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Original article

Population status, demography and habitat preferences of the threatened lipstick palm *Cyrtostachys renda* Blume in Kerumutan Reserve, Sumatra

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Abstract

Population status and demography of a population of the threatened lipstick palm *Cyrtostachys renda* in a peat swamp ecosystem of Kerumutan Reserve, Sumatra (one of the largest remaining populations) was documented at 16 different sites, covering a wide range of forest and habitat types, vegetation associations, and population sizes. Population sizes were dominated by suckers comprising 89% of the total population. Individuals with stem heights between 0 and 4 m (47.5%), stem diameters between 4 and 10 cm (82.0%), and leaf scar numbers between 0 and 60 (69.2%) dominated. Ages of individuals were estimated and used to fit a curvilinear relationship between age and stem height. Wild plants reach reproductive maturity within 25–30 years, or when they have stem heights in excess of 2.0 m, or when they have 15–25 leaf scars. They can survive more than 80 years. Cultivated plants appear to reproduce earlier and produce more seeds than wild plants. Individual growth was plant size-dependent with the adult stage being the most productive. Higher mortality was experienced by suckers, especially in continuously waterlogged conditions and locations with dense canopies. Sucker growth was faster than seedling growth, an adaptation that may allow the species to cope with periodically waterlogged conditions. Population abundances varied with habitat types; well-drained areas were the most suitable habitat. To conserve the most important remaining populations of the lipstick palm, it is crucial to protect well-drained sites in Kerumutan Reserve.

Keywords: Population status; Demography; Abundance; Survivorship; Habitat preferences; Kerumutan Reserve; Sumatra

1. Introduction

Palms are of immense significance to Indonesian people, economically the second most important group after the grasses (*Oryza* spp.). Approximately 570 palm species (of about 2600 world species) occur in this country (Uhl and Dransfield, 1987; Dransfield, 1994); an area with the largest palm species number on earth (Dransfield, 1994; Stewart, 1994). Palms are recognised as increasingly threatened (Moore, 1979; Johnson, 1996; Henderson and Borchsenius, 1997) with a total of 222 species identified by the Palm Specialist Group of the Species Survival Commission as highly threatened with extinction (Johnson, 1996). Orchids, timber species, and palms are the top three contributors to the Indonesian list of threatened plants, comprising 93, 55, and 31 species, respectively (WCMC, 1997). According to IUCN (2000) Indonesia has the second largest number of threatened species (under the categories Critically Endangered, Endangered, and Vulnerable only) after Malaysia with a total of 384 species, and perhaps as many as 513 species if the Indonesian list of threatened species recorded by the WCMC (1997) is included.

Population status, spatial occurrence, and habitat relationships of threatened plants in the tropics, even in protected areas, is a challenging task for several reasons. First, the patterns of distribution and abundance of species have not been well documented (Elias, 1986; Batianoff and Burgess, 1993;

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Bawa and Seidler, 1998; Scariot, 1999; Shapcott, 1999; Keith, 2000; Vormisto, 2002), thus the habitat and geographical ranges of species are poorly known (Kahn and Mejia, 1990; Falk and Holsinger, 1991; Keith, 2000; Vormisto, 2002). Second, a large proportion of tropical species are rare, occurring at very low population densities (Bawa and Ashton, 1991; Shapcott, 1999; Vormisto, 2002). In addition, since the 1970s tropical rare plant research has focused on providing information on the synecological relationships and distribution of endangered populations, while threatened species management requires quantitative autecological data produced from field monitoring programmes (Bradshaw, 1981; Pavlik, 1986; Cropper, 1993; Dowe et al., 1997; Keith, 2000; Higgins and Ruokolainen, 2004). Parameters such as the size and number of populations and area of occupancy form the basis for measurable criteria for further conservation actions (IUCN 1994; Tear et al., 1995; Menges and Gordon, 1996).

Primary causes of *Cyrtostachys renda* habitat loss in Sumatra are plantation development (oil palm, *Acacia mangium*, coconut, pineapple, and sagu), extraction activities (mainly logging and mining, e.g. Bawa and Seidler, 1998; Robertson and van Schaik, 2001; Fuller et al., 2004), and human settlements. Sumatra has lost nearly 10 million ha of lowland forest between 1980 and 2000 with an annual rate of deforestation of 0.91% (Achard et al., 2002; World Resources Institute, 2002). The annual deforestation rates of lowland forests in this island have increased dramatically since 1997 in part due to political and economical instability. In the Kerumutan Reserve, illegal logging and shifting habitations (enclave development) for fishing activities are the major problems. In the case of *C. renda* disturbance, the stems of adult individuals are used by local communities (fishermen) to construct bagan (shelters/temporary houses) floors.

Today Kerumutan Reserve contains the most important remaining populations of *C. renda* in which natural regeneration occurs and which supports a complete range of age and size classes. The Kerumutan peatswamp and the adjacent watershed is a very important wetland in Sumatra and has vital functions in the regulation of local and regional hydrology, maintenance of biodiversity, providing a source of renewable bioresources and habitat for various protected plant and animal species (including the endangered Sumatran tiger).

Very little is known about the ecology, habitat requirements, recruitment, and population demography of threatened palm species (Tomlinson, 1990; Ratsirarson et al., 1996; Dowe et al., 1997; Henderson and Borchsenius, 1997; Jones, 2000; Maunder et al., 2001; Vormisto, 2002), especially those occurred in peat swamp forests. Consequently, we do not know how to address specific conservation problems and how to set conservation strategies and priorities.

This research aimed to assess and monitor the population structure, status and demography (age, reproduction, growth, and survivorship) of *C. renda* and to elucidate specific ecological requirements including its habitat specificity. Such information is required to support reserve management, particularly through long-term monitoring of at least several, significant *C. renda* populations occurring on different habitat types. Long-term monitoring programs will provide the foundations for developing management prescriptions and conservation priorities for the species and its habitat.

2. Methods

2.1. Study sites and species

Kerumutan Reserve was established in 1979 based on the decree of the Indonesian Minister of Agriculture No. 350/KPTS/UM/6/79, covering a flat (0–3% in elevation) area of 120,000 ha, located between N 00°11′52″ and S 00°18′00″ and between E 102°25′20″ and E 102°37′36″, and lying between Sumatra's two major rivers: the Kampar and Indragiri Rivers (Fig. 1). It has the 'Af' climate type: tropical wet, experiencing eight consecutive wet months, all months with an average temperature above 18 °C and small seasonal temperature variations of less than 3 °C (the Koppen's System in Tarbuck and Lutgens, 2004). The average annual rainfall is 2720 mm, the daily temperature ranges from 23 °C to 34 °C, with an average humidity of 84% (Bappeda Riau and Bakosurtanal, 1998, 1998a).

Based on the water drainage qualities, Kerumutan Forest can be divided into three forest types: well-drained (five sites selected), seasonally flooded (five sites selected), and permanently waterlogged (six sites selected) peat swamp forests. Seasonally flooded forest dominates the watersheds of Kerumutan River and the adjacent streams, containing mostly low trees, such as *Syzygium incarnatum*, *S. spicatum*, *Gardenia pterocalyx*, and *Nauclea subdita*, but also higher trees such as *Calophyllum soulattri*, *Garcinia bancana*, *Campnosperma coriaceum*, *Litsea* sp., *Gluta renghas*, *G. wallichii*, and *Koompassia malaccensis*. Well-drained forest occurs behind the seasonally flooded forest consisting of at least four canopy strata: emergent/upper canopy (40–50 m), main canopy (20–35 m), subcanopy (10–20 m), and lower subcanopy (3–10 m). The dominant species includes *Shorea parvifolia*, *S. rugosa*, *K. malaccensis*, *G. renghas*, *G. wallichii*, *Combretocarpus rotundatus* (emergent); *Parastemon urophyllum*, *Adinandra polyneura*, *Palaquium xanthochymum*, *C. coriaceum* (main canopy); *Syzygium acuminatum*, *Pandanus terrestris*, *Acmena acuminatissima*, *G. bancana*, and *Eleiodoxa conferta* (subcanopy and lower stratum). Permanently waterlogged forest is dominated by *Pandanus helicopus*, *Hanguana malayana*, *Syzygium* sp. (kobu), *S. incarnatum*, *G. pterocalyx*, and *Microcos paniculata*.

The forest is dominated by a 'shallow' (Phillips, 1998) peat formation, consisting mainly of layers ranging from 0.5 to 1.5 m depth. The rock formation is composed of alluvial deposits while mineral soils are mainly organosol and red-yellow Podzol (Bappeda Riau and Bakosurtanal, 1998, 1998a). Around 30% of the area is dry during the dry season, but it is almost totally waterlogged in the wet season. The Eastern Sumatra peat swamp forest is regarded as one of the

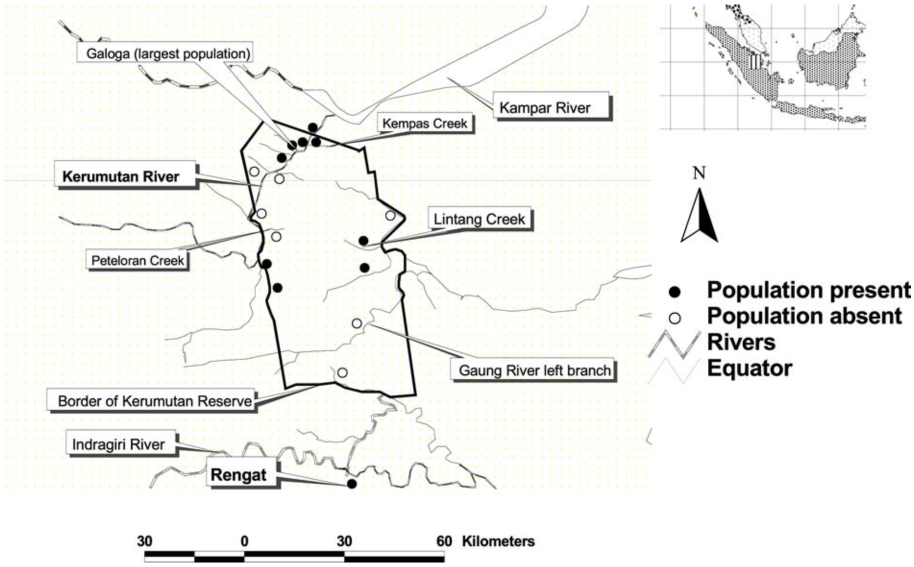

Fig. 1. Locations of the study area within Kerumutan Reserve, Sumatra.

most intact peat swamp forests remaining in Southeast Asia (Davie and Sumardja, 1997).

C. renda Blume (Arecaceae) is a monoecious, clustered or very rarely single stemmed, slender palm, up to 16 m tall and 5–14 cm in diameter, easily recognised by its bright red crownshaft. It is equatorial, distributed throughout Peninsular Malaysia, Sumatra, and Borneo, becoming a characteristic component of the lowland peatswamp ecosystems, occurring near tidal coastal areas and along river banks (Uhl and Dransfield, 1987; Widyatmoko, 2001), and the only species of the genus located west of Wallace's Line. The species has been used locally, nationally, and globally for commercial ornamental purposes (LBN, 1987) and was listed as threatened (IUCN, 1995) but was then excluded (IUCN, 2000). The young stem apex is sometimes eaten by local communities while the adult stems are used to construct bagan (shelters/temporary houses for fishing activities) floors. The hard outer wood of the stem is used for making darts. More broadly, this distinctive species may become a flagship species to promote southeast Asian peat swamp conservation. The species is protected by the Indonesian Government's Legislation No. 7 (1999) (Protection of the Indonesian Threatened Plant and Animal Species).

A clump (clone) of *C. renda* usually consists of different plant stages/ages and size classes (suckers, juveniles, and adults). Juveniles next to an adult may actually be root suckers, thus such plants (i.e. at distances equal to or less than that of the radius of the clump) were regarded as suckers rather than seedlings (based on House 1984), but single, juvenile and adult stems not associated with large clumps were counted as separate individuals. Suckers obviously use stolons to grow and escape from the dense roots of the mother plants. This assessment is an important element of the stage classifications, and it should be noted that each plant may represent a genet (a plant derived from seed) or a ramet (a separate shoot/clonal individual). IUCN (1994); Soegianto (1994); Begon et al. (1986) suggested that reproducing units within a clump should be counted as individuals, except where such units are unable to survive alone. In this case, the suitable measurement can be either basal area or crown projections. Abundance could then be represented both in terms of clump density and individual plant density (adult, juvenile, and sucker or seedling). These criteria suit the ecology and life-form of the lipstick palm.

2.2. Site selection

Fifteen sites were chosen randomly inside the study area at the Kerumutan Reserve and one site at the adjacent sanctuary to cover a wide range of population structures and sizes, vegetation associations, forest and habitat types, altitudes, and aspects. To narrow down the study area, a preliminary survey exploring the reserve was conducted to get access to various sites and cover different habitat types (including potential areas where *C. renda* might be present) before selecting the sites (Fig. 1). No herbarium records, plant collections, or existing locality records were available for *C. renda* in the Reserve before this study.

2.3. Population structure and status

2.3.1. Sampling

To assess the population structure and status of *C. renda*, a systematic parallel line sample was used to ensure that all parts of the study area were covered and the target species recorded (Krebs, 1989; Cropper, 1993). A series of 1542 transects of 100 × 10 m each covering a total forest area of 154.2 ha (0.13% of the reserve area) was established. Each locality where transects were established was located by a Garmin Global Positioning System MAP 175 and projected into the 1993/1994 boundary reconstruction map of Kerumutan Reserve with scale 1:250,000. Each selected site was divided into two blocks (both sides of the creek/river) and each side was systematically investigated using transects (100 × 10 m each) orientated on a selected compass bearing. To develop a full population structure and status, all individuals (comprising suckers, juveniles and adults) within 5 m either side of each transect were measured and counted. The accuracy of the method was improved by developing transect lines closer together, with an interval of 10 m. To avoid any problems of overlap and double counting, all recorded individuals were tagged. Sites were set up and measured in November 1996 and remeasured every 6–12 months until June 2000.

2.3.2. Measurement attributes

Measurements included the numbers of discrete clumps (from which palm frequencies and densities were determined), numbers of individual plants within each clump to determine clump sizes and tree densities, numbers of leaves (for suckers, juveniles, and adults), stem diameter at breast height (dbh) for adults to determine the basal area, height of the visible stem to the base of the leafsheath of the lowest leaf (for juveniles and adults), leaf size (length average) of the two oldest live leaves (for suckers only) (based on Ratsirarson et al., 1996), and number of leaf scars on each stemmed individual (juveniles and adults). Stem height was measured by a hagameter and stem diameter (dbh) by a diameter tape.

2.3.3. Stage-structure

Eight different stage classes were defined within the populations depending on the size (length) of the leaves for suckers (stem invisible) and the height of the stem for juveniles and adults (stem visible). Suckers were divided into three stage classes due to the wide range of their development stages (leaf sizes) and each was assumed to have different growth and mortality rates (e.g. to cope with frequent prolonged waterlogging). Juveniles had wide ranges of stem height (consisting of different ages) and were assumed to have different growth and leaf production rates, while adults had different reproductive outputs (i.e. fruit numbers produced by young and old adults as well as the difference in leaf production rates). The categories defined were sucker S_1, leaf length <100 cm; sucker S_2, leaf length 100–200 cm; sucker S_3, leaf length >200 cm; juvenile J_1, stem visible (leaf scars conspicuous), crown shafts developed, and the stem height <100 cm; juvenile J_2, immature individual with stem height 100–200 cm; adult A_1, mature individual with stem height >200–500 cm (based on the flowering/fruiting evidence of wild individuals and those of *C. renda* collections in Bogor Botanic Gardens); adult A_2, mature individual with stem height >500–800 cm; and adult A_3, mature individual with stem height >800 cm.

2.4. Demography

To estimate life tables, demographic parameters (comprising age, reproduction, growth, and survivorship) were investigated based on marked individuals in the eight known/extant sites. Information on survivorship came from censuses conducted every 6 months for suckers and annually for juvenile and mature individuals.

2.4.1. Age estimation

Age (A) of stemmed individuals was estimated from the total number of leaf scars (N) on the stem, the number of live leaves present in the crown (n), the leaf production rate (l) of an individual, and the time (a) required for a new sucker or seedling to produce a visible stem (establishment phase). The value of the establishment phase (the time taken for individuals to produce stems) is 15 years on average based on the plantation data of *C. renda* at Bogor Botanic Gardens (Registration Section). Based on Corner's (1966), formula $A = [(N + n)/l] + a$, the age of each individual with a visible stem was determined. As the number of leaf scars cannot provide an absolute age for any individual, an approximate age was estimated on the basis of leaf production averaged among individuals observed.

2.4.2. Growth

Individual growth (including stem height increment) was determined by counting the number of new leaves produced per year (Ratsirarson et al., 1996). The youngest leaf of each individual was tagged at the beginning of the research, and all new leaves produced were recorded at each census. The total height growth of the stem over time was estimated from the number of new leaves produced (based on Ratsirarson et al., 1996). Quantitative relationships among variables were analysed using regression analysis (Tomlinson, 1990). In particular, the stem height was regressed on age in a logarithmic regression. Growth rate in suckers was determined using tagged suckers from Galoga population with leaf length <1 m ($n = 40$), 1–2 m ($n = 38$), and >2 m ($n = 40$).

2.5. Habitat preference (specificity)

To determine species specific habitat requirements, the 16 sites chosen were classified into three habitat types, constituting the typical physiognomies of the Kerumutan Forest, and were differentiated on the basis of water drainage quality and ground surface characteristics. They include: *permanently waterlogged forest* (inundated all year-round), *seasonally flooded forest* (poorly drained), and *well-drained forest*. The sites chosen included both natural (intact) and disturbed (suffering from human disturbance) forests. Three habitat types were described: *natural forest*, *disturbed forest*, and *totally converted forest* in order to assess the palm abundance in different habitat qualities (based on the forest integrity or disturbance level).

3. Results

3.1. Population structure and status

The species was present in nine of the 16 sites investigated and absent from the six permanently waterlogged sites and one seasonally flooded location. The palm seems to be sensitive to changes in the water table. Although the palm tolerated seasonally flooded sites, the abundance in this type of habitat was very low. Sucker growth was very slow (ca. 15 cm per 6 months) and even lower for seedlings (ca. 5 cm per 6 months) (*unpublished data*). The growth rate was insufficient to reach the autotrophic layer (above water surface) when the water table increased and sites were waterlogged in the (next) wet season. Kahn and Mejia (1990) also found that palm density and diversity was very low in the Peruvian Amazonia forests which were periodically flooded by blackwater streams.

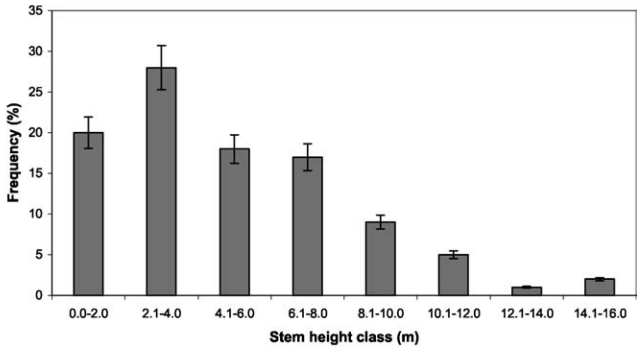

Fig. 2. Stem height-class frequency distribution of *C. renda* at Kerumutan Reserve ($n = 506$).

3.1.1. Population structure

Population structure of *C. renda* was represented in two ways: by stem height class (Figs. 2–4) and by stage class (Fig. 5). The stem height class distribution showed a preponderance of individuals in the 2.1–4.0 m height class (27.5%) and a strong right hand skew typical of populations in which recruitment and mortality were continuous and density dependent, rather than episodic. The relative frequencies of individuals in the next two classes (4.1–6.0 and 6.1–8.0 m) were

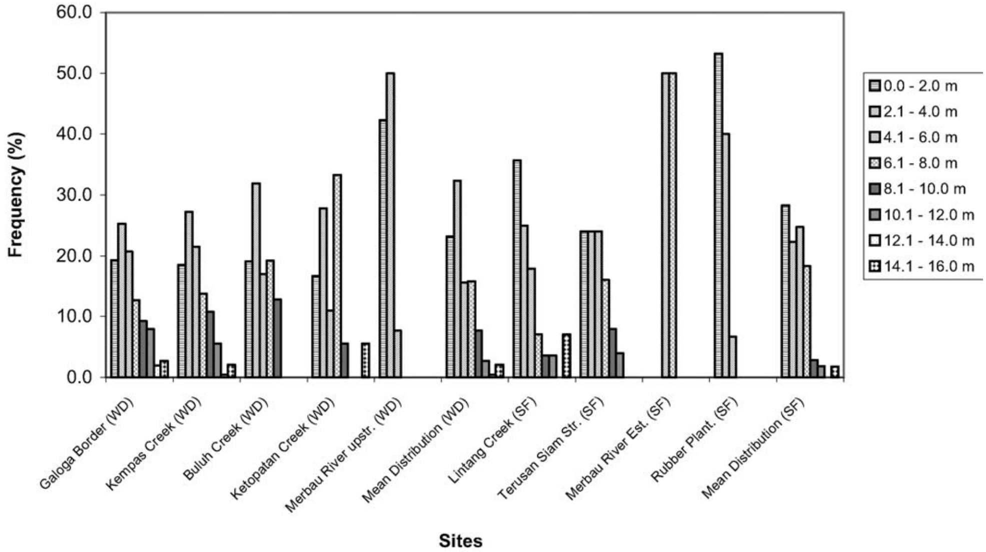

Fig. 3. Stem height-class frequency distribution (%) of *C. renda* at various sites (with different drainage qualities) within Kerumutan Reserve ($n = 506$). WD: well-drained site, SF: seasonally flooded site.

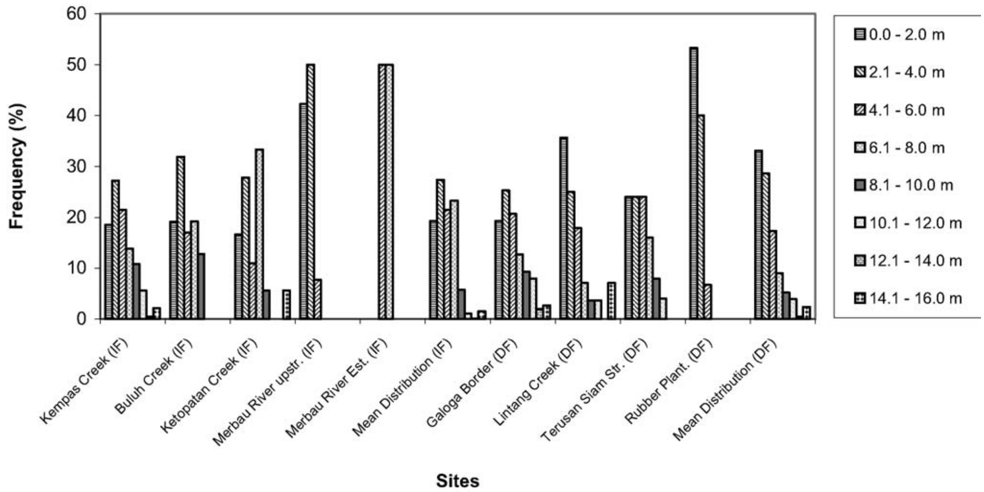

Fig. 4. Stem height-class frequency distribution (%) of *C. renda* at various sites (with different disturbance level) within Kerumutan Reserve ($n = 506$). IF: intact forest, DF: disturbed forest.

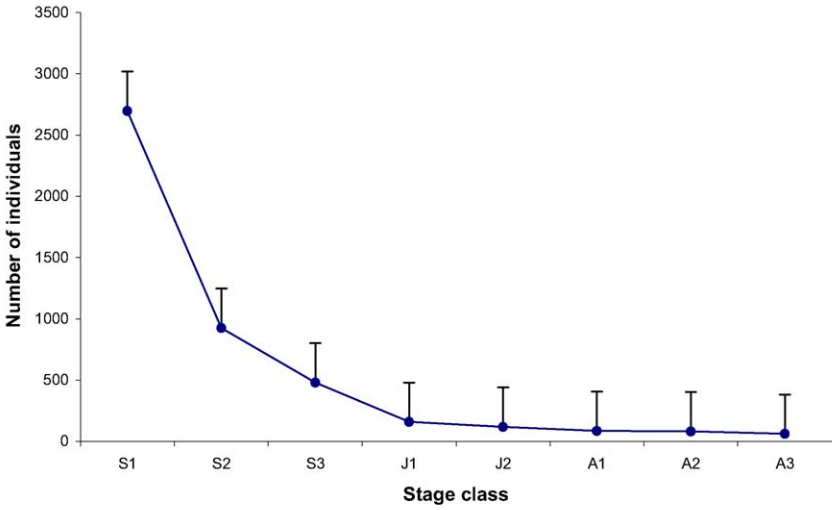

Fig. 5. Population structure of *C. renda* by stage class at Kerumutan Reserve (n = 4609, unit area = 154.2 ha). Error bars are one standard error.

also important (Fig. 2), reflecting a reduced rate of stem growth once stems found a suitable, exposed layer in the canopy. *C. renda* preferred moderate sunlight exposure, occupying the intermediate canopy, 2–10 m. At 2–4 m in height, plants started to produce flowers. Thus more energy might be allocated for reproduction than for vertical growth.

Population structure (in terms of stem height class) varied amongst sites with different drainage qualities, but younger plants tended to dominate at most sites as indicated by their mean frequency distributions (Fig. 3). At Merbau River upstream and Galoga rubber plantation, adult individuals >6 m were absent. Populations at Kempas Creek and Galoga Border comprised a full population structure of different height classes. The variations reflected local scale disturbance levels and regeneration events (Fig. 4). At Merbau River, populations were harvested relatively intensively. Population structure (in terms of stage class distribution) varied between sites but displayed the same general structure as the stem height class distributions (Fig. 5).

Abundance parameters measured in the study area (comprising clump frequency, tree density, basal area, and canopy circle area) were presented in Table 1. At high tree densities and high canopy circle areas, e.g. in Galoga Border and Kempas Creek (Table 1), where competition for light and space was assumed to be intense, sucker densities were not substantially lower, implying that suckers could tolerate low light conditions.

3.2. Demography

Individual variation of three development stages (adults, juveniles, and suckers) within *C. renda* in leaf number, stem diameter, stem height, leaf scar number, and leaf production rate were presented in Table 2. The leaf numbers of suckers varied considerably from 1 to 8. This was due to the wide range of sucker development stages: from Sucker 1 (S_1), Sucker 2 (S_2), to Sucker 3 (S_3). As the suckers grew (becoming juveniles), their leaf numbers became more stable, ranging from four to eight leaves. Mature individuals could reach 16 m in height. Leaf scar numbers varied considerably, with an average of 60.7 for adults and 21.6 for juveniles. As many as 190 leaf scars were found on some adult individuals (Table 2).

3.2.1. Age estimation

Age was estimated for all stemmed individuals (juveniles and adults), and a curvilinear relationship was seen between age and stem height of this palm (Fig. 6). The model is $Y = 7.77 \ln (X) - 21.93$, where Y = Height (m) and X = Age (year), with $R^2 = 0.81$ and $P < 0.001$. At an age of ca. 50 years (ca. 8–10 m in height) stem height increment appeared to slow. The average of stem height increment of individuals <8 m was 37.7 cm year^{-1} (an increase of 13.0 cm on average per one new leaf produced), while that of individuals >8 m was 24.8 m (an increase of 9.0 cm on average per one new leaf produced). This indicates an important difference in stem height increment within these two stages, confirming the slower growth of the older stages (shorter internodes). Similar age–height relationships had been reported in other palm species (e.g. Lieberman et al., 1988; Ratsirarson et al., 1996).

3.2.2. Reproductive behaviour

Wild plants of *C. renda* reached reproductive maturity and started to produce seeds between 25 and 30 years of age, or when they had a stem height in excess of 2.0 m (Fig. 6), or when they had between 15 and 25 leaf scars. They can survive more than 80 years (Table 2 and Fig. 6). Individuals less than 1.5 m in height or with less than 10 leaf scars (approximate age 17–18 years) never produced reproductive structures (either flowers or fruits) over the study period.

3.2.3. Plant growth

A notable difference in growth rate was found among individuals (suckers) with leaf length < 1 m, 1–2 m, and > 2 m. Individuals <1 m grew an average of 0.09 m year^{-1} (n = 40); individuals 1–2 m grew an average of 0.14 m year^{-1} (n = 38);

Table 1
Abundance parameters of *C. renda* measured in different locations within Kerumutan Reserve in association with forest (vegetation) association and habitat type

Location	Position	Forest association	Type of habitat	Number of clumps ha^{-1}	Mean number of stems clump^{-1}	Range stems clump^{-1}	Clump frequency	Number of adults ha^{-1}	Number of juveniles ha^{-1}	Stem density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Number of suckers ha^{-1}	Canopy circle area (m^2 ha^{-1})
Galoga Border	N 00°09.151′ E 102°30.052′	Anacardiaceae dominant	Well-drained forest	6.11	6.82	1–34	0.19	20.28	21.39	41.67 ± 8.14	0.167 ± 0.020	550.28	386.67 ± 39.42 (8.27)
Kempas Creek	N 00°08.977′ E 102°36.383′	Dipterocarpaceae dominant	Well-drained forest	3.16	5.42	1–19	0.11	9.04	8.07	17.11 ± 6.23	0.080 ± 0.020	106.01	207.32 ± 27.19 (9.28)
Buluh Creek	N 00°09.151′ E 102°28.80′	Pandanaceae dominant	Well-drained forest	2.69	3.36	1–11	0.15	4.23	4.81	9.04 ± 2.64	0.032 ± 0.017	48.08	74.75 ± 18.71 (9.83)
Ketopatan Creek	N 00°07.998′ E 102°26.452′	Clusiaceae dominant	Well-drained forest	0.44	4.50	1–8	0.06	1.00	1.00	2.00 ± 1.73	0.011 ± 0.003	8.56	20.34 ± 5.19 (12.12)
Merbau River upstream	S 00°06.664′ E 102°24.917′	Dipterocarpaceae dominant	Well-drained forest	0.56	3.71	1–12	0.03	0.00	2.08	2.08 ± 1.35	0.003 ± 0.001	9.44	21.96 ± 2.23 (10.56)
Lintang Creek	S 00°02.269′ E 102°36.241′	Anacardiaceae dominant	Seasonally flooded forest	1.45	3.11	2–7	0.11	1.77	2.74	4.51 ± 1.27	0.024 ± 0.002	18.39	44.41 ± 6.43 (10.17)
Terusan Siam Stream	S 00°04.120′ E 102°34.395′	Rubiaceae-Myrtaceae dominant	Seasonally flooded forest	0.61	2.50	1–9	0.05	0.55	0.98	1.03 ± 0.46	0.004 ± 0.001	9.33	15.89 ± 2.99 (10.42)
Merbau River estuary	S 00°03.510′ E 102°23.278′	Melastomataceae-Pandanaceae dominant	Seasonally flooded forest	0.29	1.00	1–1	0.03	0.29	0.00	0.29 ± 0.19	0.001 ± 0.001	2.21	3.69 ± 0.50 (12.56)
Galoga rubber plantation	N 00°09.361′ E 102°30.979′	Euphorbiaceae dominant	Seasonally flooded forest	0.60	1.50	1–4	0.04	0.41	0.48	0.89 ± 0.17	0.002 ± 0.001	11.07	7.44 ± 2.09 (8.33)
Gaung River right branch	S 00°00.614′ E 102°36.529′	Anacardiaceae-Dipterocarpaceae dominant	Seasonally flooded forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000
Sarang Unggas Creek	N 00°04.863′ E 102°27.375′	Mixed forest	Permanently waterlogged forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000
Kelantan Creek	N 00°07.913′ E 102°24.178′	Myrtaceae dominant	Permanently waterlogged forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000
Bebak Creek	N 00°03.90′ E 102°24.52′	Mixed forest	Permanently waterlogged forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000
Peteloran Creek	N 00°00.74′ E 102°26.148′	Pandanaceae dominant	Permanently waterlogged forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000
Mengkuang River	S 00°16.50′ E 102°32.98′	Anacardiaceae-Dipterocarpaceae dominant	Permanently waterlogged forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000
Gaung River left branch	S 00°08.148′ E 102°35.836′	Mixed forest	Permanently waterlogged forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.000	0.00	0.000

Mean values ± S.D. (95% confidence intervals), in parentheses: the mean canopy circle areas of individual crowns, stem density includes adults and juveniles (stemmed individuals).

Table 2
Individual variation and measurement attributes for *C. renda* at Kerumutan Reserve, Sumatra

Attribute	Measurement	Development stage*							
		A_1	A_2	A_3	J_1	J_2	S_1	S_2	S_3
Number of leaves	Mean ± S.D.	6.62 ± 0.69	7.50 ± 0.60	7.50 ± 0.59	5.68± 0.67	6.39 ± 0.84	3.38 ± 0.88	6.17 ± 0.77	6.93 ± 0.66
	Range	5–8	6–9	6–9	4–7	5–8	1–6	4–8	5–8
	Sample size	85	81	63	159	118	1747	608	303
Stem diameter (cm)	Mean ± S.D.	7.95 ± 1.40	8.84 ± 1.52	9.09 ± 1.53	4.76 ± 1.06	6.10 ± 1.33	–	–	–
	Range	4.7–12.1	5.2–12.2	5.3–14.00	2.7–8.7	3.4–10.2	–	–	–
	Sample size	85	81	63	159	118	–	–	–
Stem height (m)	Mean ± S.D.	3.54 ± 0.86	6.66 ± 0.79	10.99 ± 1.98	0.65 ± 0.19	1.62 ± 0.37	–	–	–
	Range	2.1–5	5.3–8	9.0–16.0	0.14–0.98	1.00–2.00	–	–	–
	Sample size	85	81	63	159	118	–	–	–
Number of leaf scars	Mean ± S.D.	48.34 ± 10.08	77.69 ± 25.69	126.27 ± 30.32	12.97 ± 6.66	30.27 ± 10.50	–	–	–
	Range	21–78	40–170	65–190	1–33	13–67	–	–	–
	Sample size	85	81	63	159	118	–	–	–
Age (year)	Mean ± S.D.	28.01 ± 5.36	39.25 ± 9.69	60.49 ± 10.97	18.86 ± 1.02	21.82 ± 2.23	–	–	–
	Range	20.25–51	22–82.5	37.33–83.5	16.67–21	18.50–28.50	–	–	–
	Sample size	85	81	63	159	118	–	–	–
Leaf production rate (new leaves year^{-1})	Mean ± S.D.	2.85 ± 0.62	2.94 ± 0.56	3.03 ± 0.44	2.76 ± 0.48	2.78 ± 0.49	1.62 ± 0.48	1.64 ± 0.48	1.65 ± 0.51
	Range	1–4	2–4	2–4	2–4	2–4	0–2	0–2	1–2
	Sample size	85	81	63	159	118	1747	608	303
Number of fruits per individual	Mean ± S.D.	–	46.33 ± 70.12	281.25 ± 284.95	–	–	–	–	–
	Range	–	0–127	103–705	–	–	–	–	–
	Sample size	–	3	4	–	–	–	–	–

A_1: mature individuals with stem height >200–500 cm; **A_2**: reproductive individuals with stem height >500–800 cm; **A_3**: reproductive individuals with stem height >800 cm; **J_1**: juvenile, stem visible, crown shafts developed with stem height <100 cm; **J_2**: juvenile/immature individual with stem height 100–200 cm; **S_1**: sucker, stemless, leaf length <100 cm; **S_2**: sucker, stemless, leaf length 100–200 cm; **S_3**: sucker, stemless, leaf length >200 cm. Only 2658 suckers of the total 4103 found at the study area were included in the measurement.

and individuals >2 m grew an average of 0.20 m year^{-1} (n = 40). It took individuals an average of 13 years to reach a juvenile size (approximate 2.5–3 m in height for the oldest leaves), based on specimens cultivated at Bogor Botanic Gardens. However, a juvenile with leaves 2.5–3 m in length still took some years before a visible stem developed. Thus establishment of *C. renda* required approximately 15 years.

Table 2 showed the difference of leaf production rate among plant sizes (stages). Individual growth (determined from the number of new leaves produced per year) was plant size-dependent: adult individuals (stem >2 m in height; comprising A_1, A_2, and A_3) produced 2.91 leaves (S.D. = 0.58, n = 229) per year on average, juveniles (stem ≤2 m in height; comprising J_1 and J_2) 2.77 new leaves (S.D. = 0.49, n = 277), and suckers (stemless) 1.64 leaves (S.D. = 0.48, n = 2658) per year.

3.2.4. Survivorship

Fig. 7 showed the numbers of individuals surviving in different stage classes. Mortality was higher among the early stages of the life cycle (suckers and seedlings). Mortality rate was very low in mature individuals, apart from the current harvesting rate of adults that was approximately 21 stems year^{-1} (per unit area) in the largest population on

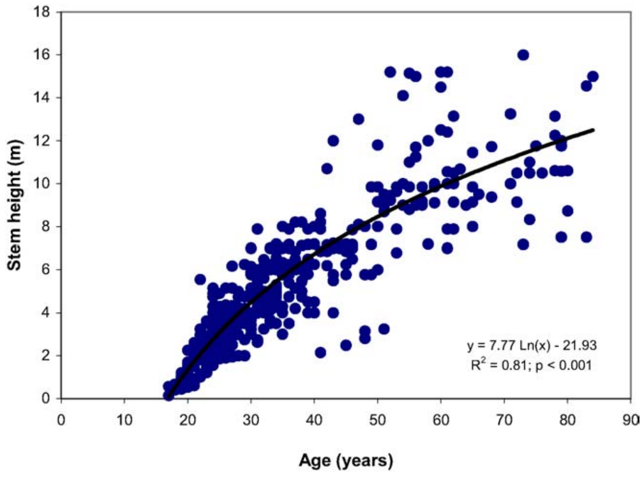

Fig. 6. Logarithmic relationship between age and stem height of *C. renda* within Kerumutan Reserve (n = 506).

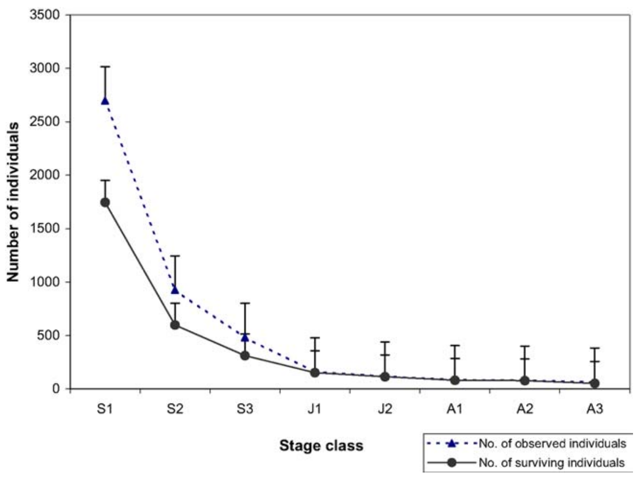

Fig. 7. Population survivorship curve for *C. renda* at Kerumutan Reserve. Unit area = 154.2 ha. Error bars are one standard error.

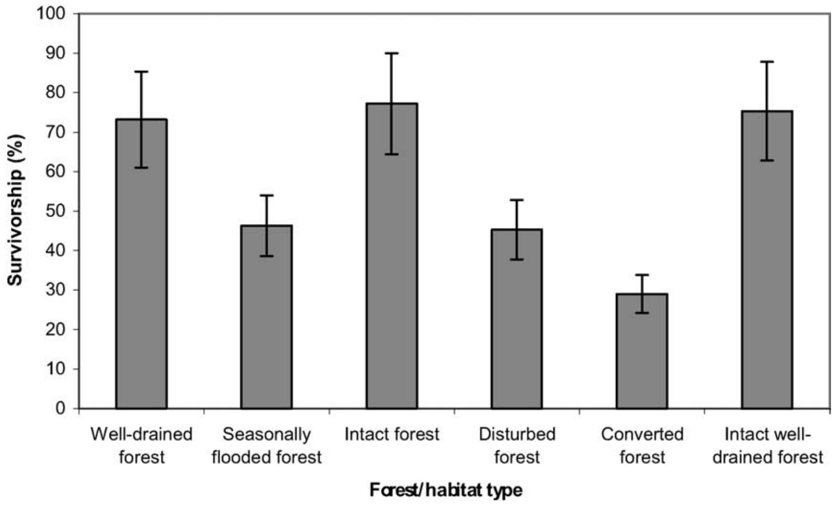

Fig. 8. Population survivorship for *C. renda* (in means and standard errors) at different drainage qualities and disturbance levels within Kerumutan Reserve.

the Galoga Border. This population had an occupancy area of ca. 200 ha. Thus there would be approximately 4056 adult individuals (200 × 20.28) in this location. The number of new individuals established in the Galoga Border population **through seed** per year ($N \times R_0$) was approximately 96, estimated from: 11% germination × 180.6 (the mean number of fruits per wild adult individual) × 124 (the number of adults in the Galoga Border population) × 3.9% (the percentage of individuals with flowers or fruit in both years of observation). Fig. 8 showed the population survivorship for *C. renda* at different drainage qualities and disturbance levels. Survivorship was significantly high in well-drained, intact forests, but was low in disturbed and seasonally flooded forests. The lowest survivorship was shown by the population from converted forest.

Based on the survivorship curve (Fig. 7) and population structure (Fig. 5), the populations of *C. renda* within Kerumutan Reserve appeared to be relatively stable or growing. However, very small vulnerable populations (with few solitary individuals) existed in some localities, e.g. Merbau River estuary (0.29 adult trees ha^{-1}) and Terusan Siam Stream (0.55 adult trees ha^{-1}) (Table 1). Extinction of the palm population was quite likely outside protected areas, due to continuing land conversion. A single extant population remained outside the reserve, adjacent to the northern boundary (Fig. 1) where no adults were found and with only a very few young individuals (0.60 clumps ha^{-1} or 0.89 juveniles ha^{-1}). At this site, there was insufficient recruitment to establish a viable population due to the absence of fertile adult individuals. This situation had mainly been caused by the conversion of the native palm habitats into oil palm, rubber plantations, and illegal logging.

3.3. Habitat preference (specificity)

Table 1 showed that *C. renda* preferred specific (well-drained) habitat types. For adults growing under suboptimal conditions (e.g. in flooded sites with low light intensity) only one new leaf was produced per year, but leaf production went up to four per year in well-drained sites exposed to moderate sunlight. Well-drained forests were preferable and supported the largest populations (Galoga Border, Kempas Creek, and Buluh Creek) with a complete age-structure. In contrast, the palm was absent from all permanently waterlogged sites. Although the palm still tolerated seasonally flooded forest, the populations were generally low and suppressed (Table 1). The palm seemed to be sensitive to changes in the water table; the mean density on well-drained sites was 2.6 clumps ha^{-1} (6.9 adults ha^{-1}), while that of seasonally flooded forests 0.6 clumps ha^{-1} (0.5 adults ha^{-1}). This species appeared to have a narrow range of ecological tolerance (amplitude) and formed a good indicator of the lowland peat swamp ecosystem. The palm behaviour pattern paralleled that of *Oncosperma horridum* and *O. tigillarum* outlined by House (1984), species that avoid poorly drained clayey substrates and occasional flooding. Several other studies had also shown that habitat specialisation was important for understanding palm abundance and distribution patterns (e.g. Kahn and Mejia, 1990; Svenning, 1999). It seems crucial to protect well-drained sites in Kerumutan Reserve if we are to conserve the main populations of the lipstick palm.

4. Discussion

The presence of substantial, healthy, recruiting populations of *C. renda* in Kerumutan Reserve (e.g. Galoga Border and Kempas Creek) indicated that the local conditions are favourable for its establishment and growth. Suckers were the most common stage class. Assuming the populations were in dynamic equilibrium, and age was related to leaf size/length (suckers) or number of leaf scars or stem height (juveniles and adults) as discussed, population structure will then be related to survivorship.

Extinction of the population was very likely outside the reserve. The inclusion of one remaining site adjacent to, but outside the reserve was intended to promote monitoring and the need for appropriate management. There was very little or no recruitment of new individuals in this site where the habitat was converted into rubber plantation by the local community. No fertile adult individuals were found in this site and the population showed an imbalance in stage/age distribution (Figs. 3 and 4). A very imbalanced stage distribution was also shown by Merbau River populations, which had no juveniles or young adults.

To some extent, disturbance seems to create a favourable environment for young individuals to grow, as light penetrates forest floor. This was indicated by the higher mean frequency distribution of juveniles (0–2 m in stem height) in disturbed forests than that of juveniles in intact forests (Fig. 4). Conversely, disturbance (e.g. illegal logging and stem cutting for constructing fishing shelters) leads to the decrease of adult individuals. Stems with lengths between 6 and 8 m were preferred by local communities because of their straightness.

The number of new leaves produced by individuals per year (which determines growth) depends on the size of the palm: adults were the most productive stage with almost three new leaves (on average) produced per year while suckers only produced approximately half as many. Ratsirarson et al. (1996) had shown a similar trend in the threatened Madagascar palm *Neodypsis decaryi* and Oyama (1990) in the neotropical dioecious palm *Chamadorea tepejilote*. However, for adults growing under suboptimal conditions (e.g. low light and flooded site) only one new leaf was produced per year, but leaf production went up to four per year on those located in well-drained sites exposed to moderate sunlight (Table 2).

The age at first reproduction in *C. renda* was earlier than that in *N. decaryi* (between 30 and 35 years; Ratsirarson et al., 1996) and *Astrocaryum mexicanum* (between 32 and 36 years; Pinero et al., 1984), but was similar to that observed in *Geonoma congesta* (between 15 and 29 years; Chazdon, 1992). In cultivation, however, *C. renda* appeared to grow faster and reproduce earlier (often with abundant seeds) than in the wild; individuals cultivated at Bogor Botanic Gardens started to produce seeds at a stem height of 1.7–1.9 m. The estimate of longevity in *C. renda* was similar to that of *Welfia georgii* (approximate 80 years to reach the maximum height; Lieberman et al., 1988), but was much younger than *N. decaryi* (200 years; Ratsirarson et al., 1996) and *A. mexicanum* (150 years; Pinero, 1988). The percentage of flowering or fruiting wild adult individuals of *C. renda* in either of the 2 years of observation was very low (11.4%), and even fewer flowered or fruited in both years (3.9%).

For plants, stage-structure is more useful for interpreting demographic data than age-structure, because reliable information on the age of immature individuals (i.e. establishment phase) is very limited. In this study, the predicted time taken for *C. renda* individuals to produce stems (15 years on average) was based on the plantation data. Thus the actual time required by wild individuals to reach juvenile stage may be longer than that of the cultivated individuals. In addition, the indeterminate growth (growth plasticity) of plants often makes the age-structure a poor predictor of future dynamics (Lefkovitch, 1965; Savage and Ashton, 1983; Ratsirarson et al., 1996). Height has been found to be a better predictor of palm fecundity than age (Ratsirarson et al., 1996). Following these authors, height was chosen as a state variable for interpreting population growth in this study.

The initial high mortality occurred between sucker leaf length classes 1 (<1 m, S_1) and 2 (1–2 m, S_2); only 34% of the individuals in S_1 survived S_2. In contrast, a significant decrease in mortality was shown by the juvenile stages (stemmed individuals); 75% of the individuals in J_1 (stem height <1 m) survived in J_2 (stem height 1–2 m). Once sucker individuals became stemmed individuals, their mortality rates decreased substantially. An apparent cessation of mortality was shown by adult individuals; 96% of the individuals in A_1 (stem height >2–5 m) survived in A_2 (stem height >5–8 m). Only approximately 5% of sucker individuals reached maturity (Fig. 7).

Higher mortality among the early stages of the life cycle (suckers and seedlings) was likely caused by high cover from falling palm and pandan leaves preventing sunlight exposure, severe competition for space, and frequent prolonged flooding/waterlogging. The establishment of abundant suckers may be a palm strategy to maintain a successful population recruitment. Leaves of young plants were susceptible to the grasshopper *Valanga nigricornis sumatrensis* and the apical meristem was eaten by rhinoceros beetles (Scarabaeidae).

Survivorship of *C. renda* seedlings seemed to be very low in the Kerumutan Reserve. Seeds were not seen to germinate in canopy gaps or open sites. Interestingly, seedlings were not found beneath the crowns of mature clumps. Germination trials conducted in Bogor Botanic Gardens (not reported here) showed that the palm requires sufficient heat (sunlight in natural situations) to germinate. The existence of an allelopathic mechanism seems unlikely. Rather, the absence of the seedlings may be due to physical constraints caused by dense suckers and juveniles at the clump bases preventing germination. Continuous leaf shedding and dense crowns may create an unfavourable light microhabitat for seed germination and seedling establishment. Seedlings that are able to grow are likely to be covered by further leaf falls of the palm and the adjacent dominant pandan leaves (*P. terrestris*). The regeneration strategy of developing new suckers and stolons rather than producing seeds appears to be more effective in swampy habitats. This was reflected in the small number of fertile adults found bearing flowers or fruits during the 1998–2000 observations (mostly >12 m in height); only 11.4% of the total mature population.

C. renda was absent from waterlogged sites and appeared that a number of factors contribute to its abundance. However, the palm tolerated seasonally flooded sites (those that were not permanently saturated), although at lower densities in small, scattered clumps. The extent of occurrence was limited by its habitat specificity and the species' ecological tolerances, and patterns of human disturbance. The palm can form an important component of the forest subcanopy layer where the surrounding canopy has been disturbed, e.g. by tree falls due to natural occurrences, such as wind storms or high rain fall, or even by illegal timber cuts. A high level of disturbance, such as logging, however, leads to the decline of populations, such as at Terusan Siam Stream.

The influence of slope on soil texture and water holding capacity partly determines the levels of available mineral nutrients, and consequently the establishment and spatial distribution of vegetation. Small variations in elevation can even be important in flat areas such as the Kerumutan forest. Soils on slopes tend to be coarser and better drained than those on flat ground where run-off creates accumulations of small soil particles (Fong, 1977; House, 1984). Soils on slopes continually lose their materials and minerals to sites below. The angle of the slope and vegetation cover affect moisture effectiveness by governing the ratio of surface run-off to infiltration (White, 1997). As drainability deteriorates, the oxidised soil profile (on a well-drained site) containing ferric oxides and oxyhydroxides is transformed into the mottled and gleyed profile of a waterlogged soil (containing iron in the ferrous state). The mean palm density on well-drained sites was 2.6 clumps ha^{-1}, that on poorly drained habitats (seasonally flooded) was 0.6 clumps ha^{-1}, while on very poorly drained (permanently waterlogged area) it was absent. *C. renda* does not develop aerial adventitious breathing roots as do many palms of wet soil habitats. Apart from human disturbance, the most important limiting factor for *C. renda* populations is soil drainage. It cannot tolerate soils that are waterlogged for long periods.

5. Conclusion

The populations of *C. renda* within Kerumutan Reserve were dominated by young plants, reflecting a growing population in which regeneration and recruitment continue in at least some sites. However habitat loss and human disturbance clearly threatened the persistence of the species. Population structures and sizes varied spatially with well-drained areas being the most favourable habitat in which the largest populations occurred (Galoga Border and Kempas Creek). By protecting this type of habitat, populations will be sustained for the long-term. This information can be used to set criteria and priorities for protecting representative suitable sites both within and outside the reserve. As suckers in several locations experienced high mortality, in situ management should focus on monitoring and managing the survival of the early stages to assist suckers to establish successfully. The relatively rapid development of sucker is the critical step in coping with waterlogged conditions. Given expected patterns of forest conversion and timber harvesting over the next few decades, the most important step is to protect high quality (well-drained) habitat in dedicated conservation reserves.

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