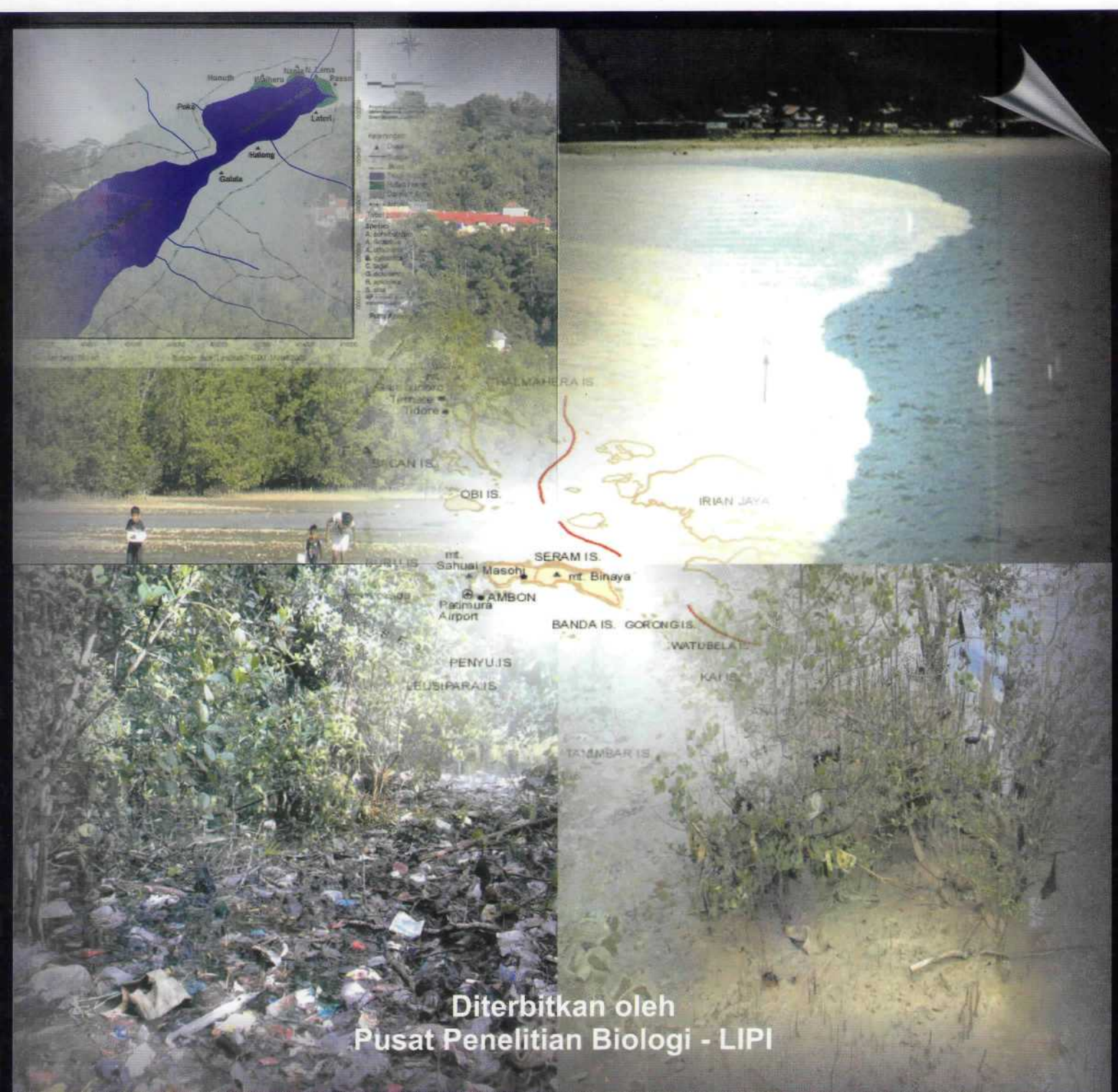


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INTERSPECIFIC ASSOCIATION PATTERNS AND EDAPHIC FACTORS' INFLUENCES: A CASE STUDY OF *Orania regalis* Zippelius IN WAIGEO ISLAND, WEST PAPUA

[Pola Asosiasi Antarspesies dan Pengaruh Faktor Edafik:
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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 tanah 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 grammifolia*, *Tabernaemontana aurantiaca*, *Intsia bijuga*, *Vatica rassak*, dan *Palaquium obovatum*) nampak berasosiasi sangat kuat dengan *O. regalis*. Palem *L. grammifolia* 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 rata-rata <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 Papuan 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 grammifolia*, *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. grammifolia* 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.

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; Hatfield *et al.*, 1996; Clark *et al.*, 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 *et al*, 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 spatial scales, e.g. at 1-100 km² (Gartlan *et al*, 1986; Swaine, 1996; Clarke *et al*, 1998, 1999; Hall *et al*, 2004). Tropical soils are not homogeneous at regional, intermediate or even local scales (Richter & Babbar, 1991; Hall *et al*, 2004) and abrupt discontinuities in the edaphic conditions are common features (Clark *et al*, 1998). Regional 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 10³ 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 different niches (niche partitioning), while 'non-equilibrium' hypotheses emphasize local fluctuations, disturbance and chance events that do not determine species composition, although they may result in expectations for relative species abundances (Hubbell, 2001; Chisholm & Burgman, 2004). Both 'equilibrium' and 'non-equilibrium' processes seem likely to contribute to the composition of most plant communities (Nakashizuka, 2001).

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 Waifo 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. Waifo 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/1996 covering a total area of 119,000 hectares, located between E 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, 2005). 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 its 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 10 m 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 Waifo Village E 130°42'46.7" S 0°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 2 m x 2 m 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):

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

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 Waifo 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 10m 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_0) 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_i) 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 $\alpha = 0.05$. If $c_i > c_d$ 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 $\pm$ 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 ($\bar{x}$ individuals ha ⁻¹)
Kamtabae River (Base camp)	Arecaceae-Fabaceae dominant	Lowland, slope, flat, adjacent to stream (river bank)	8.00 $\pm$ 2.14
Kamtabae River (North aspect)	Apocynaceae-Arecaceae dominant	Lowland, hill forest, near watershed	5.34 $\pm$ 2.28
Kamtabae River (South aspect)	Sapindaceae dominant	Lowland, flat area, undulating	3.61 $\pm$ 1.16
Kamtabae River (East aspect)	Apocynaceae-Anacardiaceae dominant	Hill forest, slope	2.24 $\pm$ 0.57
Kamtabae River (West aspect)	Fabaceae-Euphorbiaceae dominant	Hill forest, slight slope, near watershed	3.72 $\pm$ 1.62
Bamasu Waterfall 1	Fabaceae-Dipterocarpaceae dominant	River bank, stony slope	1.45 $\pm$ 1.21
Bamasu Waterfall 2	Clusiaceae-Myrtaceae dominant	Hill forest, karst, steep slope	0.61 $\pm$ 0.46
Bird Watching Camp 1	Moraceae-Myristicaceae dominant	Hill forest, karst, steep slope	0.29 $\pm$ 0.17
Bird Watching Camp 2	Euphorbiaceae dominant	Hill forest, karst, steep slope	0.60 $\pm$ 0.34
Bukit Manitalu 1	Myrtaceae dominant	Hill forest, karst, slight slope	2.18 $\pm$ 1.03
Bukit Manitalu 2	Myrtaceae-Clusiaceae forest	Hill forest, karst, slight slope	1.11 $\pm$ 0.54
Bukit Manitalu 3	Clusiaceae-Lauraceae dominant	Hill forest, slight slope, karst	2.44 $\pm$ 0.86
Waifo Village 1	Cacao plantation (planted)	Lowland forest, managed	0.20 $\pm$ 0.03
Waifo Village 2	<i>Lansium domesticum</i> dominant (planted)	Lowland forest, managed	0.17 $\pm$ 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 test	Types of Association	Strength of association (Ochiai Index)
<i>Ltcuala gramntfolia</i>	Associated	Positive	0.71
<i>Tabemaemontana aurantiaca</i>	Associated	Positive	0.68
<i>Intstab ijuga</i>	Associated	Positive	0.65
<i>Vatica rassak</i>	Associated	Positive	0.59
<i>Palaquium obovalum</i>	Associated	Positive	0.54
<i>Pomelia pinnata</i>	Associated	Positive	0.49
<i>Sommieria leucophylla</i>	Associated	Positive	0.48
<i>Cellis phlippensis</i>	Associated	Positive	0.45
<i>Artocarpus altilis</i>	Associated	Negative	0.07
<i>Semecarpus macrocarpa</i>	Associated	Negative	0.07
<i>Psychotria tripendunculata</i>	Associated	Negative	0.06
<i>Syzygium malaccensis</i>	Associated	Negative	0.05
<i>Dillenia papuana</i>	Associated	Negative	0.02
<i>Hydastele costata</i>	Associated	Negative	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
AP 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 ₂ O ₅ HCl (mg/100g)	<10	10-20	21-40	41-60	>60
P ₂ O ₅ Bray I (ppm)	<10	10-15	16-25	26-35	>35
P ₂ O ₅ Olsen (ppm)	<10	10-25	26-45	45-60	>60
K ₂ O 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
Aluminium Saturation (%)	<10	10-20	21-30	31-60	>70
pH H ₂ O	<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 (r^2) 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 (f/individual/ha ⁴)	Basal area (m ² ha ⁻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), *Pometiapiinnata* (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 *Pometiapiinnata* (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*. Dominant lower subcanopy included small trees and shrub *Aglaia lawii*, the small palms *Licuala grammifolia* 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^{-1} , while in karst habitats and hill forests it was only 0.29 individual ha^{-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 contrast. 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^{-1}) occurred in sites where Mg^{2+} contents were high, KR_{BC} : 26.50 ± 1.91

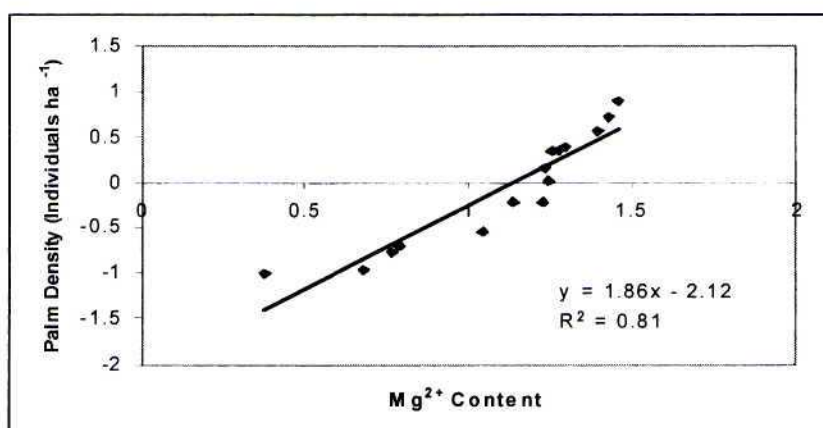


Figure 2. Relationship between Mg^{2+} content ($\text{cmol}(+)/\text{kg}$) and density of *O. regalis* (individuals ha^{-1}) within the East Waigeo Island Nature Reserve, Waigeo. Mg^{2+} content values are Log_{10} . Density values are Log_{10} individuals ha^{-1} .

cmol(+)/kg, KR_{NA} 18.50 ± 1.29 cmol(+)/kg, and KR_{WA} : 17.65 ± 0.64 cmol(+)/kg (Table 1, Table 3). 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 *O. 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^{-1}) 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. regalis* 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 grammifolia* 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 Papuan 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. grammifolia* is more widely distributed throughout Asia and Papua. However, unlike *O. regalis*, *S. leucophylla* and *L. grammifolia* 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 Waifo 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 plants 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.

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