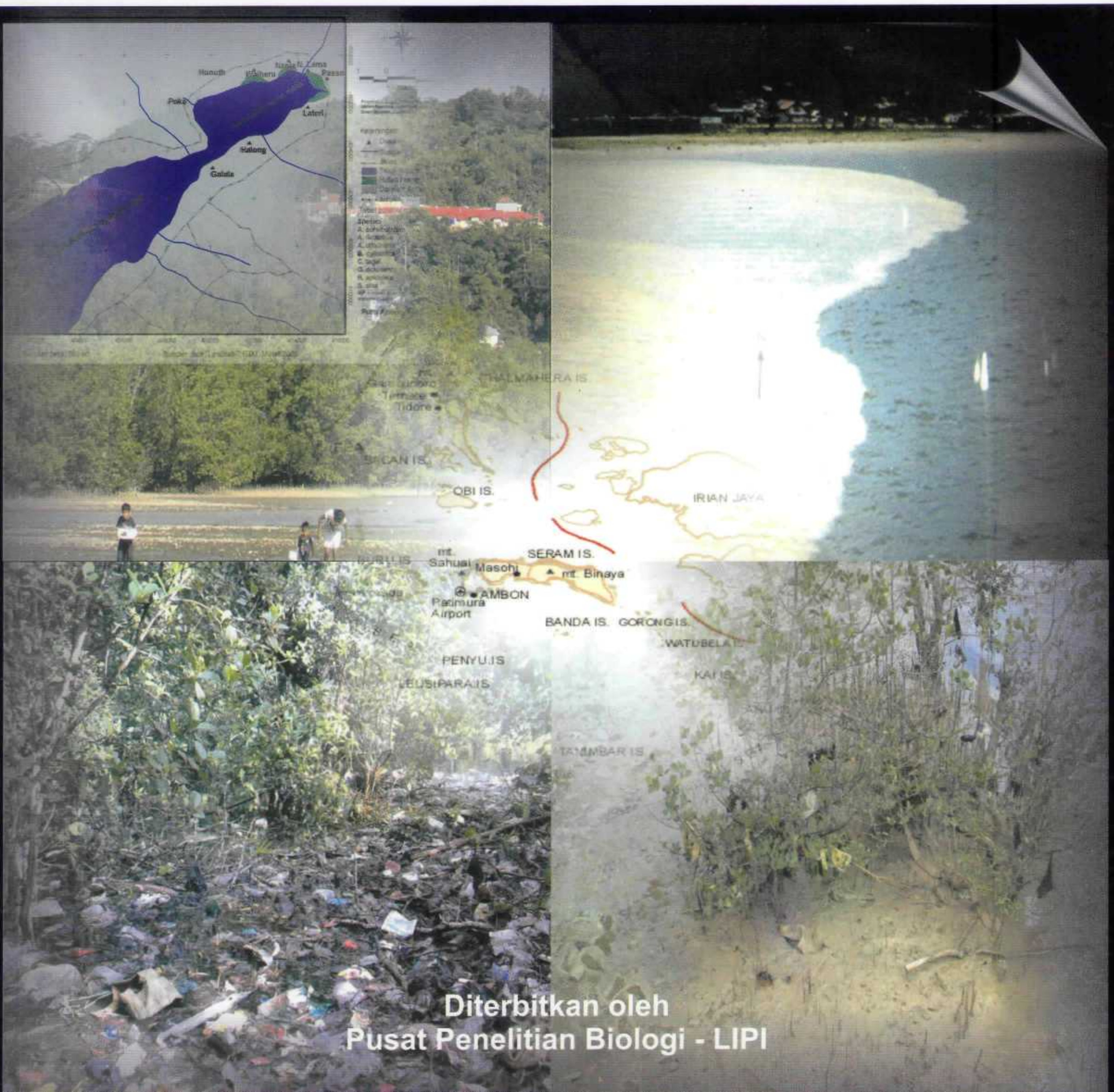
LIPI

Berita Biologi

Jurnal Ilmu-ilmu Hayati

ISSN 0126-1754
Volume 9, Nomor 5, Agustus 2009
Terakreditasi Peringkat A
SK Kepala LIPI
Nomor 180/AU1/P2MBI/08/2009



Diterbitkan oleh
Pusat Penelitian Biologi - LIPI

Berita Biologi merupakan Jurnal Ilmiah ilmu-ilmu hayati yang dikelola oleh Pusat Penelitian Biologi - Lembaga Ilmu Pengetahuan Indonesia (LIPI), untuk menerbitkan hasil karya-penelitian (original research) dan karya-pengembangan, tinjauan kembali (review) dan ulasan topik khusus dalam bidang biologi. Disediakan pula ruang untuk menguraikan seluk-beluk peralatan laboratorium yang spesifik dan dipakai secara umum, standard dan secara internasional. Juga uraian tentang metode-metode berstandar baku dalam bidang biologi, baik laboratorium, lapangan maupun pengolahan koleksi biodiversitas. Kesempatan menulis terbuka untuk umum meliputi para peneliti lembaga riset, pengajar perguruan tinggi maupun pekarya-tesis sarjana semua strata. Makalah harus dipersiapkan dengan berpedoman pada ketentuan-ketentuan penulisan yang tercantum dalam setiap nomor.

Diterbitkan 3 kali dalam setahun yakni bulan April, Agustus dan Desember. Setiap volume terdiri dari 6 nomor.

Surat Keputusan Ketua LIPI
Nomor: 1326/E/2000, Tanggal 9 Juni 2000

Pusat Penelitian Biologi—LIPI
Kompleks Cibinong Science Center (CSC-LIPI)
Jln Raya Jakarta-Bogor Km 46,
Cibinong 16911, Bogor - Indonesia
Telepon (021) 8765066 - 8765067
Faksimili (021) 8765059
e-mail: berita.biologi@mail.lipi.go.id
ksama_p2biologi@yahoo.com
herbogor@indo.net.id

Keterangan gambar cover depan: *Pembangiman perumahan di Passo dan tumpukan sampahyang mempercepat proses sedimentasi di areal hutan mangrove daerah Passo, Teluk Ambon, Maluku, sesuai makalah di halaman 481*
Suyadi - Bogor Agricultural University-SEAMEO Biotrop.

LIPI
Berita Biologi
Jurnal Ilmu-ilmu Hayati

ISSN 0126-1754
Volume 9, Nomor 5, Agustus 2009
Terakreditasi A
SKKepala LIPI
Nomor 180/AU1/P2MBI/08/2009

Diterbitkan oleh
Pusat Penelitian Biologi - LIPI

Ketentuan-ketentuan untuk Penulisan dalam Jurnal Berita Biologi

1. Karangan ilmiah asli, *hasil penelitian* dan belum pemah diterbiikan atau tidak sedang dikirim ke media lain. Makalah yang sedang dalam proses penilaian dan penyuntingan, tidak diperkenankan untuk ditarik kembali, sebelum ada keputusan resmi dari Dewan Redaksi.
2. Bahasa Indonesia. Bahasa Inggris dan asing lainnya, dipertimbangkan.
3. Masalah yang diliput, diharapkan aspek "baru" dalam bidang-bidang
   - Biologi dasar *(pure biology),* meliputi turunan-turunannya (mikrobiologi, fisiologi, ekologi, genetika, morfologi, sistematik/ taksonomi dsbnya).
   - Ilmu serumpun dengan biologi: pertanian, kehutanan, petemakan, perikanan ait tawar dan biologi kelautan, agrobiologi, limnologi, agrobioklimatologi, kesehatan, kimia, lingkungan, agroforestri.
   - *Aspek/ pendekatan biologi* harus tampak jelas.
4. Deskripsi masalah: harus jelas adanya tantangan ilmiah *(scientific challenge).*
5. Metode pendekatan masalah: standar, sesuai bidang masing-masing.
6. Hasil: hasil temuan haras jelas dan terarah.
7. Kerangka karangan: standar.
   Abstrak dalam bahasa Inggris, maksimum 200 kata, spasi tunggal, isi singkat, padat yang pada dasarnya menjelaskan masalah dan hasil temuan. Kata kunci 5-7 buah. *Hasil* dipisahkan dari *Pembahasan.*
8. Pola penulisan makalah: spasi ganda (kecuali abstrak), pada kertas berukuran A4 (70 gram), maksimum 15 halaman termasuk gambar/foto. Gambar dan foto harus bermutu tinggi; penomoran gambar dipisahkan dari foto. Jika gambar manual tidak dapat dihindari, harus dibuat pada kertas kalkir dengan tinta cina, berukuran kartu pos. Pencantuman Lampiran seperlunya.
9. Cara penulisan sumber pustaka: tuliskan nama jurnal, buku, prosiding atau sumber lainnya secara lengkap. Nama inisial pengarang(-pengarang) tidak perlu diberi tanda titik pemisah.
   a. Jurnal
      Premachandra GS, H Saneko, K Fujita and S Ogata. 1992. Leaf water relations, osmotic adjustment, cell membrane stability, epicutilar wax load and growth as affected by increasing water deficits in sorghum. *Journal of Experimental Botany* 43,1559-1576.
   b. Buku
      Kramer PJ. 1983. *Plant Water Relationship,* 76. Academic, New York.
   c. Prosiding atau hasil Simposium/Seminar/Lokakarya dan sebagainya:
      Hamzah MS dan SA Yusuf. 1995. Pengamatan beberapa aspek biologi sotong buluh *(Sepioteuthis lessoniana)* di sekitar perairan pantai Wokam bagian barat, Kepulauan Am, Maluku Tenggara. *Prosiding Seminar Nasional Biologi XI,* Ujung Pandang 20-21 Juli 1993. M Hasan, A Mattimu, JG Nelwan dan M Litaay (Penyunting), 769-777. Perhimpunan Biologi Indonesia.
   d. Makalah sebagai bagian dari buku
      Leegood RC and DA Walker. 1993. Chloroplast and Protoplast. In: DO Hall, JMO Scurlock, HR Bohlar Nordenkampf, RC Leegood and SP Long (Eds.). *Photosynthesis and Production in a Changing Environment,* 268-282. Champman and Hall. London.
10. Kirimkan 2 (dua) eksemplar makalah ke Redaksi (alamat pada cover depan-dalam) yang ditulis dengan program Microsoft Word 2000 ke atas. Satu eksemplar tanpa nama dan alamat penulis (-penulis)nya. Sertakan juga copy file dalam CD (bukan disket), untuk kebutuhan Referee/Mitra bestari. Kirimkan juga filenya melalui alamat elektronik (e-mail) resmi Berita Biologi: berita.biologi@mail.lipi.go.id dan di-Cc-kan kepada: ksama_p2biologi@yahoo.com, herbogor@indo.net.id
11. Sertakan alamat Penulis (termasuk elektronik) yang jelas, juga meliputi nomor telepon (termasuk HP) yang dengan mudah dan cepat dihubungi.

Anggota Referee / Mitra Bestari

Berita Biologi menyampaikan terima kasih
kepada para Mitra Bestari/ Penilai (Referee) nomor ini
9(5)-Agustus 2009

Dr.AndriaAgusta - *Pusat Penelitian Biologi-LIPI*
Dr. Bambang Sunarko - *Pusat Penelitian Biologi-LIPI*
Dr. Heddy Yulistiono - *Pusat Penelitian Biologi-LIPI*
Dr. Iwan Saskiawan - *Pusat Penelitian Biologi-LIPI*
Prof. (Ris.) Dr. Johanis P. Mogea- *Pusat Penelitian Biologi-LIPI*
Magdalena Litaay - *FMIPA Universitas Hasanudin*
Dr. Rasti Saraswati - *BB Sumberdaya Lahan Pertanian-Deptan*
Dr. Tukirin Partomohardjo - *Pusat Penelitian Biologi-LIPI*
Dr Yuyu Suryasari Poerba - *Pusat Penelitian Biologi-LIPI*

Referee/ Mitra Bestari Undangan

Dr. Achmad Dinoto - *Pusat Penelitian Biologi-LIPI*
Drs. Edi Mirmanto, MSc. - *Pusat Penelitian Biologi-LIPI*
Dr. Herwint Simbolon- *Pusat Penelitian Biologi-LIPI*
Dr. Ibnu Maryanto - *Pusat Penelitian Biologi-LIPI*
Dr. Kuswata Kartawinata - *Pusat Penelitian Biologi-LIPI (Purnabhakti) / UNESCO*
Dr. Niken T Murti Pratiwi - *Faperikan @ Ilmu Kelautan Institut Pertanian Bogor*
Dr. Ocky Kama Radjasa - *Faperikan @ Ilmu Kelautan Universitas Diponegoro*
Wellyzar Sjamsulrizal,PhD- *FMIPA Universitas Indonesia*

DAFTARISI

TINJAUAN ULANG **(REVIEW PAPERS**

INTERSPECIFIC ASSOCIATION PATTERNS AND EDAPHlC FACTORS' INFLUENCES: A CASE STUDY OF *Orania regalis* Zippelius IN WAIGEO ISLAND, WEST PAPUA [Pola Asosiasi Antarspesies dan Pengaruh Faktor Edafik: Studi Kasus *Orania regalis* Zippelius di Pulau Waigeo, Papua Barat]

Didik Widyatmoko
UPT Balai Kotiservasi Tumbuhan Kebun Raya Cibodas-LIPI
Jin Kebun Raya Cibodas, Sindanglaya, Cianjur 43253,
e-mail: didik_widyatmoko@yahoo.com

ABSTRAK

Ekologi komunitas tumbuhan tropika sering hanya diasumsikan dengan proses-proses yang berkaitan dengan gangguan stokastik, regenerasi, dan demografi tumbuhan. Pengaruh dan peranan komponen fisik dan biotik yang sebenarnya juga sangat berkaitan dengan bidang ini jarang mendapatkan perhatian. Akibatnya hasil studi ilmiah dalam bidang ini sangat kurang. Kondisi tan ah di daerah tropika dalam kenyataannya jauh lebih beragam dibandingkan dengan pemahaman orang selama ini, baik pada skala regional, lanskap maupun lokal. Studi ini dilakukan untuk menguji hipotesis mengenai arti penting dan pengaruh dari parameter-parameter edafik dan pola-pola asosiasi biotik terhadap kelimpahan dan distribusi palem Papuasiana *Orania regalis* Zippelius serta ko-okurensinya *(co-occurrence)* dengan spesies-spesies tumbuhan lainnya. Hasil studi ini menunjukkan bahwa sejumlah faktor edafik secara saling berkaitan mempengaruhi kelimpahan dan okurensi *O. regalis.* Palem ini mempunyai preferensi habitat yang cenderung basah, tetapi tidak tergenang, dengan konsentrasi Mg^{2+} dan Ca^{2}* tinggi. Tiga populasi terbesar terdapat di lokasi dengan kandungan Mg^{2+} sangat tinggi. Sebaliknya, konsentrasi basa yang tinggi berkorelasi erat dengan ketiadaan *(absence)* palem ini. Delapan dari 14 spesies tumbuhan tropika berasosiasi positif sedangkan enam spesies lainnya berasosiasi negatif dengan *O. regalis.* Berdasarkan Indeks Ochiai, lima spesies *{Licuala gramnifolia, Tabernaemontana aurantiaca, Intsia bijuga, Vatica rassak,* dan *Palaquium obovatum)* nampak berasosiasi sangat kuat dengan *O. regalis.* Palem *L. gramnifolia* dan *Sommieria leucophylla* menunjukkan preferensi ekologis dan habitat yang sama dengan *O. regalis. O. regalis* cenderung menempati lokasi-lokasi dengan C/N ratio rendah dan semua populasi yang ditemui tumbuh di habitat dengan C/N ratio rataan <10. Berdasarkan nilai koefisien korelasinya, konsentrasi Mg^{2+} nampak lebih berpengaruh terhadap kerapatan dan frekuensi daripada terhadap luas bidang dasar dan tajuk *O. regalis.* Pengaruh konsentrasi Ca^{2+} dan nilai C/N ratio menunjukkan pola yang sama dengan kandungan Mg^{2}*. Sebaliknya, kandungan K^{+}., Na^{+}., Al^{3+}. dan H^{+} tidak memperlihatkan pengaruh yang signifikan atau keterkaitan yang nyata dengan parameter-parameter kelimpahan palem ini. Hasil-hasil ini menunjukkan bahwa variabel-variabel edafik dan pola-pola asosiasi merupakan determinan-determinan penting dalam mengkaji kelimpahan dan okurensi spesies tumbuhan tropika.

Kata kunci: *Orania regalis,* asosiasi antar spesies, ko-okurensi, parameter edafik, Pulau Waigeo.

ABSTRACT

Tropical plant community ecology is often assumed to be driven largely by stochastic disturbance, regeneration and demographic processes. The influence and importance of physical and biotic components are rarely taken into account. Consequently, scientific findings in this field are very limited. Tropical soils are in fact more diverse than usually is recognized. This study was conducted to test hypotheses about the importance and influence of edaphic parameters and association patterns in determining the abundance and distribution of the Papuasian palm *Orania regalis* Zippelius and its co-occurrence with other plant species. The results showed that a number of interrelating edaphic factors, in combination, appeared to explain the abundance and occurrence of *O. regalis.* This palm showed a preference for wet, but well-drained soils, with high magnesium (Mg^{2+}) and calcium (Ca^{2}*) contents. The three largest colonies occurred in sites where Mg^{2}* content was high. On the other hand, high alkaline concentrations corresponded to the absence of the palm. Eight of 14 tropical plant species were positively associated while six species were negatively associated with *O. regalis.* For five species *(Licuala gramnifolia, Tabernaemontana aurantiaca, Intsia bijuga, Vatica rassak,* and *Palaquium obovatum),* the association with *O. regalis* was strong, as indicated by their Ochiai indices (>0.5). The palms *L. gramnifolia* and *Sommieria leucophylla* appeared to have similar ecological preferences and habitat requirements with *O. regalis.* The palm tended to occupy sites with lower C/N ratios and all known colonies occurred in habitats with average C/N values of less than 10. Based on the r-squared values, exchangeable Mg^{2}* appeared to have more influence on plant density and frequency than on basal area and canopy circle area. The exchangeable Ca^{2}* and C/N values showed a similar pattern to Mg^{2+} contents. However, K^{+}., Na^{+}., Al^{3+} and H^{+} contents did not show significant relationships with the palm abundance parameters. These findings suggest that edaphic variables and plant association patterns are important determinants of the abundance and occurrence of tropical plant species.

Key words: *Orania regalis,* interspecific association, co-occurrence, edaphic parameters, Waigeo Island.

^*Diterima: 13 Maret Disetujui:26 April 2009*

INTRODUCTION

Palm species is an important biotic component of tropical rain forests and often shows local or regional patterns of co-occurrence and ecological preferences (Tomlinson, 1979; House, 1984; Kahn dan 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 dan Burgman, 2006). Most tropical rain forest tree species have strongly aggregated spatial distribution patterns (Ashton, 1998; Phillips, 1998; Condit *et al,* 2000), perhaps due to a high degree of habitat specialization (Ashton, 1998; Hubbell, 2001), while 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 (Duivenvoorden, 1995; 1996).

Spatial distribution patterns may be determined by complex relationships within and between species 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 dan Peart, 2000), intermediate disturbance (Molino dan Sabatier, 2001) or variation in topography and soil water (Campbell, 1985; Swaine, 1996; Davie dan Sumardja, 1997; Clark *et al.,* 1998; Svenning, 2001). Plant co-occurrence and abundance may be determined largely by nutrient availability, heterogeneity of the biotic and abiotic environment, and microhabitat specialization (Silvertown dan Law, 1987; Ludwig dan Reynolds, 1988; Kahn dan Mejia, 1990;Hatfielde?a/., 1996; Clark *etal.,* 1998; Svenning, 1999; Webb & Peart, 2000; van der Heijden *et al,* 2003; Palmiotto *et al,* 2004). Some 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 *etal,* 1987; Suarez, 1996; Sollins, 1998; Tiessen, 1998; Potts *et al,* 2002; Halle et *al,* 2004; Palmiotto *et al,* 2004) as well as calcium, potassium and sodium contents (Suarez, 1996; Widyatmoko & Burgman, 2006). However, 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).

There has been a lack of consensus about the importance of the correlations between plant abundance and edaphic conditions at local and intermediate spans, scales, e.g. at 1-100 km^2(Gartlan *etal,* 1986; Swaine. 1996; Clarke? *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 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)

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 differen 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 conrribiat to the composition of most plant communities (Nakashizuka, 2001).

Understanding the mechanisms for species co-occurrence and habitat preference (specialization) is crucial for habitat management (Begon *et al,* 1996 Ludwig & Reynolds, 1988; Mohler, 1990;Nakashizuka 2001; Christie and Armesto, 2003; van der Heijden *et al,* 2003; Hall *et al,* 2004). Although the detection of co-occurrence or associations 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.

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 research 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 rain forest. The study focuses on the attractive palm *Orania regalis,* a New Guinean species with a disjunct geographic distribution, with a view to providing information to support management of the species. We addressed three questions. First, does *O. regalis* associate with other plant species in the Waigeo forest? Second, if so, how strong is the association? Third, do local edaphic conditions in different habitat types affect the abundance and occurrence of the species?

MATERIAL AND METHODS

Study Species

Orania regalis Zippelius (Arecaceae) or Iwul (Sundanese) is a solitary, large (up to 20 m tall with adult individual stem diameters ranging from 15 to 22 cm), erect, unarmed, pleonanthic, monoecious palm species (Uhl & Dransfield, 1987; Widyatmoko *et al*, 2007). The palm species occurs in New Guinea, particularly in the humid lowland and hill tropical rain forests at altitudes from 20 up to ca. 600 m above sea level, occupying mainly the forest subcanopy, and preferring volcanic and calcareous soils. The cabbage (mesocarp) seems to be poisonous and avoided by local people. *O. regalis* is of considerable interest, not only does it have an astonishingly disjunction geographic distribution but the inflorescence and flowers are much unspecialized within the tribe Axeceae. The ancestors of the Areceae and Cocoeae may well have been similar in form to *Orania* (Uhl & Dransfield, 1987).

Study Sites

The study area was focused on Kamtabae River (the Waifoi Forest) located within the East Waigeo Island Nature Reserve, the Raja Ampat Islands (West Papua), at altitudes range from 20 to 630 m above sea

Figure 1. Map of Waigeo Island, left figure (source: RTRW Kabupaten Raja Ampat 2005-2014, Survei Lapangan Tahun 2006, The Nature Conservancy and Conservation International Indonesia) and the detail sites studied in the island, right figure (green tree symbols). Coordinates and elevations of all sites (localities) observed were recorded. Waifoi village is located at the center of the red circle.

level where *O. regalis* mostly occurs. The camp established at Kamtabae River (E 130°43'38.2" S 0°5'53.3") was used as the reference point to explore the surrounding forests. Different directions comprising all four aspects (north, south, east, west) 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 Island Nature Reserve was established in 1996 based on the decree of the Indonesian Minister of Forestry No. 251/Kpts-II/l 996 covering a total area of 119,000 hectares, located betweenE 130°39'49"and E 130°55'54" and between S 0°02'27" and S 0°08'51". 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°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 (Figure 1). 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; Pemkab Raja Ampat and CI, 2006). However, despite it being a biologically very rich area, little is known about the Islands' plant diversity and terrestrial resources (Bappenas, 2003; Webb, 2005). Detail 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, by having extensive karst ecosystems, alluvium substrates, acid volcanic and ultrabasic rocks, with some relatively high mountains (Jepson & Whittaker, 2002; Webb, 2005; Pemkab Raja Ampat dan CI, 2006). The flora must be diverse according to the substrate and biogeographic reasons, as well as to the 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 in this island. The island ultrabasic scrub is also unique and widely known for its endemic species (Webb, 20051. Each island of the Raja Ampat has its own characteristics. especially in terms of vegetation composition and habitat types (BKSDA Papua II, 2003). Waigeo Island is botanically very important and valuable, despite ther relatively small size compared to the main island Papua (Johns, 1995; Johns, 1997; CI, 1999).

METHODS

Vegetation Structure and Composition

Two parallel belt transects of 100 m x 10m each were established on the sites studied, one at the camp Kamtabae River E 130°43'38.2" S 0°5'53.3" and another one at behind Waifoi Village E 130°42'46.7" S O°6'5.9 ". The major axis of the two transects was orientated north-south derived from a selected compass bearing (Krebs 1989; Cropper 1993). To record young plants shrubs and understorey species a series of 26 quadrats (of 2m x 2m each) were established at the study area and arranged systematically in an alternating pattern within the two belt transects developed in order to cover uniformly both sides of the axes (Mueller-Dombois & Ellenberg, 1974; Cox, 1974; Sokal & Rohlf 1981; Ludwig & Reynolds, 1988). The diameters each stem heights of all adult individuals of *O. regalis* within the two transects and heights of all of the seedlings within the quadrats (within 5 m either side of each transect) were measured and recorded. The positions of the adult palm individuals in the canopy strata (either subcanopy or lower subcanopy) were also recorded Damaged or dead individuals were not included. The location of each belt transect was recorded using a Garmin Global Positioning System MAP 175. Land slopes were measured using a clinometer (SUUNTO Optical Reading Clinometer PM-5 made in Finlandia) while soil pH and humidity were measured using a soil tester DEMETRA patent no. 193478 Electrode Measuring System, Tokyo, Japan.

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.

Fourteen 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):

$$\sqrt{a+b}\sqrt{a+c}$$

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

Test of association

Orania regalis was absent from two of the 16 observed sites. Two sites in Waifoi village were regarded as non-natural forest area (i.e. the coexisting plants have been planted with Cacao and *Lansium domesticum).* Measures of interspecific association were based on the presence and absence of species within quadrats (each of 5m x 5m). A total of 40 quadrats 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 in order to cover uniformly both sides of the axes. One transect of 100m x 1 0m was established on each site with the major axis orientated north-south. The data were then summarized in the form of a 2 x 2 contingency table.

The null hypothesis (H_o) constructed was that the distribution of *O. regalis* is independent of the other species. To test the null hypothesis of independence, the chi-square test statistic (c_t) was used (Ludwig & Reynolds, 1988). The significance of the chi-square test statistic is determined by comparison with the chi-square distribution (c_d) for 1 df at á = 0.05. If $c_t > c_d$ the null hypothesis is rejected. Rejecting the null hypothesis indicates an association between *O. regalis* 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)

Table 1. Abundance of *Orania regalis* at various locations in relation to forest (vegetation) association and habitat characteristics within the East Waigeo Island Nature Reserve. Mean abundance ± S.D. (95% Confidence Interval). The base camp established at Kamtabae River (S 00°05'53.3" E 130°43'38.2") was used as the reference point.

Location	Forest association	Habitat characteristics	Abundance (£ individuals ha"^{1})
Kamtabae River (Base camp)	Arecaceae-Fabaceae dominant	Lowland, slope, flat, adjacent to stream (river bank)	8.00 ± 2.14
Kamtabae River (North aspect)	Apocynaceae-Arecaceae dominant	Lowland, hill forest, near watershed	5.34 ±2.28
Kamtabae River (South aspect)	Sapindaceae dominant	Lowland, flat area, undulating	3.61 ±1.16
Kamtabae River (East aspect)	Apocynaceae-Anacardiaceae dominant	Hill forest, slope	2.24 ± 0.57
Kamtabae River (West aspect)	Fabaceae-Euphorbiaceae dominant	Hill forest, slight slope, near watershed	3.72± 1.62
Bamasu Waterfall 1	Fabaceae-Dipterocarpaceae dominant	River bank, stony slope	1.45 ± 1.21
Bamasu Waterfall 2	Clusiaceae-Myrtaceae dominant	Hill forest, karst, steep slope	0.61 ±0.46
Bird Watching Camp 1	Moraceae-Myristicaceae dominant	Hill forest, karst, steep slope	0.29 ± 0.17
Bird Watching Camp 2	Euphorbiaceae dominant	Hill forest, karst, steep slope	0.60 ±0.34
Bukit Manitalu 1	Myrtaceae dominant	Hill forest, karst, slight slope	2.18± 1.03
Bukit Manitalu 2	Myrtaceae-Clusiaceae forest	Hill forest, karst, slight slope	1.11 ±0.54
Bukit Manitalu 3	Clusiaceae-Lauraceae dominant	Hill forest, slight slope, karst	2.44 ± 0.86
Waifoi Village 1	Cacao plantation (planted)	Lowland forest, managed	0.20 ± 0.03
Waifoi Village 2	*Lansium domesticum* dominant (planted)	Lowland forest, managed	0.17 ± 0.02
Tanjung Bomat 1	Casuarinaceae dominant	Dry, open, ultrabasic soil	0.00
Tanjung Bomat 2	Myrtaceae dominant	Dry, open, ultrabasic soil	0.00

Table 2. Results of the association tests using the chi-square test statistic (-*-) between *Orania regalis* and the fourteen 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-square lest	Types of Association	Strength of association (Ochiai Index)
Ltcuala gramntfolla	Associated	Positive	0.71
Tabemaemontana aurantiaca	Associated	Positive	0.68
Intstab ijuga	Associated	Positive	0.65
Vatica rassak	Associated	Positive	0.59
Palaquium obovalum	Associated	Positive	0.54
Pomelia pinnata	Associated	Positive	0.49
Sommieria leucophylla	Associated	Positive	0.48
Cellis phllippensis	Associated	Positive	0.45
Artocarpus altllls	Associated	Negative	0.07
Semecarpus macrocarpa	Associated	Negative	0.07
Psychotria tripendumculata	Associated	Negative	0.06
Syzygium malaccensis	Associated	N egative	0.05
D illenia papuana	Associated	Negative	0.02
Hydhastele costata	Associated	N egative	0.02

Table 3. Results of the soil analyses conducted at six different sites within the East Waigeo Island Nature Reserve (Waigeo). KR_{BC}: Kamtabae River base camp, KR_{NA}: Kamtabae River north aspect, KR_{SA}: Kamtabae River south aspect, KR_{EA}: Kamtabae River east aspect, KR_{WA}: Kamtabae River west aspect, TB: Tanjung Bomat (Bomat Isthmus). L1 (KR_{BC}): Horizon Ao (0-13 cm), L2 (KR_{BC}): Horizon A1 (13-48.5 cm), L3 (KR_{BC}): Horizon A2 (48.5-78.5 cm), L4 (KR_{BC}): Horizon AB (78.5-148 cm). L1 (KR_{NA}): Horizon Ao (0-7 cm), L2 (KR_{NA}): Horizon A1 (7-18 cm), L3 (KR_{NA}): Horizon A2 (18-32.5 cm), L4 (KR_{NA}): Horizon AC (32.5-86.5 cm). L1 (KR_{SA}): Horizon Ao (0-20 cm), L2 (KR_{SA}): Horizon A1 (20-40 cm), L3 (KR_{SA}): Horizon A2 (40-60 cm), L4 (KR_{SA}): Horizon AB (60-80 cm). L1 (KR_{EA}): Horizon Ao (0-15 cm), L2 (KR_{EA}): Horizon A1 (15-35 cm), L3 (KR_{EA}): Horizon A2 (35-75 cm). L1 (KR_{WA}): Horizon Ao (0-16 cm), L2 (KR_{WA}): Horizon A1 (16-40 cm). L1 (TB): Horizon Ao (0-10 cm).

Parameter	KR_{BC}				KR_{NA}				KR_{SA}				KR_{EA}			KR_{WA}		TB
	L1	L2	L3	L4	L1	L2	L3	L4	L1	L2	L3	L4	L1	L2	L3	L1	L2	L1
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
Ca^{2+}	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
Mg^{2+}	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
Al^{3+}	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	0.0

recommended by Janson & Vegelius (1981) and Hubalek (1982) was used to estimate quantitatively the strength or degree of association between the species tested *(O. regalis* and the paired species), 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 or maximum association".

RESULTS

Species (Vegetation) Associations

Plant composition and structure within the East Waigeo Island Nature Reserve seemed to be very diverse, comprising a number of species and occupying at least four different canopy strata. Based on the

Tabel 4. Classifications and criteria for soil chemical properties as defined by Pusat Penelitian Tanah (1983).

Soil Properties	Very Low	Low	Medium	High	Very High
C (%)	<1.00	1.00-2.00	2.01-3.66	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 I (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 (KTK) (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 (cmol(+)/kg)	<0.4	0.4-1.0	1.1-2	2.1-8.0	>8.0
Ca (cmol(+)/kg)	<2	2-5	6-10	11-20	>20
Alkali Saturation (%)	<20	20-35	36-50	51-70	>70
Alumunium Saturation (%)	<IO	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

Table 5. Values of correlation coefficient (/--squared) between edaphic parameters and the abundance of *Orania regalis* within the East Waigeo Island Nature Reserve, Waigeo. Notes: (+) indicates a positive correlation; (-) indicates a negative correlation; *p < 0.001; sample size *(n)* = 18.

Edaphic Parameters	Frequency	Abundance Plant Density (fodividualsha⁻¹)	Basal area (m^2ha^{-1})	Canopy Circle Area ($m^2 ha^{-1}$)
pH	(-) 0.52	(-) 0.72*	(-) 0.28	(-) 0.24
C/N	(-) 0.71*	(-) 0.76*	(-) 0.30	(-) 0.28
Exch Ca^{2+}	(+) 0.62	(+) 0.65	(+) 0.47	(+) 0.51
Exch Mg^{2+}	(+) 0.78*	(+) 0.81*	(+) 0.58	(+) 0.64
Exch K^+	(+) 0.36	(+) 0.30	(+) 0.35	(+) 0.32
Na^+	(+) 0.33	(+) 0.31	(+) 0.26	(+) 0.38
Al^{3+}	0.00	0.00	0.00	0.00
H^+	(-) 0.45	(-) 0.41	(-) 0.25	(-) 0.26

importance values (IV), the forest main canopy was mainly dominated by *Tabernaemontana aurantiaca* (19.31), *Pometiapinnata* (17.78), *Palaquium obovatum* (13.16), *Celtisphillippensis* (10.92), *Intsia bijuga* (8.86), *Vatica rassak* (8.81), *Semecarpus macrocarpa* (5.60), *Artocarpus altilis* (5.42), and *Koordersiodendron pinnatum* (5.13). The subcanopy mainly consisted of *Pometiapinnata* (14.36), *Myristica lancifolia* (8.95,), *Drypetes longifolia* (6.01), *Pimelodendron amboinicum* (4.04), and *Syzygium* sp. (4.01). The other important subcanopy species included *Harpulia ramiflora*, *Lansium domesticum*, *Dysoxylum arborescens*, *Cynometra novoguineensis*, *Orania regalis*, and *Dillenia papuana.* Dominat lower subcanopy included small trees and shrub *Aglaia lawii*, the small palms *Licuala gramnifolia* and *Sommieria leucophylla*, *Ixora kerstingii*, *Garcinia dulcis*, *Maniltoa rosea*, and *M. plurijuga*, while dominant understorey species on the forest floor included *Pandanus tectorius*, *Elatostema polioneurum*, and the ferns *Nephrolepis dufii* and *Selaginella wildenowii.* Most of the land was composed by laterit ultrabasic soil.

Habitat Preference

Table 1 showed that *O. regalis* was found in specific habitat types, occurring mainly near watershed or stream but with well-drained conditions. High densities and a range of stages (sizes) occurred in river banks and watersheds but it was absent from dry ultrabasic soils, indicating its intolerance to such habitat. Although the palm tolerated calcareous soil or karst to some extent, the populations were generally low and even suppressed in this type of habitat, indicating a tolerance of sub-optimal conditions. The highest density was found on lowland, preferring slopes or slightly flat area adjacent to river banks by accommodating eight adult individuals ha', while in karst habitats and hill forests it was only 0.29 individual hal^{-1}.

Species Co-occurrence

Sixty seven possible co-occurring species were analyzed, of which 14 species were tested for association with *O. regalis.* Eight of these 14 species were positively associated while six species were negatively associated (Table 2). For five species *(Licuala gramnifolia, Tabernaemontana aurantiaca, Intsia bijuga, Vatica rassak,* and *Palaquium obovatum),* the association with *O. regalis* was strong, indicated by their indices >0.5.

Another palm species *(Sommieria leucophylla)* was positively associated with *O. regalis.* Although in some sites *Pometia pinnata* was found together with *O. regalis* (for example in Kamtabae River south and west aspects), their co-occurrence was not seen at all sites. Surprisingly, an apparently closely associated species, *Artocarpus altilis* was negatively associated with *O. regalis* (Table 2). *Koordersiodendron pinnatum, Pimelodendron amboinicum, Myristica lancifolia,* and *Pandanus tectorius* were even not associated with the palm. In fact, *O. regalis* was more common in well-drained sites and avoiding permanent waterlogged areas while P. *tectorius* seemed to adapt such conditions.

Although *Semecarpus macrocarpa and Psychotria tripendumculata* appeared to be closely associated with *O. regalis,* they were not confined to wet habitat, occurring in wider ecological contra. Unlike *O. regalis* which is a shade-tolerance species *Hydriastele costata* preferred and occupied karst. open coastal areas. The dominant species within the subcanopy (intermediate level) in the nature reserve included *Pimelodendron amboinicum, Myristica lancifolia, Pometia pinnata, Harpulia ramiflora, Cynometra novoguineensis, Orania regalis,* and *Dillenia papuana.*

Associations Between Species and Soil Characteristics

A number of interrelating edaphic factors, in combination, appeared to explain the abundance and distribution of *Orania regalis.* This palm showed a preference for wet, but well-drained soils, with high magnesium (Mg^{2+}) and calcium (Ca^{2+}) contents. The largest population (located at Kamtabae River base camp) had the highest magnesium content.

There was a strongly positive correlation between the abundance of *O. regalis* and the soil mineral Mg^{2+}content. The three largest colonies (KR_{BC} with 8 individuals ha^{1}, KR_{NA} with 5.34 individuals ha^{-1}. and KR_{WA} with 3.72 individuals ha"') occurred in sites where Mg^{2+} contents were high, KR_{BC}: 26.50$\pm$1.91

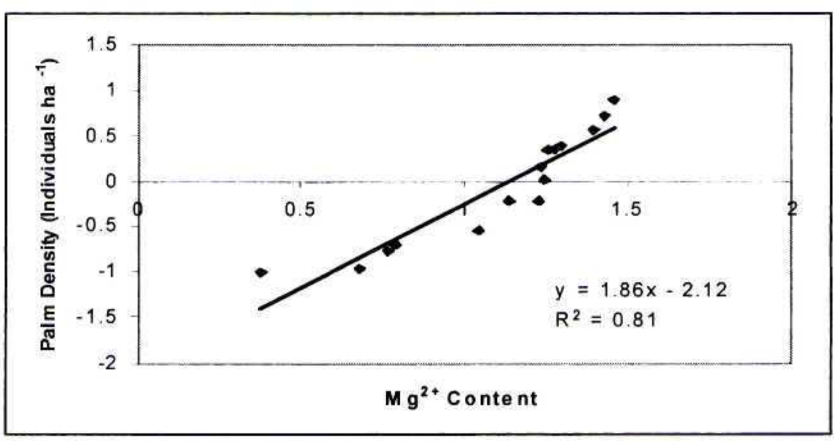


Figure 2. Relationship between Mg^{2+} content (cmol(+)/kg) and density of *O. regalis* (individuals ha^{1}) within the East Waigeo Island Nature Reserve, Waigeo. Mg^{2+} content values are Log_{10}. Density values are Log_{10} individuals ha'.

cmol(+)/kg, KR_{NA} 18.50±1.29 cmol(+)/kg, **and KR_{WA}:** 17.65±0.64 cmol(+)/kg (Table 1, Table3). According to Pusat Penelitian Tanah (1983), a Mg^{2+} content >8.0 cmol(+)/kg was categorized as "very high" (Table 4). To some extent, Ca^{2+} contents also influenced the occurrence of the palm, i.e. higher concentrations of Ca^{2+} corresponded with higher densities of *0. regalis*, although the pattern was not quite clear (Table 3). On the other hand, pH above 7 (alkaline conditions) corresponded to the absence of the palm, i.e. from Tanjung Bomat (Table 1, Table 3).

The palm tended to occur in sites with lower C/N ratios (higher N contents). All known colonies occurred in habitats with average C/N values <10. The largest colony at the Kamtabae River base camp (8.00 individuals ha^{1}) had an average C/N value of 8.5, followed by the Kamtabae River north aspect colony (5.34 individuals ha^{1}) with an average value of 9.0, while the Kamtabae River west aspect (3.72 individuals ha') contained a ratio of 8.0.

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

The adult stem diameters of *O. regalis* varied considerably, ranging from 15 to 22 cm and from 8 to 12 cm (for juveniles). Populations at Kamtabae River base camp contained the largest individuals with the mean stem diameter of 20.33 + 2.64 cm. Conversely, the populations at the Bamasu waterfall and Bukit Manitalu contained much smaller individuals with an average diameter of 15.25 + 2.01 cm.

DISCUSSION

The positive association of *Orania regalis* with high contents of Mg^{++} and Ca^{++} is similar to 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 or higher soil mineral contents. On the other hand, the association pattern of *O. regalis* is different from that of the lipstick palm *Cyrtostachys renda* (Widyatmoko & Burgman, 2006) and the bayas palms *Oncosperma horridum* and *O. tigillarum* (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* were to avoid flooded areas and poorly drained clay substrates.

Orania regalis and *Sommieria leucophylla* are long-lived species reproducing beneath a closed canopy, while *Licuala gramnifolia* is a relatively shorter-lived opportunistic species that rapidly colonizes canopy gaps. This suggests *O. regalis* and *S. leucophylla* may fill equivalent ecological roles and share membership of the same ecological guild.

The abundance of *O. regalis* 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 *O. regalis* on lowland, flat areas or slight slopes adjacent to stream banks was 8 individuals ha^{1}. In contrast, on hill forest, karsts with steep slopes far away from water courses it was only 0.6 individual ha^{1}, while on very dry, open and ultrabasic soils (such as at Bomat Isthmus) the palm was absent. The absence of *O. reaglis* from this site is an indication that this species is intolerant of high alkaline conditions, in which growth is prevented.

In addition to the apparent preference for wet but well-drained soils, *O. regalis* 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.

Slope angle and vegetative cover affect moisture effectiveness by governing the ratio of surface run-off to infiltration. As drainage deteriorates, the oxidized 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).

The palms *O. regalis, Sommieria leucophylla,* and *Licuala gramnifolia* appear to have similar ecological and habitat requirements. The three species seem to share similar population establishment strategies. Like *O. regalis, S. leucophylla* is confined to the Papuasian region. Naturally both species regenerate from seeds but not from suckers and both relatively produce abundant seeds. Their geographic distribution is also very similar. In contrast, *L. gramnifolia* is more widely distributed throughout Asia and Papua. However, unlike *O. regalis, S. leucophylla* and *L. gramnifolia* occupy lower subcanopies, thus having similar levels of sunlight exposure.

Sometimes *O. regalis* forms a prominent component of the Waigeo 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 forest clearance at Waifoi forest, has caused some colonies to decline. In heavily shaded sites of the reserve the palm occurs very scarcely with only very few adult individuals. The palm appears to be able to take advantage of unstable canopy conditions (slightly disturbed habitats) and to become established in ecologically limited spaces, although it is not a true gap exploiter.

In wet habitats 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) as most established colonies of *O. regalis* occur near water courses (streams). However, seeds were also 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 subcanopy, it is not surprising that fertile adult plans were sometimes very rare. No effective dispersers of *O. regalis* seeds were encountered during this **study** Due to relatively large seed size and poisonous mesocarp, long-distance travellers such as frugivores. granivores (pigeons) or even macaques are unlikely to be important dispersal agents.

CONCLUSIONS

The information gleaned from this study will be useful to reserve managers. Potential uses include a quantification of the palm's distribution in the reserve, an understanding of suitable habitat conditions and 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 along stream banks) are likely to be detrimental for this species. As *Orania regalis* is likely to be sensitive to changes in the hydrology of **the** landscape (particularly because of its low relief preference), any changes to groundwater conditions could have far reaching effects if they reduce the extent of humid well-drained sites within the reserve and island.

It is still unclear whether rapid drainage or intolerance to low nutrient contents determines the abundance and distribution of *O. regalis* 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 (which occurs on steep slopes or top of hills), or it may be due to its relatively slow intrinsic growth rates during the seedling stages, excluding it from these sites where plants with faster growth rates predominate. All of these are possible explanations of the research findings and thus further research is recommended.

ACKNOWLEDGEMENTS

I thank the expedition team members: Didit Okta

Pribadi, Wihermanto, Saripudin, Sudarsono, Supardi (Bogor Botanic Gardens), Rustandi (Cibodas Botanic Gardens), Deden Mudiana (Purwodadi Botanic Gardens), and I Gede Tirta (Bali Botanic Gardens) for their great assistance and cooperation. The map was drawn by Didit Okta Pribadi. I also greatly appreciate Dr. Irawati and Dr. Hery Harjono for the support and encouragement. Acknowledgements should also go to Ir. Kurung, M.M. for the permission to enter the East Waigeo Island Nature Reserve, Djefri Tibalia (BKSDA Papua II), Alberth Nebore, Irman Meilandi, Kris and Husen (CI Sorong), Gustab Gaman and Sakeus Dawa (Waifoi village) for their help and cooperation.

REFERENCES

Armbruster WS. 1995. The origins and detection of plant community structure: reproductive versus vegetative processes. *Folia Geobot. Phytotaxon* **30,** 483-497.

Ashton PS. 1998. Niche specificity among tropical trees: a question of scales. In.: *Dynamics of Tropical Communities.* D. M. Newbery, H. H. T. Prins & N. D. Brown (Editors). Blackwell Science. Oxford, UK.

Badan Perencanaan Pembangunan Nasional. 2003. *Indonesia Integrated Biodiversity Strategy and Action Plan* (IBSAP). Jakarta.

Baillie IC, Ashton PS, Court MN, Anderson JAR, Fitzpatrick EA and 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, 201-220.

Begon M, Harper JL and Townsend CR. 1996. *Ecology: Individuals, Populations and Communities,* 3rd Edition. Blackwell. Oxford, UK.

Bell G. 2000. Neutral Macroecology. *Science* **293,** 2413-2418.

Campbell GS. 1985. *Soil Physics with BASIC: Transport Models for Soil - Plant Systems.* Elsevier. Amsterdam.

Chisholm RA and Burgman MA. 2004. The unified neutral theory of biodiversity and biogeography: Comment. *Ecology* **85** (11), 3172-3174.

Christie DA and Armesto JJ. 2003. Regeneration microsites and tree species coexistence in temperate rain forests of Chiloe Island, Chile. *J. Ecol.* **91,** 776-784.

Conservation International. 1999. *The Irian Jaya Biodiversity Conservation Priority-Setting Workshop: Final Report.* Conservation International, Washington, D.C.

Clark DB, Clark DA and Read JM. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *J. Ecol.* **86,** 101-112.

Clark DB, Palmer MW and Clark DA. 1999. Edaphic factors and the landscape-scale distributions of tropical tree species. *Ecology* **80,** 2662-2675.

Condit R, Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP, Foster RB, Itoh A, LaFrankie JV, Lee HS, Losos E, Manokaran N, Sukumar R and Yamakura T. 2000. Spatial patterns in the distribution of tropical trees. *Science* **288,** 1414-1418.

Cox, GW. 1974. *Laboratory Manual of General Ecology* 2nd edition. Printed in the United States of America.

Cropper SC. 1993. *Management of Endangered Plants.* Jenkin Buxton Printers Pty Ltd. Melbourne.

Davie J and Sumardja E. 1997. The protection of forested coastal wetlands in Southern Sumatra: a regional strategy for integrating conservation and development. *Pac. Conserv. Biol.* 3, 366-378.

Duivenvoorden JF. 1995. Tree species composition and rain forest - environment relationships in the middle Caqueta, Colombia, NW Amazon. *Vegetatio* **120,** 91-113.

Duivenvoorden JF. 1996. Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. *Biotropica* 28, 142-158.

Edmunds J, Cushing JM, Costantino RF, Henson SM, Dennis B and Desharnais RA. 2003. Park's *Tribolium* competition experiments: a non-equilibrium species coexistence hypothesis. *J. Anim. Ecol.* 72, 703-712.

Fong FW. 1977. Edaphic conditions under Bertam *(Eugeissona tristis* Griff.) on Seraya Ridge Forests. *Trop. Ecol.* **18,** 60-70.

Gartlan S, Newbery DM, Thomas DW and Waterman PG. 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest reserve, Cameroon. *Vegetatio* **65,** 131-148.

Gentry AH. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Miss. Bot. G.* 75, 1-34.

Groeneveld J, Enright NJ, Lamont BB and Wissel C. 2002. A spatial model of coexistence among three *Banksia* species along a topographic gradient in fire-prone shrublands. *J. Ecol.* 90, 762-774.

Hall JS, McKenna JJ, Ashton PMS and Gregoire TG. 2004. Habitat characterizations underestimate the role of edhapic factors controlling the distribution of *Entandrophragma. Ecology* **85** (8), 2171-2183.

Harms KE, Wright SJ, Calderon O, Hernandez A and Herre EA. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404,** 493-495.

Hatfield JS, Link WA, Dawson DK and Lindquist EL. 1996. Coexistence and community structure of tropical trees in a Hawaiian montane rain forest. *Biotropica* **28** (4), 746-758.

Higgs AJ and Usher MB. 1980. Should reserves be large or small? *Nature* **285,** 568-569.

House AP. 1984. The Ecology of *Oncosperma horridum* on Siberut Island, Indonesia. *Principes* **28** (2), 85-89.

Hubalek Z. 1982. Coefficients of association and similarity based on binary (presence-absence) data: an evaluation. *Biol. Rev.* 57, 669-689.

Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography: Monographs in Population Biology.* Princeton University Press. Princeton, NJ.

Janson S and Vegelius J. 1981. Measures of ecological association. *Oecologia* **49,** 371-376.

Jepson P and Whittaker RJ. 2002. Ecoregions in Context: A critique with special reference to Indonesia. *Conservation Biology* 16 (1), 42-57.

Johns RJ. 1995. Malesia - An introduction. *Curtis's Botanical Magazine* **12 (2),** 53 - 62.

Johns RJ. 1997. *Background Papers for the Study of the*

Flora and Vegetation of the N. E. Kepala Burung, Irian Jaya, Indonesia. Royal Botanic Gardens. Kew.

Kahn F and Mejia K. 1990. Palm communities in wetland forest ecosystems of Peruvian Amazonia. *Forest Ecology and Management* 33 & 34, 169-179.

Krebs CJ. 1989. *Ecological Methodology.* Harper & Row Publishers. New York.

Ludwig JA and Reynolds JF. 1988. *Statistical Ecology, A Premier on Methods and Computing.* John Wiley and Sons. New York.

Mohler CL. 1990. Co-occurrence of Oak Subgenera: implications for niche differentiation. *Bull. Torrey Bot. Club* **117** (3), 247-255.

Molino JF and Sabatier D. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* **294,** 1702-1704.

Moraes MR. 1996. Diversity and distribution of palms in Bolivia. *Principes* **40** (2), 75-85.

Morisita M. 1959. Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci. Kyushu Univ., Ser. E (Biol.)* 3 (1), 65-80.

Mueller-Dombois D and Ellenberg H. 1974. *Aims and Methods of Vegetation Ecology.* John Wiley & Sons Inc. New York.

Nakashizuka T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends Ecol. Evol.* 16 (4), 205-210.

Olsen SR and Sommers LE. 1982. Phosphorus. In: *Methods in Soil Analysis, Part 2 Chemical and Microbiological Properties. A.* L. Page (Editor). American Society of Agronomy. Madison, WI.

Palmiotto PA, Davies SJ, Vogt KA, Ashton MS, Vogt DJ and Ashton PS. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *J. Ecol.* **92,** 609-623.

Pemerintah Kabupaten Raja Ampat dan Conservation International Indonesia. 2006. *Atlas Sumberdaya Wilayah Pesisir Kabupaten Raja Ampat, Provinsi Irian Jaya Barat.* Pemerintah Kabupaten Raja Ampat dan C! Indonesia. Sorong.

Phillips VD. 1998. Peatswamp ecology and sustainable development in Borneo. *Biodiversity and Conservation* 7 (5), 651-671.

Potts MD, Ashton PS, Kaufman LS and Plotkin JB. 2002. Habitat patterns in tropical rainforests: a comparison of 105 plots in Northwest Borneo. *Ecology* **83, 2782-**2797.

Poulsen AD. 1996. Species richness and density of ground herbs within a plot of lowland rainforest in north-west Borneo. *Journal of Tropical Ecology* **12,** 177-190.

Pusat Penelitian Tanah. 1983. *Kriteria Sifat Kimia Tanah.* Departemen Pertanian, Badan Penelitian dan Pengembangan Pertanian. Bogor.

Real R and Vargas M. 1996. The probabilistic basis of Jaccard's Index of Similarity. *Syst. Biol.* **45** (3), 380-385.

Richter DD and Babbar LI. 1991. Soil diversity in the tropics. *Adv. Ecol. Res.* **21,** 315-389.

Schluter D. 1984. A variance test for detecting species associations with some example applications. *Ecology* **65,** 998-1005.

Silvertown J and Law R. 1987. Do plants need niches? Some recent developments in plant community ecology. *Trends Ecol. Evol. 2* (1), 24-26.

Silvertown J, Holtier S, Johnson J and Dale P. 1992. Cellular automaton models of interspecific competition for space - the effect of pattern on process. *J. Ecol.* **80,** 527-534.

Sokal RR and Rohlf FJ. 1981. *Biometry: The Principles and Practice of Statistics in Biological Research* .W.H Freeman and Company. New York.

Sollins P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* **79,** 23-30.

Suarez DL. 1996. Magnesium and calcium. In: *Methods of Soil Analysis, Part 5 Chemical Methods.* J. M. **Bigham** (Editor). Soil Science Society of America. Madison,. Wl, 575-602

Svenning JC. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol-* **87,** 55-65.

Svenning JC. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification Neotropical rain forest palms (Arecaceae). *Bot* **.Rev 67,** 1-53.

Swaine MD. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *J. Ecol.* **84.** 419-428.

Tarbuck EJ and Lutgens FK. 2004. Earth Science 9[th] Editor (Chapter 18. Climate). Pearson Prentice Hall Companion Website.

Tiessen H. 1998. Resilience of phosphorus transformations in tropical forests and derived ecosystems. Irr *Soils of Tropical Forest Ecosystems Characteristics. Ecology and Management. A.* Schulte & D. Ruhiyat (Editors) Springer-Verlag. Berlin, 92-98.

Tomlinson PB. 1979. Systematics and ecology of the **Palmae** *Ann. Rev Ecol. Syst.* **10,** 85-107.

Tomlinson PB. 1990. *The Structural Biology of Palm* Clarendon Press Oxford. Oxford.

Tucker R. 1992. Experiences with *Cyrtostachys rends Mooreana Journal of Palm* 2, 11-16.

Uhl NW and Dransfield J. 1987. *Genera Palmarum: A Classification of Palms Based on the Work of* ***Haroia*** *E. Moore, Jr.* The L. H. Bailey Hortorium and The International Palm Society. Lawrence, Kansas.

Van der Heijden MGA, Wiemken A and Sanders IR. 2003. Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plant. *New Phytol.* **157,** 569-578.

Vitousek P and Sanford RL. 1986. Nutrient cycling in moist tropical forests. *Annu. Rev. Ecol. Syst.* **17, 137-167**

Vormisto J. 2002. Palms as rainforest resources: how evenl> are they distributed in Peruvian Amazonia" *Biodiversity and Conservation* **11,** 1025-1045.

Webb CO. 2005. Vegetation of the Raja Ampat Islands, Papua. Indonesia. *A Report to the Nature Conservancy. Revision 1.5.*

Webb CO and Peart DR. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *J. Ecol* **88,** 464-478.

White RE. 1997. *Principles and Practice of Soil Science The Soil as a Natural Resource,* 3[rd] Edition. Blackwell Science Ltd. 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 MA, Guhardja E, Mogea JP.

Walujo EB and Setiadi D. 2005. Population status, demography and habitat preferences of the threatened lipstick palm *Cyrtostachys renda* Blume in Kerumutan Reserve, Sumatra. *Ada Oecologica* 28: 107-118.

Widyatmoko D and Burgman MA. 2006. Influences of edaphic factors on the distribution and abundance of a rare palm *(Cyrtostachys renda)* in a peat swamp forest in eastern Sumatra, Indonesia. *Austral Ecology* 31 (8): 964-974.

Widyatmoko D, Pribadi DO, Wihermanto, Saripudin, Sudarsono, Supardi, Rustandi, Mudiana D and Tirta IG. 2007. Eksplorasi dan Studi Keragaman Flora Cagar Alam Pulau Waigeo Timur dan Taman Wisata Alam Sorong, Papua Barat. An Expedition Report *(unpublished).* Pusat Konservasi Tumbuhan Kebun Raya Bogor - LIP1. Bogor.