E. *H. wendlandiana* and F. *L. ramsayi* seedlings at sites A2 - 62% canopy openness (□), A3 - 52% (▲), B - 43% (Δ), C - 31% (●), D - 27% (○) and E - 80% (■).

of *C. moti* survived at sites with 62% canopy openness than 27% openness. The net recruitment of *A. australasica* and *H. wendlandiana* seedlings was not significantly different between sites. More *L. ramsayi* seedlings were recorded at more shaded sites (Fig. 2F). These results showed that canopy gaps created by Cyclone Larry may stimulate the recruitment of *C. australis* and *C. moti*. Clearly, major cyclone disturbances that create canopy gaps (increasing light intensity) stimulate recruitment of certain species in most plant communities (Bullock, 2000; Fenner & Thompson, 2005; Harper, 1977; Uhl *et al.,* 1987; Whitmore, 1998).

The early seedling stage is most susceptible to mortality in *A. australasica* and is a major mortality risk factor in the other study species (Fig. 3). Most seedlings of all study species survived in 'Less shade or open areas' following Cyclone Larry. Moreover, disturbance factors following cyclones, including predation, diseases, litter, mud, debris and logs, were not significant

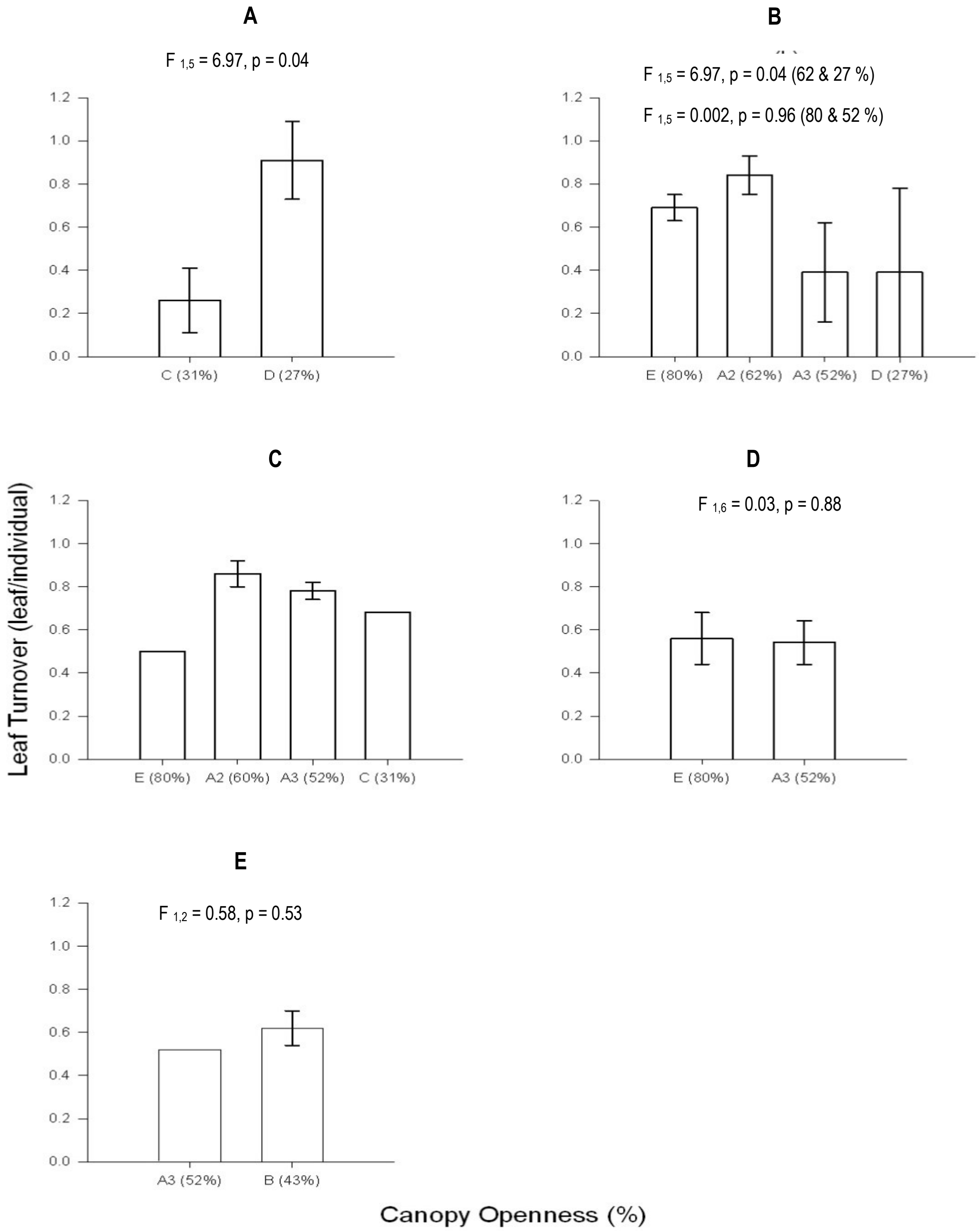


Fig. 5. Leaf turnover (mean ± SEM) of A. *A. australasica*, B. *C. australis,*C. *C. moti*, D. *H. wendlandiana* and E. *L. ramsayi* at sites A2, A3, B, C, D and E under different canopy openness (%) during 1.5-2 year study*; C. australis* in Site A3 and E.

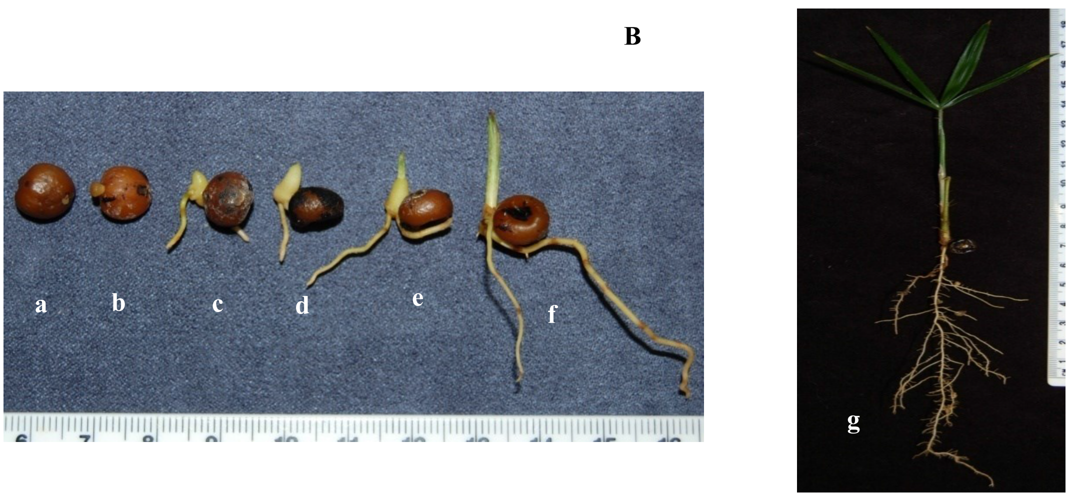
(Fig. 3). These results support the importance of light availability for seedling recruitment and survivorship (Augspurger, 1984). However, the thick litter layer that accumulates following cyclones can restrict recruitment and seedling survivorship (Guzman-Grajales & Walker, 1991; Yih *et al.*, 1991).

Seedlings of the palm species showed different growth responses in relation to the light environment, with sigmoidal response being a common pattern. The height of *A. australasica*, *C. australis*, *C. moti* and *L. ramsayi* seedlings did not respond significantly to different light intensities. *H. wendlandiana* seedlings grew more rapidly under 52% canopy openness than more open canopies (80%). The mean height of this species at site E (80% open) decreased during the last census as the oldest leaves of some samples were shed. *C. moti* and *L. ramsayi* retained their leaves longer in larger gaps, which would maximize light capture for photosynthesis, while *C. australis* had short leaf longevity. *A. australasica* had high leaf longevity in more open sites, while the leaf longevity of *H. wendlandiana* did not respond significantly to light conditions. The growth rates suggested that the palm seedlings were slow-growing species (Tomlinson, 1990). In other studies by Augspurger (1984) and Poorter and Boot (1998), 10 neotropical tree seedlings and seven rainforest seedlings, responded to higher canopy openness by increasing their leaf turnover and this enabled the plants to replace their

A

a–b= 40; b–d= 28; d–f= 64; f–h= 67 days; approximate germination period = 199 ± 7 days (*ca.* 7 months)

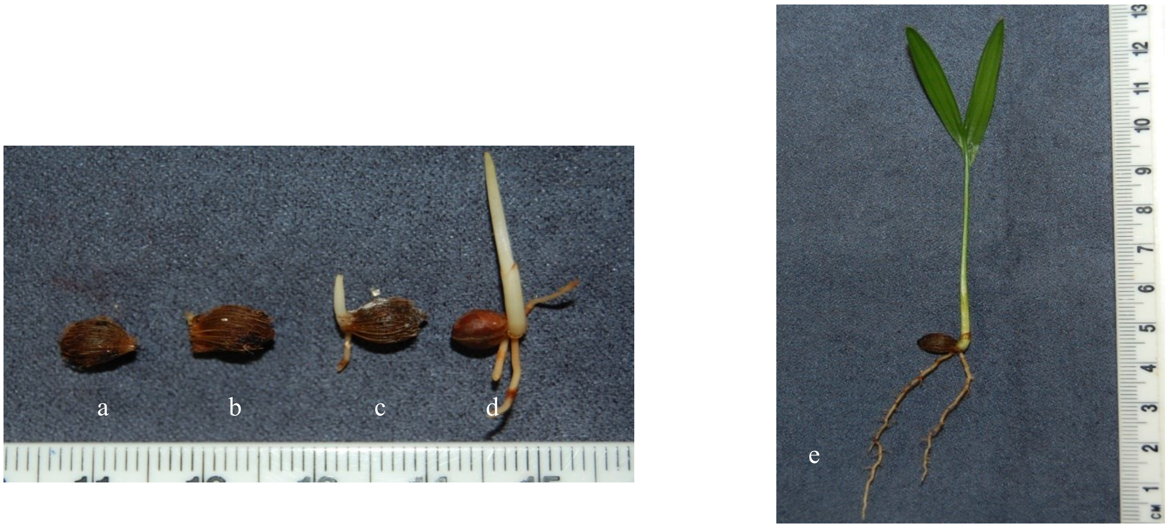
B



a–b= 11; b–d= 22; d–e= 12; e–f = 36; f–g = 81 days; germination period= 163 ± 26 days (*ca.* 6 months)

Fig. 6. Germination pattern of A. *A. australasica* and B. *C. australis.* The germination period was determined from 3 samples of germinated seeds from the germination experiments that were conducted at the same study period and were published elsewhere in Latifah *et al.* (2014); a-h = germination stages from seed to 1-eophyll/first leaf seedling stage; the numbers indicated the number of days.

A



a-b= 88; b-c= 16; c-d= 15; d-e= 88 days; germination period= 206 ± 17 days (*ca.* 7 months)

B

a-b= 87; b-c= 23; c-f= 20; f-h = 107 days; germination period= 237 ± 15 days (*ca.* 8 months)

Fig. 7. Germination patterns of A. *H. wendlandiana* and B. *L ramsayi* var. *tuckeri*. The germination period was determined from 3 samples of germinated seeds from the germination experiments that were conducted at the same study period and were published elsewhere in Latifah *et al*. (2014); a-h = germination stages from seed to 1-eophyll/ first leaf seedling stage; the numbers indicated the number of days.

Table 6. Observations of the life history stages of five palms from July 2007 to December 2009 at study sites (A2, A3, B, C, E) in north Queensland.

Live Events	*A. australasica*	*C. australis*	*C. moti*	*H. wendlandiana*	*L. ramsayi*
			Average (individuals/100m^2)		
Mature plants producing flowers/fruits	1	1	1	1	13
Juveniles survived previous cyclones	4	3	6	3	6
Seedlings/recruits	3	8	10	14	44
Flowering	tntc[1] Jul-Oct 2008 & Jul-Oct 2009 (C)	tntc Aug-Nov 2007 & Aug-Nov 2009 (one female; biennial; A3) Aug-Nov 2007, Aug-Nov 2008 & Aug-Nov 2009 (one male; annual; A3) Not flowering between Aug-Nov 2007 & 2008, flowering in Jul-Oct 2009 (one male & one female; biennial; E)	tntc Jul-Sep 2008 and Jul-Sep 2009 (biennial; A3)	tntc Apr 2008-2009 (A3) Jul 2008-2009 (E)	tntc Feb-Apr 2008-2009 (A2) Feb-Mar 2008-2009 (B)
Fruiting (Young fruit stage)	865 fruits	295 fruits Oct-Nov 2007 & 2009 (A3) Aug 2009 (E)	218 fruits Sep-Oct 2008-2009 (A3)	991 fruits May 2008-2009 (A3) Sep 2008-2009 (E)	23,488 fruits Mar-Apr 2008-2009
Fruiting [End-season (mature) stage]	208 fruits	55 fruits Nov-Dec 2007 & Nov-Dec 2009 (A3) Sep 2009 (E)	69 fruits Nov-Dec 2008-2009 (A3)	220 fruits Sep-Oct 2008-2009 (A3) Nov-Dec 2008-2009 (E)	2,172 fruits Apr-Jun 2008-2009 (A2) May-Aug 2008-2009 (B)
Seed dispersal (by non-predator agents or by predators)	865 fruits	256 fruits Nov-Dec 2007 & 2009 (A3) Dec 2009 (E)	218 fruits Sep-Dec 2008 to Feb 2009 (A3)	991 fruits Nov 2008-2009 (A3) Nov-Dec 2008-2009 (E)	23,488 fruits Aug 2008-2009 (A2) May-Sep 2008-2009 (B)
Seed dispersal by cassowaries	Not observed	18 seeds, 80% germination[2] (Feb 2008; A); 5 seeds, no germination (May 2008; A) 4 seeds, no germination (Jun 2008; A); 68 seeds, 60% germination (Jul 2009)	Not observed	Not observed	1 seedling (Dec 2007; A) 1 seedling (Nov 2008; A)
Germination period (Fig. 6)	7 months	6 months	Not observed	7 months	8 months
Seedling pool[3]	4	15	8	21	47
Juvenile pool[3]	4	3	6	4	7

[1]tntc = too numerous to count; [2]Tested under temperature-controlled room conditions; [3]predicted number of the surviving seedlings and juveniles at the end of study

unproductive leaves with new, productive leaves for harvesting light.

Cassowaries play an important role in palm seed dispersal. Seeds of *C. australis*, *L. ramsayi*, *A. alexandrae* and *P. elegans* were dispersed by cassowaries. The seeds were able to germinate after they passed through the cassowary gut. Seeds of *C. australis* were found most frequently in cassowary dung. Stocker and Irvine (1983) also found seeds of *C. australis*, *C. moti*, *C. radicalis* and *Linospadix microcarya* in cassowary dung and found that moderate to high germination occurred (except *C. australis*, no germination data provided). *C. radicalis* and *L. microcarya* were found most frequently in the dung (Stocker & Irvine, 1983). Bradford and Westcott (2010) also reported that all *Normanbya normanbyi* seeds germinated after passing through a cassowary's gut compared to 80% germination of control seeds.

CONCLUSION

Palm study species had regeneration strategies or growth forms such as a clustering growth habit in *A. australasica* and *H. wendlandiana* or tilting in *L. ramsayi* which favoured persistence. The recruitment of the seedlings of *C. australis* and *C. moti* was higher in gaps with more light; however, the recruitment of *L. ramsayi* was higher in sites with lower canopy openness. 'Less shade or open areas' was a minor mortality risk factor suggesting the importance of light availability for seedling recruitment and survivorship. In the current study, the growth rate of palm seedlings was not significantly different among study sites.

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