

Influences of edaphic factors on the distribution and abundance of a rare palm (*Cyrtostachys renda*) in a peat swamp forest in eastern Sumatra, Indonesia

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Abstract Tropical plant community ecology is often assumed to be driven largely by stochastic disturbance, replacement and demographic processes despite a general lack of information about the physical environment. Tropical soils are more diverse, at regional, intermediate and local scales than usually is recognized. This study was conducted to test hypotheses about the importance of edaphic parameters in determining the abundance and distribution of the rare lipstick palm *Cyrtostachys renda* Blume and its co-occurrence with other plants. Eight of 11 tropical tree species were positively associated with *C. renda*. For *Gluta renghas*, *Shorea parvifolia*, *Eleiodoxa conferta*, *Pandanus terrestris* and *Korthalsia flagellaris*, the association with the palm was strong. The palms *E. conferta* and *K. flagellaris* appeared to have similar ecological and habitat requirements. The lipstick palm is adapted to specific edaphic conditions related to soil quality and drainage. It prefers fine sand, well-drained soil and low mineral content, reflected in associations between these variables and stem density, clump density, clump size, frequency, basal area and canopy circle area. High levels of soil Ca⁺⁺, Mg⁺⁺ and K⁺ are associated with sites where the palm is absent. The C/N ratio of soils appears to influence palm densities and sizes. All known populations occur in habitats with C/N-values less than 19, with the largest populations in areas with C/N-values of 13. Our findings suggest that edaphic variables are important determinants of the abundance and distribution of this tropical peat swamp forest species.

Key words: *Cyrtostachys renda*, Kerumutan Reserve, interspecific association, soil quality, spatial distribution pattern.

INTRODUCTION

Habitat management depends on understanding the mechanisms for species co-occurrence (Begon *et al.* 1996) and habitat preference or specialization (Ludwig & Reynolds 1988; Mohler 1990; Nakashizuka 2001; Christie & Armesto 2003; van der Heijden *et al.* 2003; Hall *et al.* 2004). The detection of significant associations among or between species and environmental variables (including edaphic factors) does not provide a causal understanding, but can be used to generate hypotheses of possible underlying causal factors.

Hypotheses regarding species co-occurrence invoke ‘equilibrium’ and ‘non-equilibrium’ explanations (Svenning 1999; Nakashizuka 2001; Groeneveld *et al.*

2002; Edmunds *et al.* 2003). Equilibrium hypotheses assume that species co-occur by occupying different niches (niche partitioning), while ‘non-equilibrium’ hypotheses emphasize local fluctuations, disturbance and chance events that do not determine species composition, although they may result in expectations for relative species abundances (Hubbell 2001; Chisholm & Burgman 2004). Both ‘equilibrium’ and ‘non-equilibrium’ processes seem likely to contribute to the composition of most plant communities (Nakashizuka 2001).

Condit *et al.* (2000) suggested that most tropical rain forest tree species have strongly aggregated spatial distribution patterns, perhaps due to a high degree of habitat specialization (Ashton 1998; Hubbell 2001). Spatial patterns may be determined by complex relationships within and between species seed dispersal (Bell 2000), competition for pollinators (Armbruster 1995; Svenning 1999), recruitment (Harms *et al.* 2000), density dependence (Webb & Peart 2000), intermediate disturbance (Molino & Sabatier 2001) or variation in topography and soil water (Swaine 1996; Clark *et al.* 1998; Svenning 2001).

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In any given situation, plant co-occurrence and abundance may be determined largely by resource availability, heterogeneity of the abiotic environment and microhabitat specialization (Silvertown & Law 1987; Ludwig & Reynolds 1988; Kahn & Mejia 1990; Hatfield *et al.* 1996; Clark *et al.* 1998; Svenning 1999; Webb & Peart 2000; van der Heijden *et al.* 2003; Palmiotto *et al.* 2004). However, very little information is available about soil conditions and the microhabitat specialization of tropical trees (House 1984; Gentry 1988; Duivenvoorden 1995).

Some studies have shown that tropical plant species distributions and community composition are correlated with soil nutrient status (Poulsen 1996; Clark *et al.* 1998; Svenning 2001) such as phosphorus and magnesium content (Vitousek & Sanford 1986; Baillie *et al.* 1987; Sollins 1998; Tiessen 1998; Potts *et al.* 2002; Hall *et al.* 2004; Palmiotto *et al.* 2004). However, there is still a lack of consensus about the importance of the correlations at local and intermediate spatial scales, e.g. at 1–100 km² (Gartlan *et al.* 1986; Swaine 1996; Clark *et al.* 1998, 1999; Hall *et al.* 2004). Tropical soils are not homogeneous at regional, intermediate or even local scales (Richter & Babbar 1991; Hall *et al.* 2004) and abrupt discontinuities in the edaphic conditions are common features (Clark *et al.* 1998). Regional/intermediate spatial scales refer to strong environmental discontinuities (habitats) while local spatial scales refer to environmental conditions that vary at scales less than 10³ m, such as tree-fall gaps and local topographic variation (Svenning 1999).

Palms are important elements of many tropical forests and often show local or regional patterns of association (Kahn & Mejia 1990; Moraes 1996; Svenning 1999) and ecological preferences (Tomlinson 1979; House 1984). Some palms appear to be adapted to specific edaphic conditions, such as soil quality, drainage and formation (House 1984; Moraes 1996). Duivenvoorden (1995, 1996) noted that most trees of the well-drained upland habitat in Colombian Amazonia are likely to be soil generalists rather than specialists, implying limited importance of microhabitat specialization for maintaining tree species richness.

The interspecific association test is a simple species-based approach for preliminarily defining community types that can be recognized by a small assemblage of common species. If sets of species are found to co-occur, and the occurrence of these sets can be related to habitat factors, such information will provide more compelling evidence for niche processes structuring the community than does a single species approach.

The objective of this study was to test hypotheses about the tendency of palm species to co-occur and to assess the potential importance of edaphic parameters in determining species abundance and distribution in a tropical lowland peat swamp forest. The study

focuses on *Cyrtostachys renda*, a rare palm species of the Kerumutan Forest, Sumatra, with a view to providing information to support management of the species. We addressed three questions. First, does *C. renda* associate with other plant species in the Kerumutan Forest? Second, if so, how strong is the association? Third, do local edaphic conditions in different habitat types affect the abundance and distribution of the species?

METHODS

Study species

The lipstick palm *C. renda* Blume (Arecaceae) is a monoecious, clustered or very rarely single stemmed, slender palm, up to 15 m tall and with adult individual stem diameters ranging from 5 to 14 cm. The species is equatorial, confined to lowland peat swamp forests usually near tidal coast areas and along river banks (Uhl & Dransfield 1987; Widyatmoko 2001) at altitudes from 0 up to about 500 m above sea level (Uhl & Dransfield 1987). *C. renda* is the only representative of its genus to occur west of Wallace's Line. It occurs in Southern Thailand, Peninsular Malaysia, Sumatra, and Borneo, and is a characteristic component of south-east Asian lowland peat swamp forests, while the other *Cyrtostachys* species are all from New Guinea and the Solomons (Uhl & Dransfield 1987). The eastern coastal area of Borneo appears to be the eastern geographical limit of this species. There are no herbarium or existing locality records for the species from the islands of Siberut, Mentawai and Pagai.

Study sites

Kerumutan Reserve (Eastern Sumatra) supports lowland peat swamp tropical rain forests, one of the most intact peat swamp forests remaining in South-east Asia (Davie & Sumardja 1997). The reserve topography is flat (elevation: 0–3%), varying from 5 to 68 m above sea level, and covering an area of 120 000 ha (N 00°11'52"–S 00°18'00" and E 102°25'20" – E 102°37'36"). It has the 'Af' climate type, experiencing eight consecutive wet months. All months have an average temperature above 18°C (ranging from 23°C to 34°C). It has small seasonal temperature variations of less than 3°C (the Koppen's System, Tarbuck & Lutgens 2004); with an average annual rainfall of 2720 mm and an average humidity of 84% for the period between 1992 and 1997 (Bappeda Tingkat I Propinsi Riau dan Bakosurtanal 1998a,b). The area 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 the mineral soils are mainly organosol and red-yellow Podzol. Around 30% of the area is dry during the dry season, but it is almost totally waterlogged in the wet season.

Today, Kerumutan Reserve contains one of the largest remaining populations of *C. renda* in which natural regeneration occurs and a complete range of age and size classes can be found. Some successful recruitment occurs in several sites where suckers and juveniles are abundant, while in other locations of apparently suitable habitat, the species is absent. The reserve is located between Sumatra's two major rivers: the Kampar and Indragiri Rivers (Fig. 1). The Kerumutan River flows across the northern part and western border of the Reserve.

Fifteen sites were chosen inside the study area at the Kerumutan Reserve and one site at an adjacent sanctuary to cover a wide range of population occurrences and sizes, vegetation associations (based on the dominant species/individual abundance), forest and habitat types, altitudes, and aspects. A preliminary survey of the reserve was conducted before selecting the sites. Vegetation associations (above ground characteristics) of each location were determined to describe different forest association types floristically and structurally. Each site where quadrats 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 using ArcView GIS 3.2. The research was conducted from February 1999 to June 2000.

Interspecific association (co-occurrence)

Association patterns among co-occurring species were tested using the chi-squared test statistic by constructing the hypothesis that two species are not associated at some predetermined probability level. The strength of each association was tested using the Ochiai Index as recommended by Ludwig and Reynolds (1988). Eleven species were tested for association from 56 observed.

Test of association

The species was absent from seven of the 16 observed sites (Fig. 1). A site in Galoga's rubber plantation was excluded because it is regarded as an unnatural forest area (i.e. the coexisting plants have been planted). Measures of interspecific association were based on the presence and absence of species within quadrats (each of 5 m × 5 m). A total of 160 quadrats were sampled from all known populations of *C. renda* within the reserve (eight sites) with different vegetation types (20 quadrats per site). Quadrats were arranged systematically in an alternating pattern within the belt transects in order to cover uniformly both sides of the axes. One transect of 100 m × 10 m was established on each site with the major axis orientated north-south. The data were then summarized in the form of a 2 × 2 contingency table.

The null hypothesis (H_0) was that the distribution of *C. renda* is independent of the other species. To test

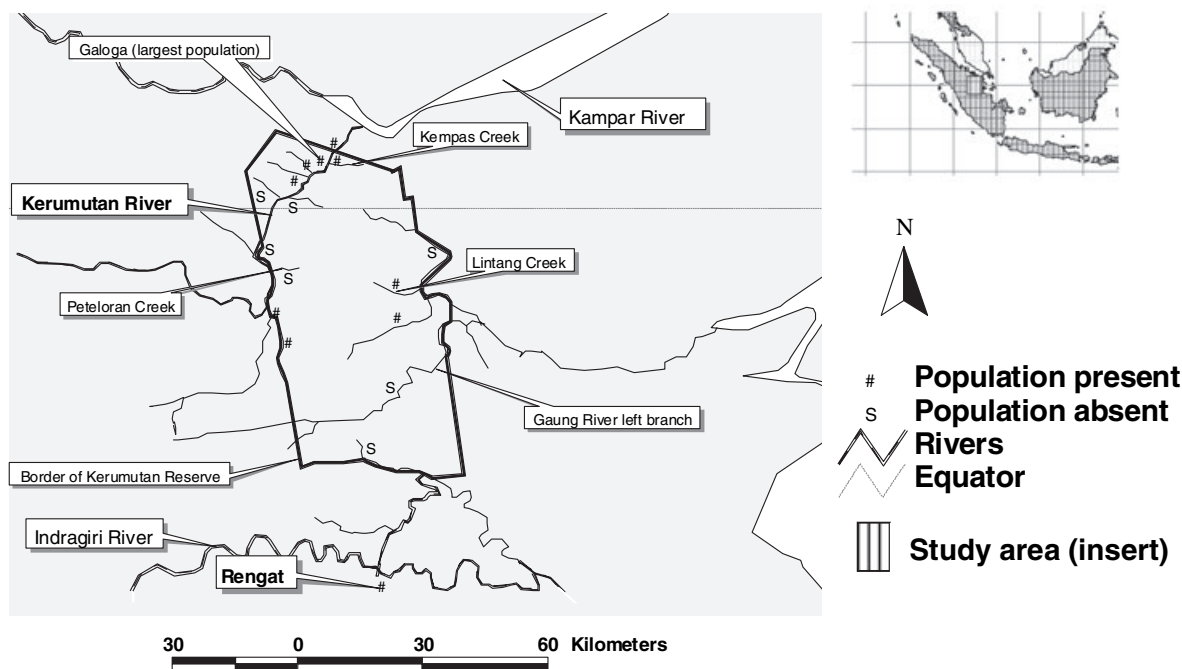


Fig. 1. Locations of the study area within Kerumutan Reserve, Sumatra, from which soils were sampled from each locality.

the null hypothesis of independence, the chi-squared test statistic (χ^2) was used (Ludwig & Reynolds 1988). The significance of the chi-squared test statistic is determined by comparison with the chi-squared distribution (χ^2) for 1 d.f. at $\alpha = 0.05$. If $\chi^2 > \chi^2_{\alpha}$ the null hypothesis is rejected. Rejecting the null hypothesis indicates an association between *C. renda* and the paired species, implying that the two species co-occur at a frequency greater than expected by random association. Positive or negative associations were determined by comparing the value of observed occurrences ($O_{(a)}$) to that of expected occurrences ($E_{(a)}$). If observed is greater than expected, there is a positive association (the pair of species occurred together more often than expected if independent).

Measure of the degree of association

A measure of association (the Ochiai Index) recommended by Janson and Vegelius (1981) and Hubalek (1982) was used to estimate quantitatively the strength or degree of association between the species tested, as the association test can only determine whether the species tested are associated or not associated. The value of the Ochiai Index is equal to 0 at 'no association' and 1 at 'complete association'.

Soil analyses

To assess possible interactions between edaphic factors and palm occurrences and abundances, soils were sampled from each locality in which the quadrats were sampled (one sample per transect). The precise site of each soil pit was chosen randomly within the quadrats of each transect. For *C. renda*, surface and subsurface soil levels appear to be more important than the deeper soil profile since the feeding roots are close to the surface. Thus soil samples were taken from two depths, surface (2–5 cm) and subsurface (>5–75 cm), mainly from the A horizon, while the layer of pure organic matter (O horizon) was excluded. The size of the pit was approximately 20 cm in diameter, while the amount of soil taken from each horizon was approximately 720 g and was used to determine various chemical and physical parameters. Values of the two surfaces were calculated to give mean profile values (following House 1984; White 1997). Where present, leaf litter and the humus layer were removed before soil sampling. Soil samples were sieved through a 2-mm mesh sieve to remove roots and stones. Chemical and physical analyses were carried out on oven-dried samples (105°C) in the Centre for Soil and Agroclimate Research, Bogor, Indonesia. Soil pH was measured on a 1:2.5 soil-distilled water mix. Exchangeable base cations (Ca^{++} , Mg^{++} and K^+) were

extracted from the soil using a neutral (pH 7) salt extractant of 1 N NH_4 -acetate in a mechanical vacuum extractor (Centurion International, Lincoln, NE, USA; Suarez 1996). Total C and N were determined using a dry combustion technique on a Leco CHN-600 elemental analyser (following Olsen & Sommers 1982). The physical structure of the soils was determined by removal of clay using ultrasonics and sedimentation while sand content was measured by sieving and washing (Suarez 1996; White 1997). Soil moisture content was determined by heating the soil samples in the oven at 38°C for 24 h (Campbell 1985; White 1997).

Correlation statistics were used to assess associations between edaphic parameters and the abundances of *C. renda*. Each edaphic parameter was correlated with the average palm density and size in the transect from which the soil sample was taken. The sample from which the correlations were calculated was relatively small ($n = 16$).

RESULTS

Forest (vegetation) associations

Sixteen detailed forest associations were described from the 16 localities sampled in this study belonging to 10 floristically different forest association types (Table 1). The most common tree families were Pandanaceae, Dipterocarpaceae, Anacardiaceae, Myrtaceae and Clusiaceae. Pandanaceous forests were dominated by *Pandanus terrestris* and *Pandanus helicopus*, Dipterocarp forests by *Shorea parvifolia* and *Shorea rugosa*, Anacardiaceous forests by *Gluta reinghas*, *G. wallichii* and *G. aptera*, Myrtaceous (pole) forests by *Syzygium incarnatum* and *S. spicatum*, while Clusiaceous forest was dominated by *Garcinia bancana* and *Calophyllum soulattri*. Mixed forests had high species diversity with no clearly dominant species, while Myrtaceous forests appeared to have the least species. The forest associations were reflected in the results of the interspecific association tests (Table 2) in which *G. reinghas* (Anacardiaceae), *S. parvifolia* (Dipterocarpaceae) and *Eleiodoxa conferta* (Arecaceae) were most strongly associated with *C. renda*.

Habitat preference

Table 1 showed that *C. renda* was found in specific habitat types. High densities and a range of sizes occurred in well-drained forest but the species was absent from all permanently waterlogged sites. Although the palm tolerated seasonally flooded forest, the populations in this type of habitat were generally

Table 1. Densities and sizes of *Cyrtostachys renda* at various locations in relation to forest (vegetation) association and habitat type within Kerumutan Reserve, Sumatra

Location	Position	Forest association	Type of habitat	No. clumps per hectare	Mean no. stems per clump	No. adults per hectare	No. juveniles per hectare	No. suckers per hectare	Range stems per clump
Galaga Border	N 00°09.151' E 102°30.052'	Anacardiaceae dominant	Well drained forest	6.11 ± 3.27	6.82 ± 5.13	20.28 ± 8.61	21.39 ± 9.20	550.28 ± 90.34	1–34
Kempas Creek	N 00°08.977' E 102°36.383'	Dipterocarpaceae dominant	Well drained forest	3.16 ± 2.49	5.42 ± 3.02	9.04 ± 6.58	8.07 ± 6.67	106.01 ± 26.38	1–19
Buluh Creek	N 00°09.151' E 102°28.80'	Pandanaceae dominant	Well drained forest	2.69 ± 1.40	3.36 ± 2.11	4.23 ± 2.85	4.81 ± 2.99	48.08 ± 14.57	1–11
Ketopatan Creek	N 00°07.998' E 102°26.452'	Clusiaceae dominant	Well drained forest	0.44 ± 0.28	4.50 ± 2.07	1.00 ± 1.73	1.00 ± 1.70	8.56 ± 3.36	1–8
Merbau River upstream	S 00°06.664' E 102°24.917'	Dipterocarpaceae dominant	Well drained forest	0.56 ± 0.69	3.71 ± 2.23	0.00	2.08 ± 1.35	9.44 ± 5.02	1–12
Lintang Creek	S 00°02.269' E 102°36.241'	Anacardiaceae dominant	Seasonally flooded forest	1.45 ± 1.21	3.11 ± 1.09	1.77 ± 1.42	2.74 ± 1.56	18.39 ± 6.11	2–7
Terusan Siam Stream	S 00°04.120' E 102°34.395'	Rubiaceae- Myrtaceae dominant	Seasonally flooded forest	0.61 ± 0.46	2.50 ± 1.28	0.55 ± 0.49	0.98 ± 0.61	9.33 ± 4.47	1–9
Merbau River estuary	S 00°03.510' E 102°23.278'	Melastomataceae- Pandanaceae dominant	Seasonally flooded forest	0.29 ± 0.17	1.00 ± 0.48	0.29 ± 0.19	0.00	2.21 ± 2.01	1–1
Galaga rubber plantation	N 00°09.361' E 102°30.979'	Euphorbiaceae dominant	Seasonally flooded forest	0.60 ± 0.34	1.50 ± 0.34	0.00	0.89 ± 0.17	11.07 ± 5.53	1–4
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
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
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
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
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
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
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

Mean ± SD (95% confidence interval).

low and suppressed, indicating a tolerance of suboptimal conditions. The mean palm density on well-drained sites was 2.6 clumps per hectare (6.9 adults per hectare), while in seasonally flooded forests it was 0.6 clumps per hectare (0.5 adult hectare).

Species co-occurrence

Fifty-six species were encountered, of which 11 species were tested for association with *C. renda*. Eight of these 11 species were positively associated while two species were negatively associated (Table 2). For five species (*G. renghas*, *S. parvifolia*, *E. conferta*, *P. terrestris* and *Korthalsia flagellaris*), the association with the lipstick palm was strong, indicated by their indices >0.5.

Another palm, *Korthalsia paucijuga*, was positively associated with *C. renda*. Although in some sites *K. paucijuga* and *S. rugosa* were found together with *C. renda* (for example in the Galoga Border and Kempas Creek sites), their co-occurrence was not seen at all sites. Surprisingly, two apparently closely associated species, *S. incarnatum* and *P. helicopus*, were negatively associated with *C. renda*. In fact, *C. renda* was more common in well-drained sites, avoiding waterlogged areas within lowland peat swamp tropical rain forests (Widyatmoko *et al.* 2005). Although *S. parvifolia* appeared to be closely associated with *C. renda*, it was not confined to peat swamp ecosystems, occurring in wider ecological contexts. Unlike *C. renda*, *S. parvifolia* (up to 60 m high) occupied the highest canopy stratum. The dominant species within the lower subcanopy (intermediate level) in Kerumutan Forest included *P. terrestris*, *P. helicopus*, *S. incarnatum*, *Syzygium* sp. and *Gardenia pterocalyx*. The upper subcanopy was occupied mainly by *Callophyllum soulattri*, *Tetramerista glabra* and *Camptosperma coriacea*, while the main canopy was dominated by *Koompassia malaccensis*, *G. renghas*, *G. wallichii*, *S. parvifolia* and *S. rugosa*.

Associations between species and soil characteristics

The results of chemical and physical analyses of soils of the study area indicated that well-drained areas (Galoga Border, Kempas Creek and Buluh Creek) had the lowest levels of soil moisture, Ca⁺⁺, Mg⁺⁺, K⁺, C/N ratio and clay, but the highest content of fine sand and N. Soil pH and C content varied slightly amongst sites.

Several interrelating edaphic factors, in combination, appeared to explain the abundance of *C. renda*. This palm showed a preference for sandy (Fig. 2), well-drained soils (Table 1) with low mineral content (Fig. 3,4). The three largest populations, Galoga Border, Kempas Creek and Buluh Creek had the lowest mineral content.

The soil minerals Ca⁺⁺, Mg⁺⁺ and K⁺ appeared to be most closely related to clump size, frequency and clump density (Table 3). There were strongly negative correlations between clump size and frequency and the three soil minerals' content (Table 3, Fig. 4). High

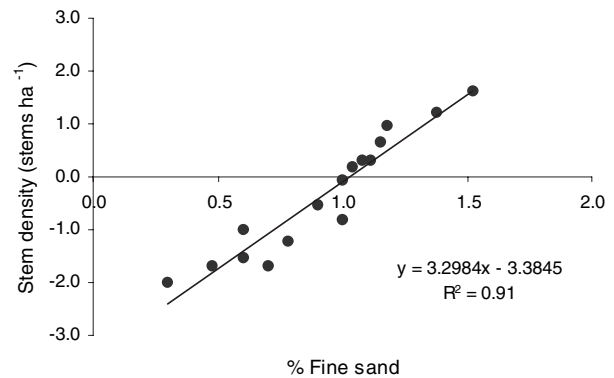


Fig. 2. Relationship between soil sand content (% fine sand) and stem density of *C. renda* within Kerumutan Reserve, Sumatra. Soil sand content values are Log₁₀. Density values are Log₁₀ stems ha⁻¹.

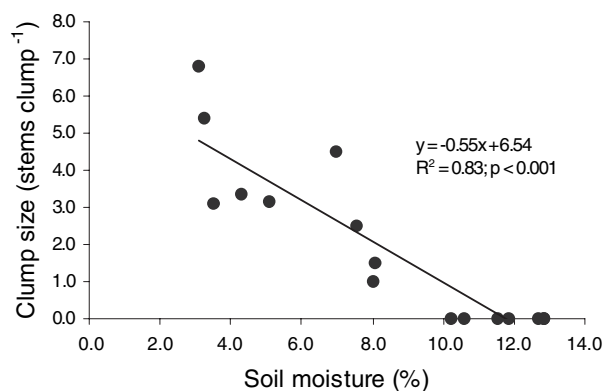
Table 2. Results of the association tests using the chi-squared test statistic (χ^2) between *Cyrtostachys renda* and the 11 co-occurring species. Values of the Ochiai Index are equal to 0 at 'no association' and to 1 at 'complete/maximum association'

Paired species	Result of chi-squared test	Types of association	Strength of association (Ochiai Index)
<i>Gluta renghas</i>	Associated	Positive	0.66
<i>Shorea parvifolia</i>	Associated	Positive	0.66
<i>Eleiodoxa conferta</i>	Associated	Positive	0.64
<i>Pandanus terrestris</i>	Associated	Positive	0.55
<i>Korthalsia flagellaris</i>	Associated	Positive	0.51
<i>Korthalsia paucijuga</i>	Associated	Positive	0.47
<i>Shorea rugosa</i>	Associated	Positive	0.47
<i>Licuala paludosa</i>	Associated	Positive	0.30
<i>Syzygium incarnatum</i>	Associated	Negative	0.04
<i>Pandanus helicopus</i>	Associated	Negative	0.07
<i>Memecylon lucida</i>	No significant result	-	0.11

Table 3. Values of correlation coefficient (*r*-squared) between edaphic parameters and the abundance of *Cyrtostachys renda* within Kerumutan Reserve, Sumatra

Edaphic parameters	Abundance					
	Frequency (clumps per hectare)	Clump density (stems per hectare)	Stem density (stems per clump)	Clump size (m ² ha ⁻¹)	Basal area (m ² ha ⁻¹)	Canopy circle area
pH	0.04	0.02	0.05	0.02	0.16	0.05
% Moisture	(-) 0.84*	(-) 0.80*	(-) 0.62	(-) 0.83*	(-) 0.56	(-) 0.57
Exchangeable Ca ⁺⁺	(-) 0.85*	(-) 0.79*	(-) 0.65	(-) 0.91*	(-) 0.67	(-) 0.69
Exchangeable Mg ⁺⁺	(-) 0.82*	(-) 0.72	(-) 0.59	(-) 0.93*	(-) 0.59	(-) 0.61
Exchangeable K ⁺	(-) 0.85*	(-) 0.73	(-) 0.58	(-) 0.92*	(-) 0.59	(-) 0.60
% N	0.05	0.06	0.06	0.20	0.05	0.05
C/N	(-) 0.71	(-) 0.69	(-) 0.36	(-) 0.75*	(-) 0.30	(-) 0.28
% Fine sand [†]	0.80*	0.88*	0.91*	0.88*	0.89*	0.85*
% Silt [‡]	(-) 0.10	(-) 0.09	(-) 0.12	(-) 0.24	(-) 0.10	(-) 0.10
% Clay [§]	(-) 0.52	(-) 0.82*	0.04	(-) 0.51	(-) 0.56	(-) 0.59

(-) indicates a negative correlation; **P* < 0.001; [†]>20–250 µm, [‡]2–20 µm, [§]<2 µm; sample size (*n*) = 16.

**Fig. 3.** Relationship between soil C/N ratio and clump size of *C. renda* within Kerumutan Reserve, Sumatra.

levels of Ca⁺⁺, Mg⁺⁺ and K⁺ corresponded to the absence of the palm (Tables 1,3).

Fine sand was closely associated with stem density, clump density, clump size, frequency, basal area and canopy circle area (Table 3). The relationship with stem density was particularly close. Figure 2 indicated that sand content in the soil (determining its water drainage properties) determined the palm abundance. Clay was closely associated with clump density (Table 3).

Based on the *r*-squared values, moisture appeared to have more influence on clump size (Fig. 3), clump density and frequency than on stem density, basal area and canopy circle area (Table 3; Fig. 3). On the other hand, pH, silt and N content did not show significant or important relationships with palm abundance parameters, suggesting the species is adapted to a wide range of pH.

The C/N ratio was more closely associated with palm density, palm frequency and clump size than was N content (Table 3). All known populations occurred

in habitats with C/N-values <19 (Fig. 5). The habitats where the three largest populations occurred have C/N-values of 13 (Galoga Border and Kempas Creek) and 11 (Buluh Creek).

The adult stem diameters of *C. renda* varied considerably, ranging from 4.7 to 14.0 cm and from 3.1 to 10.2 cm (for juveniles). Populations at Lintang and Ketopatan Creeks were small but contained the largest individuals (mean stem diameter = 10.33 and 9.41 cm respectively). The largest population at the Galoga Border contained individuals averaging 8.25 cm.

DISCUSSION

The positive association of *C. renda* with low levels of Ca⁺⁺, Mg⁺⁺ and K⁺ is similar to that of the bayas palm *Oncosperma horridum* and *Oncosperma tigillarum*. These palms were shown by House (1984) to avoid flooded areas and poorly drained clay substrates. The pattern for *C. renda* is different from that of the Malayan rain forest bertam palm *Eugeissona tristis* (Fong 1977) and the Amazonian palms *Phytelephas macrocarpa* and *Astrocaryum murumuru* var. *murumuru* (Vormisto 2002) which prefer fertile soils. *C. renda* and *O. horridum* are long-lived species reproducing beneath a closed canopy, while *E. tristis* is a relatively short-lived opportunistic species that rapidly colonizes canopy gaps. This suggests *C. renda* and *O. horridum* may fill equivalent ecological roles and share membership of the same ecological guild.

The densities of *C. renda* and *O. horridum* (House 1984) decrease with cation content while those of *E. tristis* increase with the cation exchange capacity (Fong 1977). Soil cation exchange potential is linked with soil drainage capacity (White 1997). Well-drained soils have high sand fractions and low cation concentrations. In some of the habitats of *C. renda*, the

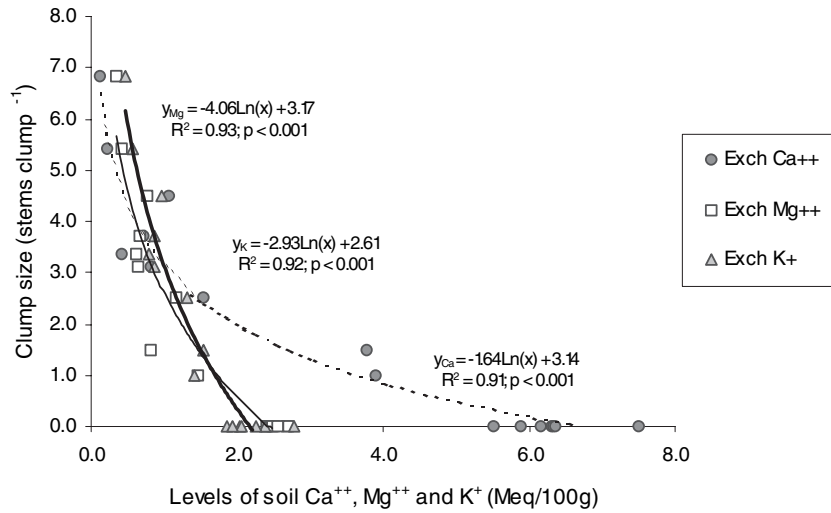


Fig. 4. Relationship between clump size of *C. renda* and levels of Ca⁺⁺, Mg⁺⁺ and K⁺ within Kerumutan Reserve, Sumatra.

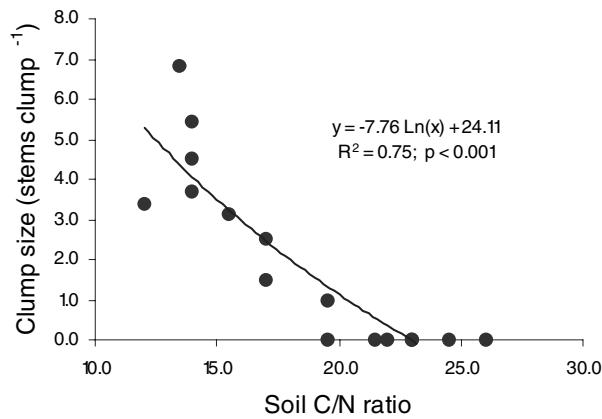


Fig. 5. Relationship between soil moisture and clump size of *C. renda* within Kerumutan Reserve, Sumatra.

accumulations of peaty organic materials overlay decomposed granite fines, such as yellow clay and humic sands derived from eroded sand stones (Tucker 1992). The absence of *C. renda* from all permanently waterlogged forests is a strong indication that this species is intolerant of waterlogged conditions, in which seed germination is prevented.

C. renda may overcome apparent low soil nutrient levels by self-mulching. There was abundant leaf litter from crown falls either within clumps or at their base, providing the surface feeding roots with newly released nutrients, preventing excessive surface mineral leaching (particularly from frequent flooding) and reducing competition from seedlings and young plants of other species. Competition from other species is also reduced by the dense root mats this species develops.

It is unclear whether rapid drainage or tolerance to low nutrients determines the distribution of *C. renda* (as these factors are strongly correlated) and what

drives this association. If tolerance to low nutrients is the case, the absence of the palm from sites with high nutrient content may be due to water inundation (i.e. the palm is intolerant of waterlogging). It may be due to its slow intrinsic growth rates, excluding it from these sites where plants with faster growth rates predominate, or it may simply be because the palm tolerates nutrient poor soils more easily than potential competitors. All of these are possible explanations of our finding and we recommend further research.

In addition to the apparent preference for well-drained soils, *C. renda* appeared to be more common in sites with lower electrical conductivity and low concentrations of major nutrients. Mineral concentrations (Ca⁺⁺, Mg⁺⁺ and K⁺) in permanently waterlogged sites were substantially higher than in the other two habitat types. Soil pH did not correlate with density and frequency of *C. renda*, concordant with independent observations that it grows very well in cultivation where the soil pH is highly variable.

The influence of slope on soil texture and water holding capacity partly determines the levels of available mineral nutrients, and thus the establishment and spatial distribution of vegetation. Even small variations in elevation can be important in flat landscapes like 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 (House 1984; Hall *et al.* 2004). Slope angle and vegetative cover affect moisture effectiveness by governing the ratio of surface run-off to infiltration (White 1997). As drainage deteriorates, the oxidized soil profile of well-drained sites is transformed into the mottled and gleyed profile of a waterlogged soil. The mean palm density on well-drained sites is 2.6 clumps per hectare. On poorly drained, seasonally flooded habitat it is 0.6 clumps per hectare, while on very poorly

drained or permanently waterlogged areas the palm is absent.

The palms *C. renda*, *E. conferta* and *K. flagellaris* appear to have similar ecological and habitat requirements. The three species are 'clustering' palms, sharing similar growth form and population establishment strategies. Like *C. renda*, *K. flagellaris* is almost entirely confined to lowland peat swamp forests. Both species regenerate from suckers and less frequently from seeds. Their geographical distribution is also very similar, from Malay Peninsula, Sumatra, to Borneo. Similarly, *E. conferta* is distributed throughout this region, particularly in peat swamp forests where water movement occurs, indicating the same habitat specificity as *C. renda*. *E. conferta* produces seeds and suckers, as do *C. renda* and *K. flagellaris*. The three species mainly occupy lower subcanopies, thus having similar exposure to moderate levels of sunlight. However, unlike *C. renda* and *K. flagellaris*, *E. conferta* produces abundant seeds in this reserve.

Sometimes *C. renda* forms a prominent component of the forest vegetation, such as in drainage lines and stream banks of the reserve where the sunlight penetrates or where the surrounding canopy has been disturbed (for instance by tree falls due to wind storms and high rain fall). However, a high level of disturbance, such as logging, may cause populations to decline, such as at Terusan Siam Stream (Table 1). In the heavily shaded sites of the reserve it occurs as very poorly formed clumps with very few stems. The palm appears to be able to take advantage of unstable canopy conditions (disturbed habitats) and to become established in ecologically limited spaces (minor disturbed sites), although it is not a true gap exploiter.

In swampy habitats, it seems that vegetative propagation (by developing new suckers and stolons) is most important for clump maintenance and expansion, while seed dispersal and germination must be important for the establishment of new clumps far removed from reproductive adults. However, seeds were not seen to germinate in canopy gaps. Curiously, seedlings were also absent beneath the crowns of mature clumps. Together with continuous leaf shedding, the dense crowns create a microhabitat of heavy shade that is unfavourable for seed germination and seedling establishment. This was reflected by a low percentage of fertile adults found bearing flowers or fruits during the 1998–2000 observations, only 11% of the total mature population (Widyatmoko *et al.* 2005). As light exposure is important for flowering and successful fruit set, and because the crowns of this palm occupy mainly the lower subcanopy, it is not surprising that fertile adult plants were very rare. No effective dispersers of the palm seeds were encountered during this study. However, long-distance travellers such as frugivores, granivores (pigeons) or macaques could be important dispersal agents.

The information gleaned from this study will be useful to managers. Potential uses include a quantification of the palm's distribution in the reserve, an understanding of suitable habitat conditions (niche preferences) which can guide enrichment planting programs, and possible use of the palm as an indicator of habitat conditions. Human activities that cause large scale or very regular disturbance (particularly on well-drained areas) are likely to be detrimental for this species. As the species is likely to be sensitive to changes in the hydrology of the landscape (particularly because of its low relief), any changes to groundwater conditions could have far-reaching effects if they reduce the extent of seasonally dry locations within the lowland peat swamps.

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REFERENCES

- Armbruster W. S. (1995) The origins and detection of plant community structure: reproductive versus vegetative processes. *Folia Geobot. Phytotaxon.* **30**, 483–97.
- Ashton P. S. (1998) Niche specificity among tropical trees: a question of scales. In: *Dynamics of Tropical Communities* (eds D. M. Newbery, H. H. T. Prins & N. D. Brown) pp. 491–514. Blackwell Science, Oxford.
- Baillie I. C., Ashton P. S., Court M. N., Anderson J. A. R., Fitzpatrick E. A. & Tinsley J. (1987) Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in Central Sarawak. *Malay. J. Trop. Ecol.* **3**, 201–20.
- Bappeda Tingkat I Propinsi Riau dan Bakosurtanal (1998a) Neraca Sumberdaya Lahan Spasial Daerah Kabupaten Kampar, Propinsi Riau, 75pp.

- Bappeda Tingkat I Propinsi Riau dan Bakosurtanal (1998b) Neraca Sumberdaya Lahan Spasial Daerah Kabupaten Indragiri Hulu, Propinsi Riau, 95pp.
- Begon M., Harper J. L. & Townsend C. R. (1996) *Ecology: Individuals, Populations and Communities*, 3rd edn. Blackwell, Oxford.
- Bell G. (2000) Neutral macroecology. *Science* **293**, 2413–18.
- Campbell G. S. (1985) *Soil Physics with BASIC: Transport Models for Soil – Plant Systems*. Elsevier, Amsterdam.
- Chisholm R. A. & Burgman M. A. (2004) The unified neutral theory of biodiversity and biogeography: comment. *Ecology* **85**, 3172–4.
- Christie D. A. & Armesto J. J. (2003) Regeneration microsites and tree species coexistence in temperate rain forests of Chiloe Island, Chile. *J. Ecol.* **91**, 776–84.
- Clark D. B., Clark J. A. & Read J. M. (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *J. Ecol.* **86**, 101–12.
- Clark D. B., Palmer M. W. & Clark D. A. (1999) Edaphic factors and the landscape-scale distributions of tropical tree species. *Ecology* **80**, 2662–75.
- Condit R., Ashton P. S., Baker P. *et al.* (2000) Spatial patterns in the distribution of tropical trees. *Science* **288**, 1414–18.
- Davie J. & Sumardja E. (1997) The protection of forested coastal wetlands in Southern Sumatra: a regional strategy for integrating conservation and development. *Pac. Conserv. Biol.* **3**, 366–78.
- Duivenvoorden J. F. (1995) Tree species composition and rain forest – environment relationships in the middle Caqueta, Colombia, NW Amazon. *Vegetatio* **120**, 91–113.
- Duivenvoorden J. F. (1996) Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. *Biotropica* **28**, 142–58.
- Edmunds J., Cushing J. M., Costantino R. F., Henson S. M., Dennis B. & Desharnais R. A. (2003) Park's *Tribolium* competition experiments: a non-equilibrium species coexistence hypothesis. *J. Anim. Ecol.* **72**, 703–12.
- Fong F. W. (1977) Edaphic conditions under Bertam (*Eugeissona tristis* Griff.) on Seraya Ridge Forests. *Trop. Ecol.* **18**, 60–70.
- Gartlan S., Newbery D. M., Thomas D. W. & Waterman P. G. (1986) The influence of topography and soil phosphorus on the vegetation of Korup Forest reserve, Cameroon. *Vegetatio* **65**, 131–48.
- Gentry A. H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Miss. Bot. G.* **75**, 1–34.
- Groeneveld J., Enright N. J., Lamont B. B. & Wissel C. (2002) A spatial model of coexistence among three *Banksia* species along a topographic gradient in fire-prone shrublands. *J. Ecol.* **90**, 762–74.
- Hall J. S., McKenna J. J., Ashton P. M. S. & Gregoire T. G. (2004) Habitat characterizations underestimate the role of edaphic factors controlling the distribution of *Entandrophragma*. *Ecology* **85**, 2171–83.
- Harms K. E., Wright S. J., Calderon O., Hernandez A. & Herre E. A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**, 493–5.
- Hatfield J. S., Link W. A., Dawson D. K. & Lindquist E. L. (1996) Coexistence and community structure of tropical trees in a Hawaiian montane rain forest. *Biotropica* **28**, 746–58.
- House A. P. (1984) The Ecology of *Oncosperma horridum* on Siberut Island, Indonesia. *Principes* **28**, 85–9.
- Hubalek Z. (1982) Coefficients of association and similarity based on binary (presence-absence) data: an evaluation. *Biol. Rev.* **57**, 669–89.
- Hubbell S. P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Monographs in Population Biology. Princeton University Press, Princeton.
- Janson S. & Vegelius J. (1981) Measures of ecological association. *Oecologia* **49**, 371–6.
- Kahn F. & Mejia K. (1990) Palm communities in wetland forest ecosystems of Peruvian Amazonia. *For. Ecol. Manage.* **33/34**, 169–79.
- Ludwig J. A. & Reynolds J. F. (1988) *Statistical Ecology, A Premier on Methods and Computing*. John Wiley and Sons, New York.
- Mohler C. L. (1990) Co-occurrence of Oak Subgenera: implications for niche differentiation. *Bull. Torrey Bot. Club* **117**, 247–55.
- Molino J. F. & Sabatier D. (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* **294**, 1702–4.
- Moraes M. R. (1996) Diversity and distribution of palms in Bolivia. *Principes* **40**, 75–85.
- Nakashizuka T. (2001) Species coexistence in temperate, mixed deciduous forests. *Trends Ecol. Evol.* **16**, 205–10.
- Olsen S. R. & Sommers L. E. (1982) Phosphorus. In: *Methods in Soil Analysis, Part 2 Chemical and Microbiological Properties* (ed. A. L. Page) pp. 414–16. American Society of Agronomy, Madison.
- Palmiotto P. A., Davies S. J., Vogt K. A., Ashton M. S., Vogt D. J. & Ashton P. S. (2004) Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *J. Ecol.* **92**, 609–23.
- Phillips V. D. (1998) Peatswamp ecology and sustainable development in Borneo. *Biodiv. Conserv.* **7**, 651–71.
- Potts M. D., Ashton P. S., Kaufman L. S. & Plotkin J. B. (2002) Habitat patterns in tropical rainforests: a comparison of 105 plots in Northwest Borneo. *Ecology* **83**, 2782–97.
- Poulsen A. D. (1996) Species richness and density of ground herbs within a plot of lowland rainforest in north-west Borneo. *J. Trop. Ecol.* **12**, 177–90.
- Richter D. D. & Babbar L. I. (1991) Soil diversity in the tropics. *Adv. Ecol. Res.* **21**, 315–89.
- Silvertown J. & Law R. (1987) Do plants need niches? Some recent developments in plant community ecology. *Trends Ecol. Evol.* **2**, 24–6.
- Sollins P. (1998) Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* **79**, 23–30.
- Suarez D. L. (1996) Magnesium and calcium. In: *Methods of Soil Analysis, Part 5 Chemical Methods* (ed. J. M. Biggam) pp. 575–602. Soil Science Society of America, Madison.
- Svenning J. C. (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol.* **87**, 55–65.
- Svenning J. C. (2001) On the role of microenvironmental heterogeneity in the ecology and diversification of Neotropical rain forest palms (Arecaceae). *Bot. Rev.* **67**, 1–53.
- Swaine M. D. (1996) Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *J. Ecol.* **84**, 419–28.
- Tarbut E. J. & Lutgens F. K. (2004) *Earth Science*, 9th edn (Chapter 18. Climate). Prentice Hall, N. J. Pearson Prentice Hall Companion Website. [Cited 19 Oct 2006.] Available from URL: http://wps.prenhall.com/esm_tarbut_escience_9/0,4781,258966-main,00.html

- Tiessen H. (1998) Resilience of phosphorus transformations in tropical forests and derived ecosystems. In: *Soils of Tropical Forest Ecosystems Characteristics, Ecology and Management* (eds A. Schulte & D. Ruhayat) pp. 92–8. Springer-Verlag, Berlin.
- Tomlinson P. B. (1979) Systematics and ecology of the palmas. *Ann. Rev. Ecol. Syst.* **10**, 85–107.
- Tucker R. (1992) Experiences with *Cyrtostachys renda*. *Mooreana J. Palm.* **2**, 11–16.
- Uhl N. W. & Dransfield J. (1987) *Genera Palmarum: A Classification of Palms Based on the Work of Harold E. Moore, Jr.* The L. H. Bailey Hortorium and The International Palm Society, Lawrence.
- van der Heijden M. G. A., Wiemken A. & Sanders I. R. (2003) Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. *New Phytol.* **157**, 569–78.
- Vitousek P. & Sanford R. L. (1986) Nutrient cycling in moist tropical forests. *Annu. Rev. Ecol. Syst.* **17**, 137–67.
- Vormisto J. (2002) Palms as rainforest resources: how evenly are they distributed in Peruvian Amazonia? *Biodiv. Conserv.* **11**, 1025–45.
- Webb C. O. & Peart D. R. (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *J. Ecol.* **88**, 464–78.
- White R. E. (1997) *Principles and Practice of Soil Science, the Soil as a Natural Resource*, 3rd edn. Blackwell Science, Oxford.
- Widyatmoko D. (2001) *Autecology and conservation management of a rare palm species: The case study of lipstick palm cyrtostachys renda blume in Kerumutan Wildlife Sanctuary, Sumatra* (PhD Thesis). Bogor Agricultural University, Bogor.
- Widyatmoko D., Burgman M. A., Guhardja E., Mogeja J. P., Walujo E. B. & Setiadi D. (2005) Population status, demography and habitat preferences of the threatened lipstick palm *Cyrtostachys renda* Blume in Kerumutan Reserve, Sumatra. *Acta Oecol.* **28**, 107–18.