Habitat and ecological preferences of *Hydriastele costata* (Palmae) in Waigeo Island, West Papua

Didik Widyatmoko

Cibodas Botanic Gardens, Indonesian Institute of Sciences (LIPI),
Jl. Kebun Raya Cibodas, Sindanglaya, Cianjur 43253, Indonesia
didik_widyatmoko@yahoo.com

ABSTRACT. The research was conducted to test hypotheses about the significance and influence of edaphic parameters and association patterns in governing the occurrence and abundance of the karst palm *Hydriastele costata* and its co-occurrence with other plant species in Waigeo Island, West Papua. The results indicate that a number of interrelating edaphic factors influence the palm's occurrence and abundance. The palm showed a preference for dry, well-drained soil, with high magnesium (Mg^{2+}) content. Most colonies occurred in localities where Mg^{2+} content was very high. High alkaline concentrations also strongly corresponded to the presence of the emergent palm. Six of 15 tropical plant species were positively associated while the rest were negatively associated with *H. costata*. Four species (*Casuarina rumphiana*, *Decaspermum bracteatum*, *Baeckea frutescens*, and *Pinanga rumphiana* were strongly associated with *H. costata*, as indicated by their high association degrees using the Ochiai indices. The palm *P. rumphiana* appears to have similar habitat requirements as *H. costata*. The xerophytic palm *H. costata* tended to occupy sites with medium carbon/nitrogen (C/N) ratios where all sampled populations occurred in habitats with average C/N values more than 10. Based on the *r*-squared values, exchangeable Mg^{2+} and calcium (Ca^{2+}) appeared to have more influence on plant density and frequency than on crown and basal areas. The exchangeable Ca^{2+} contents showed a similar pattern to Mg^{2+} concentrations. Curiously, potassium (K^{+}), sodium (Na^{+}), aluminium (Al^{3+}) and hydrogen (H^{+}) contents did not show significant relationships with the palm abundance parameters.

Keywords. Association, co-occurrence, habitat preferences, *Hydriastele costata*, palms, Waigeo, West Papua

Introduction

Understanding the mechanisms for species co-occurrence and habitat preference (specialisation) is crucial for habitat management (Begon et al. 1996, Ludwig & Reynolds 1988, Mohler 1990, Nakashizuka 2001, Christie & Armesto 2003, van der Heijden et al. 2003, Hall et al. 2004). Although the detection of co-occurrence or association among or between species and environmental variables does not provide a causal understanding (Morisita 1959, Schluter 1984, Silvertown et al. 1992, Real & Vargas 1996), it can be used to generate hypotheses of possible underlying causal factors.

Palms often show local or regional patterns of co-occurrence and ecological preferences (Tomlinson 1979, House 1984, Kahn & Mejia 1990, Moraes 1996, Svenning 1999). Some palms appear to be adapted to specific edaphic conditions, such as soil quality, drainage and type (House 1984, Tomlinson 1990, Moraes 1996, Widyatmoko & Burgman 2006). Most tropical rain forest tree species have strongly aggregated spatial distribution patterns due to a high degree of habitat specialisation (Ashton 1998, Phillips 1998, Condit et al. 2000, Hubbell 2001). However, Duivenvoorden (1995, 1996) argued 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 specialisation for maintaining tree species richness.

There has been a lack of consensus about the importance of the correlations between plant abundance and edaphic conditions at local and intermediate spatial scales, e.g., at 1–100 km^2 (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 edaphic conditions are common features (Clark et al. 1998). Regional or intermediate spatial scales refer to strong environmental discontinuities (habitat types) while local spatial scales refer to environmental conditions that vary at scales less than 10^3 m, such as treefall gaps and local topographic variation (Svenning 1999).

Plant co-occurrence and abundance may be determined largely by nutrient availability, heterogeneity of the biotic and abiotic environment, and microhabitat specialisation (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). Some other studies have shown that tropical plant species distributions and community composition are correlated with soil nutrient status (Tucker 1992, Poulsen 1996, Clark et al. 1998, Svenning 2001, Widyatmoko 2001, Widyatmoko & Burgman 2006, Widyatmoko et al. 2007) such as magnesium and phosphor (Olsen & Sommers 1982, Vitousek & Sanford 1986, Baillie et al. 1987, Suarez 1996, Sollins 1998, Tiessen 1998, Potts et al. 2002, Hall et al. 2004, Palmiotto et al. 2004) as well as calcium, potassium, and sodium contents (Suarez 1996, Widyatmoko & Burgman 2006).

Spatial distribution patterns may also be determined by complex relationships within and between species, including seed dispersal (Bell 2000), competition for pollinators (Armbruster 1995, Svenning 1999), recruitment and regeneration (Harms et al. 2000, Christie & Armesto 2003, Widyatmoko et al. 2005), density dependence (Webb & Peart 2000), intermediate disturbance (Molino & Sabatier 2001) or variation in topography and soil water (Campbell 1985, Swaine 1996, Davie & Sumardja 1997, Clark et al. 1998, Svenning 2001). Very little information is available about the roles and influences of soil conditions and biotic associations on plant abundance and co-occurrence (Higgs & Usher 1980, House 1984, Gentry 1988, Duivenvoorden 1995).

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 emphasise 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).

The interspecific association test is a simple species-based approach for preliminarily defining community types that can be recognised 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 research was to (1) test hypotheses about the significance and influence of edaphic parameters in governing the occurrence and abundance of the important karst palm *Hydriastele costata* F.M.Bailey in a tropical lowland rain forest of Waigeo Island, West Papua, and (2) assess the tendency of the palm to co-occur with other plant species. We addressed three questions to answer. First, do local edaphic conditions in different habitat types affect the occurrence and abundance of *H. costata*? Second, does the palm species associate with other plant species in the Waigeo forest? Third, if so, how strong is the association? Such information is required to support the reserve management system, particularly through long-term monitoring of significant populations of the species occurring on different habitat types. Long-term monitoring programs will provide foundations for developing management prescriptions and conservation priorities for the valuable species and its habitat.

Materials and methods

Study species

Hydriastele costata (Arecaceae) is a solitary, erect, straight, unarmed, tall (up to 20–30 m), pleonanthic, monoecious palm species (Uhl & Dransfield 1987, Widyatmoko et al. 2007). The palm species occurs in New Guinea, Bismarck Archipelago and northern Australia, particularly in the humid lowland and hill tropical rain forests at altitudes from 0 up to 500 m above sea level, occupying mainly the forest upper canopy, preferring coastal calcareous soils. *H. costata* is not only of interest from an ecological point of view, but also in terms of economic significance since it provides a number of benefits. The palm is used as an ornamental plant, the stem is used for constructing local houses (floors and laths), while the hard outer part of the stem is locally used for making spears.

Study sites

The study focused on the Waifoi Forest and Kamtabae River located within the East Waigeo Nature Reserve, the Raja Ampat Islands, West Papua (Fig. 1), at altitudes ranging from 0 to 500 m above sea level, where *H. costata* mostly occurs. The camp established at Kamtabae River (130°43’38.2”E 0°5’53.3”S) was used as the reference

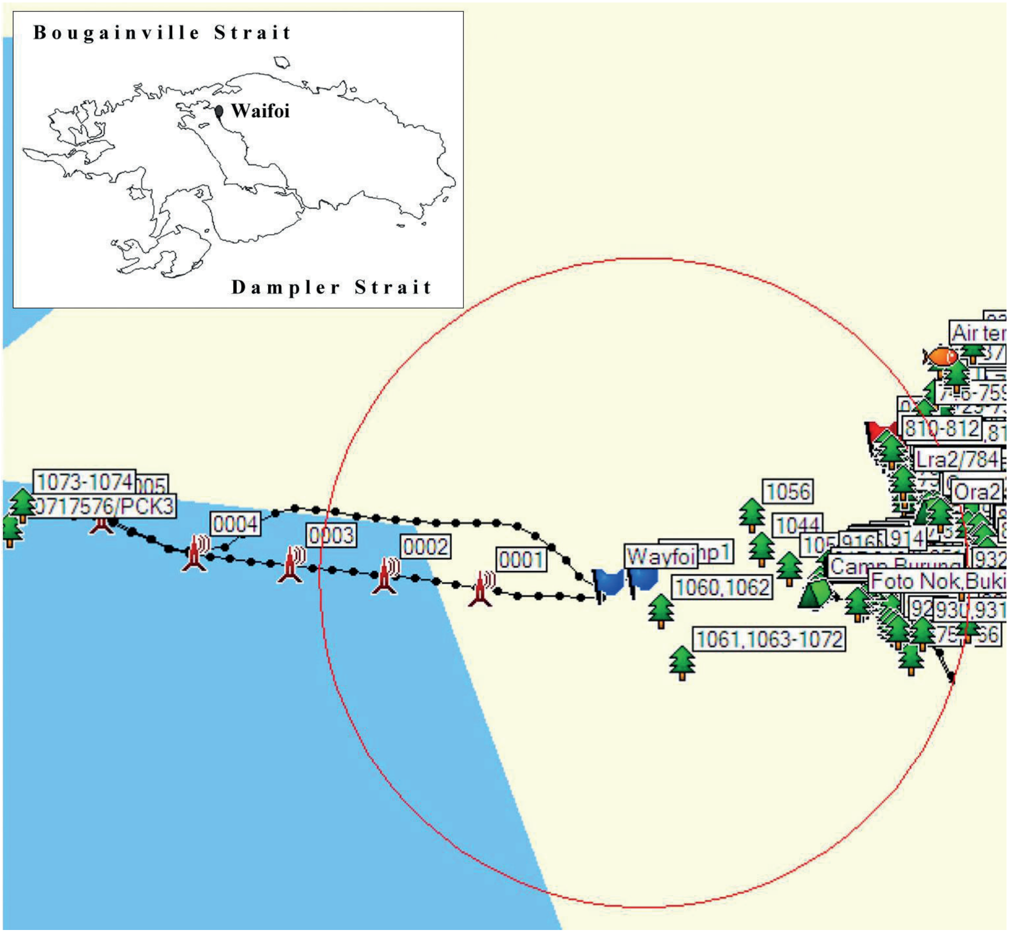

Fig. 1. The study area where coordinates and elevation of all sites studied (tree symbols) were recorded; Waifoi (Wayfoi) village is at the center of the circle. Inset shows locality of Waifoi on Waigeo.

point to explore the surrounding forests. Different directions comprising all four aspects were covered in order to comprehensively cover the study area. Lowland and hill forests of mixed-age indigenous vegetation, with slopes ranging from 30 to 70%, dominated the inland nature reserve topography.

East Waigeo Nature Reserve was established in 1996 based on the decree of the Indonesian Minister of Forestry No. 251/Kpts-II/1996 covering a total area of 119,000 hectares, located between 130°39’49”E and 130°55’54”E and between 0°02’27”S and 0°08’51”S. 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 32°C). Waigeo only has small seasonal temperature variations of less than 3^{0}C (the Koppen’s System, Tarbuck & Lutgens 2004); with an average humidity of 85% during June 2007.

Waigeo Island is one of the four major islands of the Raja Ampat Archipelago. The waters and environment around Waigeo Island have been known as the most biodiverse marine area in the world, especially in terms of coral reefs and fish species (Webb 2005, Pemerintah Kabupaten Raja Ampat & Conservation International Indonesia 2006). However, despite it being a biologically very rich area, little is known about the Islands' plant diversity and terrestrial resources (Badan Perencanaan Pembangunan Nasional - Bappenas 2003, Webb 2005). Detailed surveys focusing on the plant diversity will provide important baseline data for managing and conserving the Islands' biodiversity sustainably (Webb 2005).

Geologically, Waigeo Island is interesting, in having extensive karst ecosystems, alluvium substrates, acid volcanic and ultrabasic rocks, with some relatively high mountains (Jepson & Whittaker 2002, Webb 2005, Pemerintah Kabupaten Raja Ampat & Conservation International Indonesia 2006). The flora must be diverse according to the substrate and biogeographic reasons, as well as habitat characteristics which range from submontane forests to sago swamps and mangroves (via forests on karst and acid volcanics). Hill forests on volcanic substrates and karst formations extensively occur on this island. The island ultrabasic scrub is also unique and widely known for its endemic species (Webb 2005). Each island of the Raja Ampat has its own characteristics, especially in terms of vegetation composition and habitat types. Waigeo Island is botanically very important and valuable, despite its relatively small size compared to the main island of Papua (Johns 1995, Johns 1997, CI 1999).

Selection of habitat types

In order to study *H. costata* habitat preferences, eight habitat types were selected: coastal line (seashore), coastal hill slope, coastal hill top, inland river bank, inland hill slope, inland hill top, disturbed forest (most native species present), and converted forest (most native species removed). The characteristics of each habitat type (including slope, soil formation, elevation soil pH, average humidity, and average temperature) were described and recorded.

Vegetation structure and composition

A series of 24 belt transects (of 100 m × 10 m each) was established at the eight habitat types selected (i.e., three transects on each habitat), stretching from the camp at the Kamtabae River (130°43'38.2"E 0°5'53.3"S) to behind the Waifoi Village (130°42'46.7"E 0°6'5.9"S). Locations of each habitat type and belt transect were recorded using a Garmin Global Positioning System MAP 175. The major axes of all transects were orientated north-south derived from a selected compass bearing (Krebs 1989, Cropper 1993). All stemmed individuals of *H. costata* within each transect were counted. Damaged or dead individuals were not included. Land slopes were measured using a clinometer (SUUNTO Optical Reading Clinometer PM-5), while soil pH and humidity were measured using a soil tester Demetra patent no. 193478 Electrode Measuring System. Soil profiles were sampled by using a soil sampler the Belgium auger 1 m. Soil analyses were conducted at the Soil Research Center, Bogor. The level of forest (habitat) disturbance was determined on the basis of the proportion of the remaining native species.

Interspecific association (co-occurrence)

Association patterns among co-occurring species were tested using the chi-square test statistic by constructing the hypothesis that two species are not associated at some predetermined probability level. Fifteen plant species were tested for association from 67 observed. The strength of each association was tested using the Ochiai Index (OI) as recommended by Ludwig & Reynolds (1988):

$$OI = \frac{a}{\sqrt{a + b}\sqrt{a + b}}$$

Where:
a = the number of plots where both species (*H. costata* and the paired species) occur;
b = the number of plots where *H. costata* occurs, but not the paired species; and
c = the number of plots where the paired species occurs, but not *H. costata*.

Test of association. The palm was absent from one of the eight observed habitat types. The site was in the Waifoi village and was regarded as non-natural forest area (i.e., the coexisting plants have been planted with *Theobroma cacao*). Measures of interspecific association were based on the presence and absence of species within quadrats developed. A total of 144 quadrats of 5 m × 5 m each were sampled from the observed sites within the reserve with different vegetation types and associations. Quadrats were arranged systematically in an alternating pattern within the belt transects (of 100 m × 10 m each) in order to cover uniformly both sides of the axes (Mueller-Dombois & Ellenberg 1974, Cox 1974, Sokal & Rohlf 1981, Ludwig & Reynolds 1988). The data were then summarised in the form of a 2 × 2 contingency table.

The null hypothesis (H_o) constructed was that the distribution of *H. costata* is independent of the other species. To test the null hypothesis of independence, the chi-square test statistic (χ_t) was used (Ludwig & Reynolds 1988). The significance of the chi-square test statistic is determined by comparison with the chi-square distribution (χ_d) for 1 df at $\alpha = 0.05$. If $\chi_t > \chi_d$ the null hypothesis is rejected. Rejecting the null hypothesis indicates an association between *H. costata* 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 strength of association. The Ochiai Index (a measure of association) was used to quantify the strength of association between the species tested (i.e., *H. costata* and the paired species), as the association test can only determine whether the species tested are associated or not associated, but not the degree of the association. The index was recommended by Janson & Vegelius (1981) and Hubalek (1982) as it proved less biased. The value of the Ochiai Index is equal to 0 at no association and 1 at complete or maximum association.

Results

Habitat preferences

H. costata seemed to prefer specific habitat types. Highest densities occurred on hill slopes and tops near the coastal area (Table 1, Fig. 2). In contrast, the palm was suppressed at the shore and even absent from converted forest where most native species have been removed and replaced by *Theobroma cacao* (Fig. 2). Although the palm tolerated minor forest disturbance, the populations were generally low in this type of habitat, indicating a tolerance of sub-optimal conditions. The highest density was found on ultrabasic soil, on steep slopes and dry-open canopy gaps, where there were 72.4 adult individuals ha^{-1} (Table 1).

Species co-occurrence

Sixty seven possible co-occurring species were analysed, of which 15 species were tested for association with *H. costata*. Six of these 15 tested species were positively associated while the rest were negatively associated (Table 2). For the six species (*Casuarina rumphiana* Miq., *Decaspermum bracteatum* (Roxb.) A.J.Scott, *Baeckea frutescens* L., *Pinanga rumphiana* (Mart.) J.Dransf. & Govaerts, *Exocarpos latifolius* R.Br., and *Myrsine rawacensis* A.DC.), the association with *H. costata* was strong,

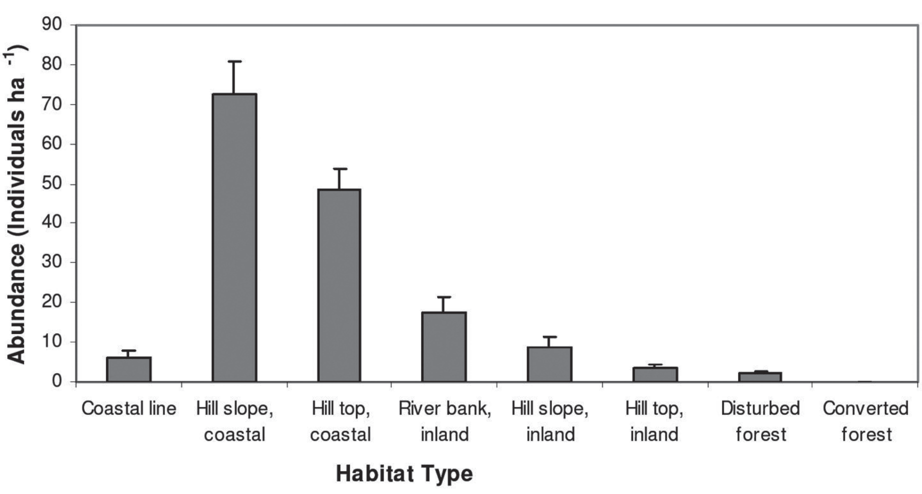

Fig. 2. Population densities of *Hydriastele costata* at different habitat types within the East Waigeo Nature Reserve, the Raja Ampat Islands, West Papua.

Table 1. The abundance of *H. costata* at various habitat types within the East Waigeo Nature Reserve, the Raja Ampat Islands, West Papua. Mean abundance ± S.D. (95% Confidence Interval).

Habitat type	Abundance (ha^{-1})	Habitat characteristics	Altitude (m asl)	Soil pH	Av. Humidity (%)	Av. Temp (°C)
Coastal line/shore	6.2 ± 1.6	0–30% slope, tidal influences, mud formation	0–10	6.2	82 ± 8.17	30.9
Hill slope, coastal	72.4 ± 5.4	30–80% slope, dry, open (wide canopy gaps), karst, ultrabasic soil	20–100	7.2	65 ± 7.02	31.9
Hill top, coastal	48.3 ± 5.3	30–60% slope, very dry, wide canopy gaps, karst, ultrabasic soil	100–150	7.2	63 ± 6.24	31.7
River bank, inland	17.5 ± 3.9	0–30% slope, lowland, alluvium, frequent floods	30–40	6.0-6.9	89 ± 8.29	28.5
Hill slope, inland	8.6 ± 2.9	30–70% slope, hill forest, alluvial deposit, volcanic soils	40–120	6.6–7.0	84 ± 6.72	28.3
Hill top, inland	3.4 ± 1.1	30–60% slope, hill forest, alluvial deposit	120–170	6.1–6.2	82 ± 9.02	27.6
Disturbed forest	2.2 ± 0.3	10–40%, most native species remained, *Lansium domesticum* planted	60–100	6.4–6.8	81 ± 6.48	29.1
Converted forest	0	10–40%, most native species removed, cacao planted	20–60	6.1–6.3	74 ± 6.01	29.6

indicated by their >0.5 indices. Although in some sites *Livistona brevifolia* Dowe & Mogea and *Licuala graminifolia* Heatubun & Barfod were found together with *H. costata*, their co-occurrence was not consistent. Surprisingly, the apparently closely associated species *Styphelia abnormis* (Sond.) F.Muell. and *Wendlandia buddlejacea* F.Muell. were negatively associated with *H. costata*. Unlike *Orania regalis* Blume ex Zipp., which is a shade-tolerance species, *H. costata* prefers and occupies karst and open coastal areas. As a consequence, their association degree was very low (Table 2).

A number of interrelating edaphic factors appeared to explain the occurrence

Table 2. Results of the association tests using the chi-square test statistic (χt) between *H. costata* and the fifteen co-occurring species. Values of the Ochiai Index are 0 at "no association" and 1 at "complete (maximum) association".

Paired species	Result of chi-square test	Types of Association	Strength of association (Ochiai Index)
Casuarina rumphiana	Associated	Positive	0.69
Decaspermum bracteatum	Associated	Positive	0.67
Baeckea frutescens	Associated	Positive	0.62
Pinanga rumphiana	Associated	Positive	0.61
Exocarpos latifolius	Associated	Positive	0.55
Myrsine rawacensis	Associated	Positive	0.52
Styphelia abnormis	Associated	Negative	0.43
Wendlandia buddlejacea	Associated	Negative	0.42
Ploiarium sessile	Associated	Negative	0.31
Livistona brevifolia	Associated	Negative	0.24
Decaspermum fruticosum	Associated	Negative	0.19
Licuala graminifolia	Associated	Negative	0.16
Pometia pinnata	Associated	Negative	0.15
Sommieria leucophylla	Associated	Negative	0.11
Orania regalis	Associated	Negative	0.07

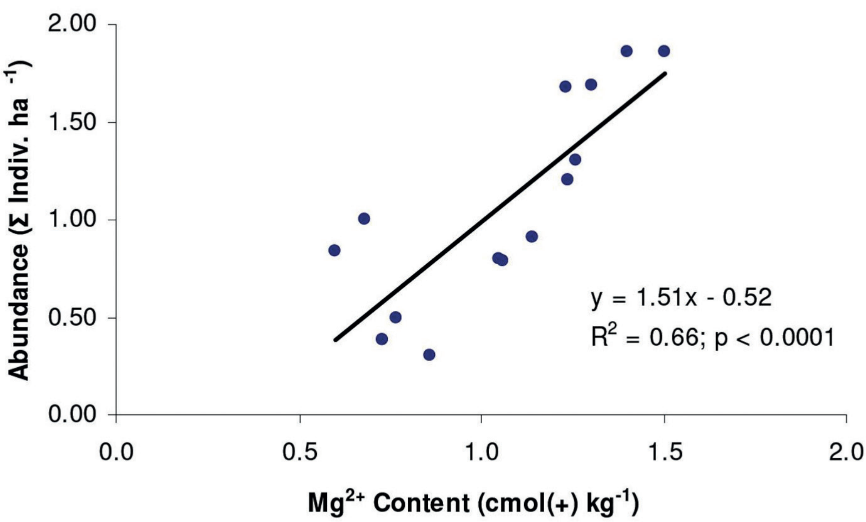

Fig. 3. Relationship between Mg^{2+} content and density of *Hydriastele costata* within the East Waigeo Nature Reserve, Waigeo. Mg^{2+} content values are Log_{10} and abundance values are Log_{10} individuals ha-1.

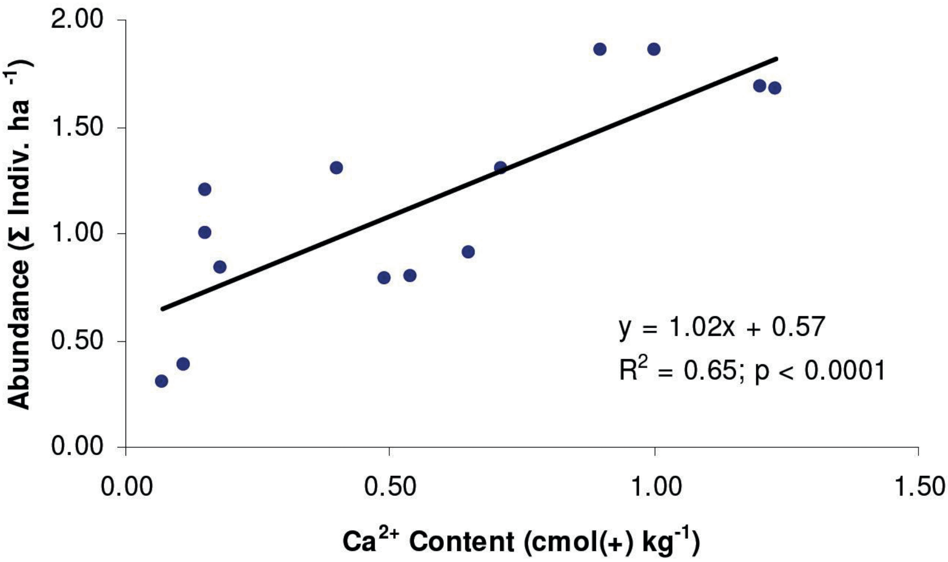

Fig. 4. Relationship between Ca^{2+} content and density of *H. costata* within the East Waigeo Nature Reserve, Waigeo. Ca^{2+} content values are Log_{10} and abundance values are Log_{10} individuals ha^{-1}.

Table 3. Results of the soil analyses conducted at six different habitat types within the East Waigeo Nature Reserve, Waigeo, West Papua. *Hill slope, coastal*: Horizon Ao (0–13 cm), A1 (13–48.5 cm), A2 (48.5–78.5 cm), AB (78.5–148 cm). *Hill top, coastal*: Horizon Ao (0–7 cm), A1 (7–18 cm), A2 (18–32.5 cm), AC (32.5–86.5 cm). *Hill slope, inland*: Horizon Ao (0–20 cm), A1 (20–40 cm), A2 (40–60 cm), AB (60–80 cm). *Hill top, inland*: Horizon Ao (0–15 cm), A1 (15–35 cm), A2 (35–75 cm). *River bank, inland*: Horizon Ao (0–16 cm), A1 (16–40 cm). *Coastal line*: Horizon Ao (0–10 cm).

Para meter	Hill slope, coastal				Hill top, coastal				Hill slope, inland				Hill top, inland			River bank, inland		Coastal line
	Ao	A1	A2	AB	Ao	A1	A2	AC	A0	A1	A2	AB	Ao	A1	A2	Ao	A1	Ao
pH	6.6	6.8	6.9	7.1	6.6	6.8	7.0	7.1	6.0	6.1	6.6	6.9	6.1	6.1	6.2	6.4	6.8	7.2
C/N	8	8	10	8	7	9	9	11	8	9	8	8	12	9	8	8	8	12
Ca2+	10	8.0	5.6	7.5	16	17	13	10	1.4	1.3	1.5	0.8	11.7	10.5	10.7	2.5	1.4	3.3
Mg2+	25	29	25	27	20	18	19	17	4.8	4.0	2.4	6.1	5.9	8.2	13.9	18.1	17.2	11.3
K+	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1
Na+	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.2	0.3	0.2	0.2	0.3
Al3+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
H+	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.1	0.1	0.1	0.1	0.1	0.1

and abundance of *H. costata*. This palm showed a preference for ultrabasic soils, steep slopes, and dry-open canopy gaps, with high magnesium (Mg^{2+}) and calcium (Ca^{2+}) contents. The largest population occurred on hill slopes where the highest magnesium content was recorded (Table 3). There was a strongly positive correlation between the abundance of *H. costata* and the soil mineral Mg^{2+} content (Fig. 3). The three largest populations (coastal hill slopes, coastal hill tops, and inland river bank) occurred in sites where Mg^{2+} contents were high (Table 3). According to the Soil Research Center (1983), a Mg^{2+} content >8.0 cmol(+)/kg was categorised as "very high" (Table 4). To some extent, Ca^{2+} contents also influenced the occurrence of *H. costata*, i.e., higher concentrations of Ca^{2+} corresponded with higher densities of the palm (Fig. 4), although the trend was not as clear as that for Mg^{2+}. Curiously, K^+, Na^+, Al^{3+} and H^+ concentrations did not show significant relationships with *H. costata* abundance parameters. The palm tended to occur in sites with lower C/N ratios (higher N contents). All observed populations occurred in habitats with average C/N values <10.

Table 4. Classification and criteria for soil chemical properties as defined by the Soil Research Center (1983).

Soil Properties	Very Low	Low	Medium	High	Very High
C (%)	<1.00	1.00–2.00	2.01–3.00	3.01–5.00	>5.00
N (%)	<0.10	0.10–0.20	0.21–0.50	0.51–0.75	>0.75
C/N	<5	5–10	11–15	16–25	>25
P_2O_5 HCl (mg/100g)	<10	10–20	21–40	41–60	>60
P_2O_5 Bray 1 (ppm)	<10	10–15	16–25	26–35	>35
P_2O_5 Olsen (ppm)	<10	10–25	26–45	45–60	>60
K_2O HCl 25% (mg/100g)	<10	10–20	21–40	41–60	>60
Cation Exchange Capacity (cmol(+)/kg)	<5	5–16	17–24	25–40	>40
K^+ (cmol(+)/kg)	<0.1	0.1–0.2	0.3–0.5	0.6–1.0	>1.0
Na^+ (cmol(+)/kg)	<0.1	0.1–0.3	0.4-0.7	0.8–1.0	>1.0
Mg^{2+} (cmol(+)/kg)	<0.4	0.4–1.0	1.1–2	2.1–8.0	>8.0
Ca^{2+} (cmol(+)/kg)	<2	2–5	6–10	11–20	>20
Alkali Saturation (%)	<20	20–35	36–50	51–70	>70
Alumin. Saturation (%)	<10	10–20	21–30	31–60	>70
pH H_2O	<4.5 – 5.5 Acid	5.6 – 6.5 Slightly Acid	6.6 – 7.5 Neutral	7.6 – 8.5 Slightly Alkaline	>8.5 Alkaline

The largest colony at the coastal hill slopes had an average C/N value of 8.5, followed by the coastal hill tops colony with an average value of 9.0 (Table 3).

Based on the *r*-squared values, exchangeable Mg^{2+} appeared to have more influence on plant density and frequency than on basal area and crown area (Table 5). The exchangeable Ca^{2+} concentrations showed a very similar pattern to Mg^{2+} contents, while C/N values seemed to have a negative correlation with frequency and density (i.e., higher values of C/N correlated with lower plant densities). Soil pH appeared to have more influence on plant density than on plant frequency. On the other hand, K^+, Na^+, Al^{3+} and H^+ contents did not show significant relationships with the palm abundance parameters, as indicated by their low correlation coefficients (Table 5).

Discussion

The positive association of *H. costata* with high contents of Mg^{2+} and Ca^{2+} is similar to that of the Papuasian palm *Orania regalis* (Widyatmoko 2009), the Malayan rain forest bertam palm *Eugeissona triste* Griff. (Fong 1977) and the Amazonian palms *Phytelephas macrocarpa* Ruiz & Pav. and *Astrocaryum murumuru* Wallace var. *murumuru* (Vormisto 2002) which prefer higher soil mineral contents. On the other hand, the association pattern of *H. costata* is different from that of the lipstick palm *Cyrtostachys renda* Blume (Widyatmoko & Burgman 2006) and the bayas palms *Oncosperma horridum* Scheff. and *O. tigillarium* (Jack) Ridl. (House 1984) which prefer low levels of Ca^{2+}, Mg^{2+} and K^+. Widyatmoko & Burgman (2006) showed that *C. renda* preferred sandy, well-drained soils with low mineral contents, while House (1984) found that *O. horridum* and *O. tigillarum* did not avoid flooded areas and poorly drained clay substrates.

Table 5. Values of correlation coefficient (*r*-squared) between edaphic parameters and abundance of *H. costata* within the East Waigeo Nature Reserve, Waigeo. Notes: (+) indicates a positive correlation; (-) indicates a negative correlation; * $p < 0.0001$; sample size (*n*) = 14.

Edaphic Parameters	Frequency	Density (Σ Individuals ha^{-1})	Basal Area (m^2 ha^{-1})	Canopy Circle Area (m^2 ha^{-1})
pH	(-) 0.52	(+) 0.61*	(-) 0.31	(-) 0.30
C/N	(-) 0.60*	(-) 0.62*	(-) 0.27	(-) 0.31
Exch. Ca^{2+}	(+) 0.62*	(+) 0.65*	(+) 0.41	(+) 0.41
Exch. Mg^{2+}	(+) 0.63*	(+) 0.66*	(+) 0.54	(+) 0.47
Exch. K^+	(+) 0.32	(+) 0.38	(+) 0.33	(+) 0.29
Na^+	(+) 0.41	(+) 0.35	(+) 0.39	(+) 0.36
Al^{3+}	0.00	0.00	0.00	0.00
H^+	(-) 0.34	(-) 0.39	(-) 0.28	(-) 0.24

Unlike *Licuala graminifolia* which is a relatively shorter-lived opportunistic species that rapidly colonises canopy gaps, *H. costata* is a slower-growing, long-lived species constituting an emergent canopy layer. Unlike *H. costata*, *L. graminifolia* occupies lower subcanopies, thus having different levels of sunlight exposure. *Licuala graminifolia* is more widely distributed throughout Papua. To some extent, *H. costata*, *Pinanga rumphiana* and *Casuarina rumphiana* may fill equivalent ecological roles and share membership of the same ecological guild. *Hydriastele costata* and *P. rumphiana* seem to share similar population establishment strategies, and both species naturally regenerate from seeds but not from suckers and both species produce relatively abundant seeds.

The abundance of *H. costata* seemed to increase with the cation exchange capacity. Soil cation exchange potential is linked with soil drainage capacity and well-drained soils contain high sand fractions (White 1997). The mean density of *H. costata* on hill slopes adjacent to coastal area was 72.4 individuals ha^{-1}, while on hill slopes far away from coastal area (inland) it was only 8.6 individual ha^{-1}. The absence of *H. costata* from converted forest is an indication that this species is intolerant of habitat disturbance, in which growth is prevented. In addition to the apparent preference for dry, well-drained soils, *H. costata* appeared to be more common in sites with higher electrical conductivity and higher concentrations of major nutrients, especially Mg^{++} and Ca^{++}. Surprisingly, K^+ and Na^+ contents did not correlate significantly with the palm density and frequency. This may be due to the very low contents of these minerals at various sites studied.

Hydriastele costata often forms a prominent component of the coastal Waigeo vegetation. However, a high level of disturbance, such as forest clearance behind the Waifoi forest, has caused some colonies to decline. In heavily shaded inland sites of the reserve, the palm very scarcely occurs with only very few individuals found. The palm is not a true gap exploiter and appears to be unable to take advantage of unstable canopy conditions (i.e., slightly disturbed habitats) and to become established in ecologically limited spaces.

Slope angle and vegetative cover affect moisture effectiveness by governing the ratio of surface run-off to infiltration. As drainage deteriorates, the oxidised soil profile of well-drained sites is transformed into the mottled and gleyed profile of a wet soil. 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. 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, White 1997, Hall 2004).

It seems that generative propagation through seed germination is most important for colony maintenance, while seed dispersal must be important for the establishment of new colonies far removed from reproductive adults through water transport (hydrochory). Seeds were sometimes seen to germinate in canopy gaps. Curiously, seedlings were often absent beneath the crowns of mature individuals. As light exposure is important for flowering and successful fruit set, and because the crowns of this palm occupy mainly the upper canopy, it is not surprising that fertile adult plants were relatively abundant. No effective dispersers of *H. costata* seeds were encountered during this study. Due to small seed size, long-distance travellers such as frugivores and granivores (pigeons) are likely to be potential dispersal agents.

Conclusion

Relationship between Mg^{2+} and Ca^{2+} content and the occurrence and abundance of *H. costata* was detected. Four species *(Casuarina rumphiana, Decaspermum bracteatum, Baeckea frutescens,* and *Pinanga rumphiana*) were strongly associated with *H. costata*, indicating the same habitat requirements and ecological preferences. However, it is still unclear whether rapid drainage or intolerance to low nutrient content determines the occurrence and abundance of *H. costata* and what factors drive the interspecific association. If intolerance to low nutrients is the case, the absence of the palm from sites with high nutrient contents may be due to rapid water shortage, particularly on steep slopes and hill tops. Otherwise, it may be due to its slow intrinsic growth rates during the seedling stages, excluding it from sites where plants with faster growth rates predominate. All of these are possible explanations of the research findings and thus further research is recommended. The information gleaned from this study will be useful to reserve managers to quantify the palm's occurrence and abundance in the reserve, guide an effective monitoring program, and possible use of the palm as an indicator of habitat conditions.

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