

热带亚热带森林生态系统研究

第四集

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中国科学院
鼎湖山森林生态系统定位研究站编

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**TROPICAL AND SUBTROPICAL
FOREST ECOSYSTEM**

4

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低地和山地自然森林生态系统的生态关系和相互影响*

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摘 要

东南亚热带和亚热带地区亚高山上部的自然气候顶极植被是以常绿森林占优势。在裸露的生境和贫瘠的土壤上, 山地森林的群落外貌通常是属于硬叶——旱生型, 而且其结构(建筑和图式)比低地森林较为简单。这些特征在世界各地低海拔的一定土壤的和自然地理的顶极森林中同样都可以见到。例如东南亚的Kerangas森林、Kerapah森林和Padang疏林以及亚马孙低地的Caatinga森林和Bana疏林, 它们都是分布在极为恶劣的土壤和生境上的。人们对形成这些森林的特殊性状的有关生态因子是什么尚无一致的看法。结果人们对生态学的问题和管理的原则未能充分地认识, 而且土地利用的政策和客观上的需要也不十分协调。山地和低地的相互关系过去甚少被人研究, 但由于当前热带山地和低地的森林正迅速地受到破坏, 因此这个问题日益受到重视。研究的需要是迫切的, 但是改变人们的态度则更为重要。急须采取的政治措施就是要马上制止对山地和低地森林和植被的破坏。

- 一、沙捞越与文莱 Kerangas/Kerapah 森林和山地森林的植物区系的关系
- 二、沙捞越与文莱 Kerangas/Kerapah 森林和山地森林的群落外貌的关系
- 三、沙捞越与文莱 Kerangas/Kerapah 森林和山地森林的群落结构的关系
- 四、低地森林和山地森林相互影响的可能的因素
- 五、低地森林和山地森林相互影响与中国发展的关系
- 六、结论

总而言之, Kerangas/Kerapah 低地硬叶森林和山地森林对环境保护是有重要意义的。由于生境和土壤条件不宜, 因此这些森林生态系统是脆弱的, 其抗性、弹性和可塑性都比较低。所以这些贫瘠的低地森林和山地森林土地利用的主要原则是:

- (一) 保护功能必须绝对优先于生产功能(参阅 Bruenig, 1974);
- (二) 尽可能不要改变管理措施, 充分发挥森林自然调节的能力;
- (三) 土地利用规划必须是综合性的, 在探讨当地的低地森林和山地森林的关系时, 必须同时考虑地区性的沿海森林和内陆森林的相互影响。

要把上述原则付诸实践, 必须在当前科学知识水平的条件上, 在森林生态系统水平(低水平)、当地景观水平和地区水平等方面进行结构、相互作用的功能和反馈机理等的科学研究。

* 本文曾于1985年10月21—25日在中国四川成都举行的“热带和亚热带山区生态和发展国际学术会议”上宣读。王铸豪摘译。

LOWLAND-MONTANE ECOLOGICAL RELATIONSHIPS AND
INTERDEPENDENCIES BETWEEN NATURAL
FOREST ECOSYSTEMS*

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Abstract

The natural climatic climax vegetation of the upper submontane altitudinal zones in Southeastasian subtropical and tropical areas is a predominantly evergreen forest. Generally, on exposed sites and poor soils, the physiognomy is sclerophyll-xeromorph and the structure (architecture and pattern) more simple than in lowland forest. These features throughout the world are similarly found in certain edaphic and physiographic climax forests at low altitude. Examples are the Kerangas and Kerapah forests and Padang woodlands in Southeast Asia and the Caatinga forest and Bana woodlands in the Amazonian lowlands, which occur on extremely unfavourable soils and sites. There is no common agreement yet on the ecological factors which are responsible for the peculiar features of these forests. Consequently, the ecological and management implications are not well understood and land-use policies correspondingly inconsistent with needs. The highland-lowland interactions have been little studied but their reality is being increasingly felt throughout the tropics as the highlands and lowlands are being deforested at a progressive rate. Research needs are urgent, but even more critical is the need for change of people's attitude. Immediate political action is needed to stop deforestation and vegetation abuse both in the highlands and in the lowlands.

1. FLORISTIC AFFINITIES BETWEEN KERANGAS / KERAPAH AND
MONTANE FORESTS IN SARAWAK AND BRUNEI

Ordination of 55 Kerangas and Kerapah forest stands, selected as mature, fully stocked samples of their type in Sarawak and Brunei (Fig. 1) revealed patterns of tree species soil type and of leaf size distribution (BRUENIG, 1966, 1970, 1974). The soil type pattern (Fig. 2) indicated a gradient of water storage and drainage conditions along the X-axis. On the left are excessively drained, very deep sandy soils of coastal terraces ("giant podzol", quartzopsamment, orthic or humic podzol). Toward the center, drainage is moderate and rootable soil depth decreases

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(medium to shallow humic to gleyic podzol, leached ultisol). To the right beyond the reference axis 16-27, hydromorphic features increase with an altitudinal gradient to 1125 m in stand 54 and 735 m in the reference stand 56, and histosols develop on flats (51, 55, 57) or on quartzitic sandstone dip-slopes (54). The corresponding gradient toward acid, oligotrophic, dystic histosols formation in the lowlands goes vertically upward and occupies the upper right quadrangle. The Mulu N. P. terrace catena is the series 28 to 32.

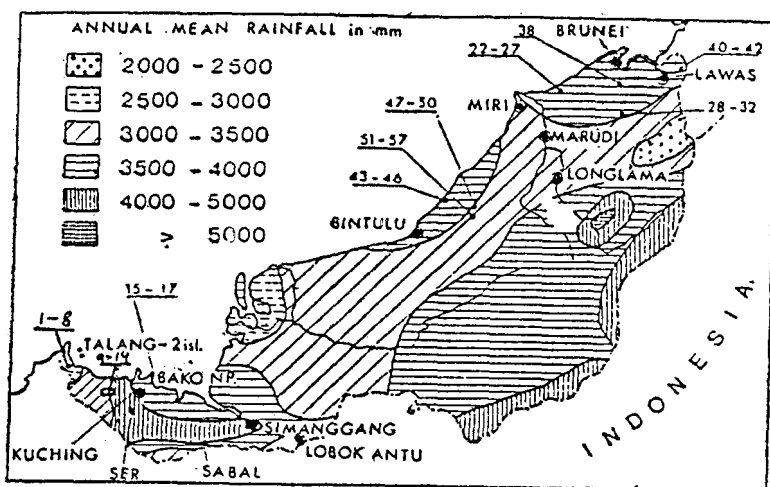


Fig. 1. Mean annual rainfall and location of 57 sample Kerangas and Kerapah forest stands of some limestone forest plots SER and of the 20 ha Sabal forest plot in Sarawak und Brunei, Borneo.

The peat swamp series begin in the heterogenous center (31 = peripheral Ramin Mixed Swamp) and proceeds towards the coastal terrace Kerapah reference stand (type 36, Alan forest), but then turns toward the submontane histosols, with 372 and 373 (Alan bunga forest) close to the Alan bunga kerapah on the Melinau terrace in Mulu N. P.

Downward from the center, the soils become more clayey, often deeper rooted and the common nutrient deficiency is probably less pronounced and the ecological consequences are less severe.

A characteristic feature of the soils in the ordination is the tendency to form surface rawhumus and peat (upper right quadrant). The causal mechanisms are probably the same in the lowland and montane sclerophyll forests. The coriaceous litter, rich in polyphenols (non-hydrolysable tannins) and acids resists abiotic and biotic decomposition typically in most forest formations in Borneo. In Kerangas forest, a surface raw-

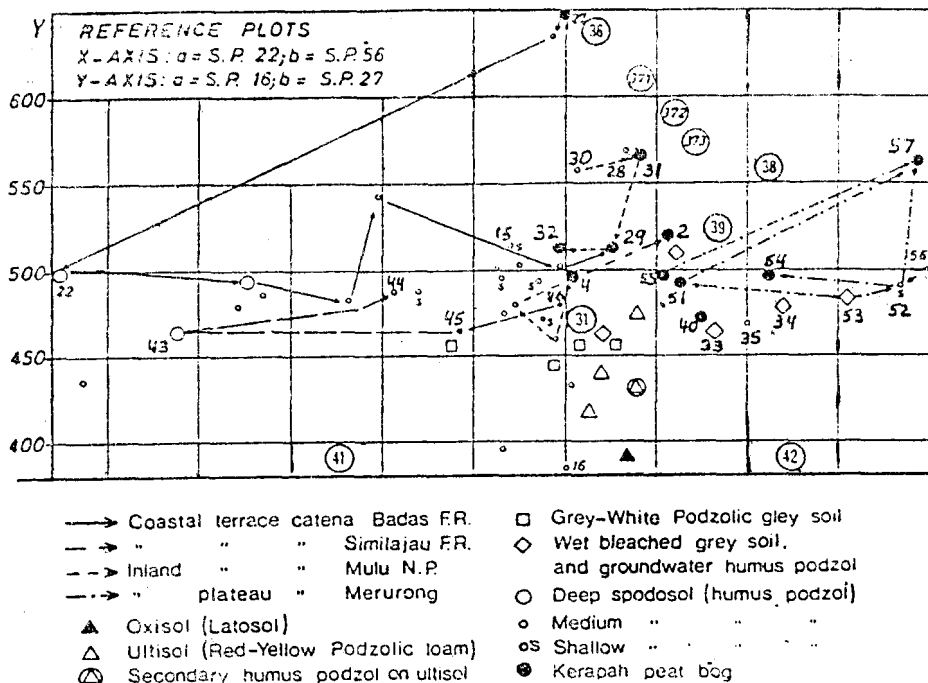


Fig. 2. Distribution of soil types in a floristic ordination of 55 Kerangas and Kerspah sample stands in Sarawak and Brunei (from BRUENIG, 1966 and 1974). The circled numbers 31 to 39 are the location of the phasic communities (association groups) of the lowland peat swamp series, 41 and 42 the location of Mixed Dipterocarp forest on more sandy (41, ultisol) or clayey (42, oxisol) soil.

humus layer of 5 to 20 cm accumulates, more on periodically dry podzols and usually somewhat less on bleached, often gley-type ultisols. The reason possibly is lower biological activity in these soils. Deeper rawhumus or peat may develop under conditions of extremely fluctuating water content, with saturation alternating with dry conditions and of extreme oligotrophy (BRUENIG and SANDER, 1983). Such conditions exist in the centers of pleistocene terraces or on flat plateaus where drainage is impeded, or on siliceous sandstone dipslopes over a wide range of altitude (BRUENIG, 1966 and 1974).

Some of the sample stands lie in the area of Mulu National Park closely southwest of the Kerangas forest sample plot of PROCTOR et al. (1983a) and are in line with the altitudinal sequence from the terraces in the Badas-Sungei Ingei basin across the Melinau terraces to Gunung Mulu (Fig. 3). The notable scarcity of comparative descriptive studies of humid tropical forest stands at a range of altitudes (PROCTOR et al. 1983a)

encourages to present the information available from the author's kerangas studies for this area.

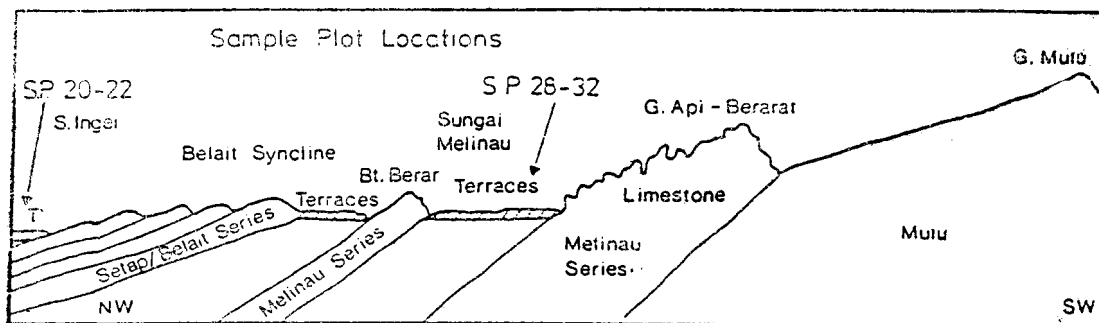


Fig. 3. Cross-section through the Belait Syncline (Ulu Ingei, Brunei) and Mulu National Park (from Fig. 5 of the Gunung Mulu N. P. Management and Development Plan, 1982) with the locations of sample plots 20-22 and 28-32 on the pleistocene terraces. The section runs NW-SE.

2. PHYSIOGNOMIC AFFINITIES BETWEEN KERANGAS/KERAPAH AND MONTANE/FORESTS

A distinct and congruent pattern emerged when a leaf size index was superimposed on the same floristic similarity ordination (Fig. 4). The leaf size index was calculated as the mean of the percent stand basal area and number of species in each of the leaf size classes according to WEBB, adding the class "notophyll" to RAUNKIAER's scheme WEBB, 1959). Plotting the classes leptophyll, microphyll and mesophyll showed distinct peak areas (Fig. 4). Leptophylls peaked in the submontane histosol area, but omitting 51 and 55 due to the aberrant occurrence of *Shorea albida* Sym., previously considered an coastal peat swamp forest endemic (ANDERSON, 1961). The mesophyll class peaks in the coastal histosols, due to the somninance of *S. albida*, and in the more clayey ultisols and oxisols with Mixed Dipterocarp and Riparian flood-plain forest. The microphyll class characterizes a broad belt along the X-axis with a boomerang-shaped peak on the shallow to medium deep, sandy humic podzols (the kerangas soils proper) represented by the Similajau catena in Fig. 5, top.

GRUBB and TANNER (1976) consider the dominant leaf size class according to WEBB (1959) as the consistently most useful character to define forest formation types (equal to formation or nano-ecosystem level of ELLENBERG, 1973). Their sequence mesophyll = lowland rainforest, noto- or mesophyll = lower montane rainforest, microphyll = upper montane rainforest and nanophyll = subalpine rainforest corresponds closely to the se-

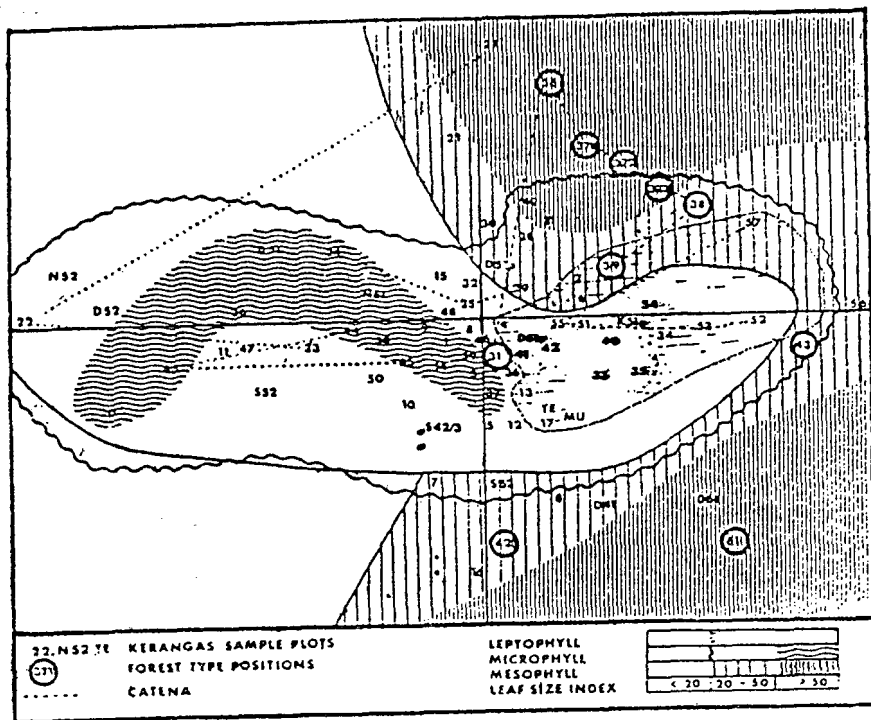


Fig. 4. The pattern of distribution of stands with leaf size index $L = 0.5 (G \% + Spp \%) > 50, 20-50, > 20$ for the leaf size classes leptophyll, microphyll and mesophyll. The darker shaded or hatched areas indicate peaks of the proportion of the respective leaf size class (from BRUENIG, 1966 and 1974).

quence from mesic, relatively favourable to periodically xeric, unfavourable sites in lowland Kerangas and Kerapah forests as illustrated in Fig. 5 and 6.

This trend toward micro- and nanophyll or leptophyll or acicular leafage or phyllodes, culminating in the submontane-montane kerapah (S. P. 40, 57) and similarly in exposed ridge-top kerangas (S. P. 15) and kerapah (S. P. 29 and others), is associated with other functional, biochemical and physiognomic features which could be adaptations to episodic moisture stress (BRUENIG, 1970, 1971; MEDINA et al., 1978; MEDINA, 1983). Some of the properties of some of the kerangas and montane tree species, such as numerous large stomata on small, coriaceous leaves and needles, improve drought tolerance but also permit high transpiration rates if conditions are favourable, which also helps with nutrient supply.

The trends to increased sclerophylly in it's various manifestations (BRUENIG, 1970) is, in kerangas and with increasing

altitude, associated with increased evergreenness of tree species. This may be related to a suspected longevity of leaves and serve as a nutrient conserving mechanism.

3. ARCHITECTURAL AFFINITY BETWEEN KERANGAS/KERAPAH AND MONTANE FOREST IN SARAWAK AND BRUENEI

Associated with increasing sclerophylly along the gradients of decreasing favourableness of soil and site in the lowlands with increasing altitude on mountains is a decline in forest stature. Fig. 5 gives an impression of the change with examples from:

- (1) Coastal Kerangas: Similajau Forest Reserve, northeast of Bintulu (Fig. 1), coastal holocene and pleistocene terraces (S. P. 46 to 44), and Bako N. P. (Fig. 1) with a low-stature, low-biomass forest on shallow humus podzol (S. P. 15) derived from thick-bedded siliceous sandstone. On exposed ridge-tops follows an open woodland similar to the montane summit forest (BRUENIG, 1965).
- (2) Inland Kerangas/Kerapah in Mulu N. P. on pleistocene terraces southwest adjacent to PROCTOR's Kerangas plot, with an instable transition in S. P. 29.
- (3) Submontane Kerangas (S. P. 52, 57, 51) and Kerapah (S. P. 57, raised bog) and lower montane "moss forest" on the Merurong Plateau east of Bintulu (Fig. 1) with an instable but highly divers transition zone, containing aberrant Shorea albida Sym., in 51. On exposed ridge-tops follow an open woodland to scrub (BRUENIG, 1966 and 1974).

The microphyll, mossy upper montane and summit forest plots in Mulu N. P., as described by MARTIN (1977) and PROCTOR et al. (1983, 1984) are similar to 52-57 and 15 with respect to: crown sizes, tree height, canopy architecture (aerodynamic roughness), life sizes and crown architecture. There is a notable similarity of the change of crown architectural types along the gradients from lowland Mixed Dipterocarp forest on favourable sites and Kerangas/Kerapah forest on poor sites and from comparably rich submontane/montane Conifer-Broadleaf forest on favourable sites to submontane Kerangas/Kerapah and submontane/montane moss forest (see Fig. 5). If crown architecture is related to tree functioning under environmental impact, especially stress (BRUENIG, 1976; FISHER 1984), similar environmental conditions may be involved (see chapt. 4).

Results of field measurements by KLINGE and BRUENIG in Amazonian lowland forest showed that leaf area, leaf weight and crown/canopy volume declined less than wood volume and weight along a site gradient of increasing unfavourableness from tall

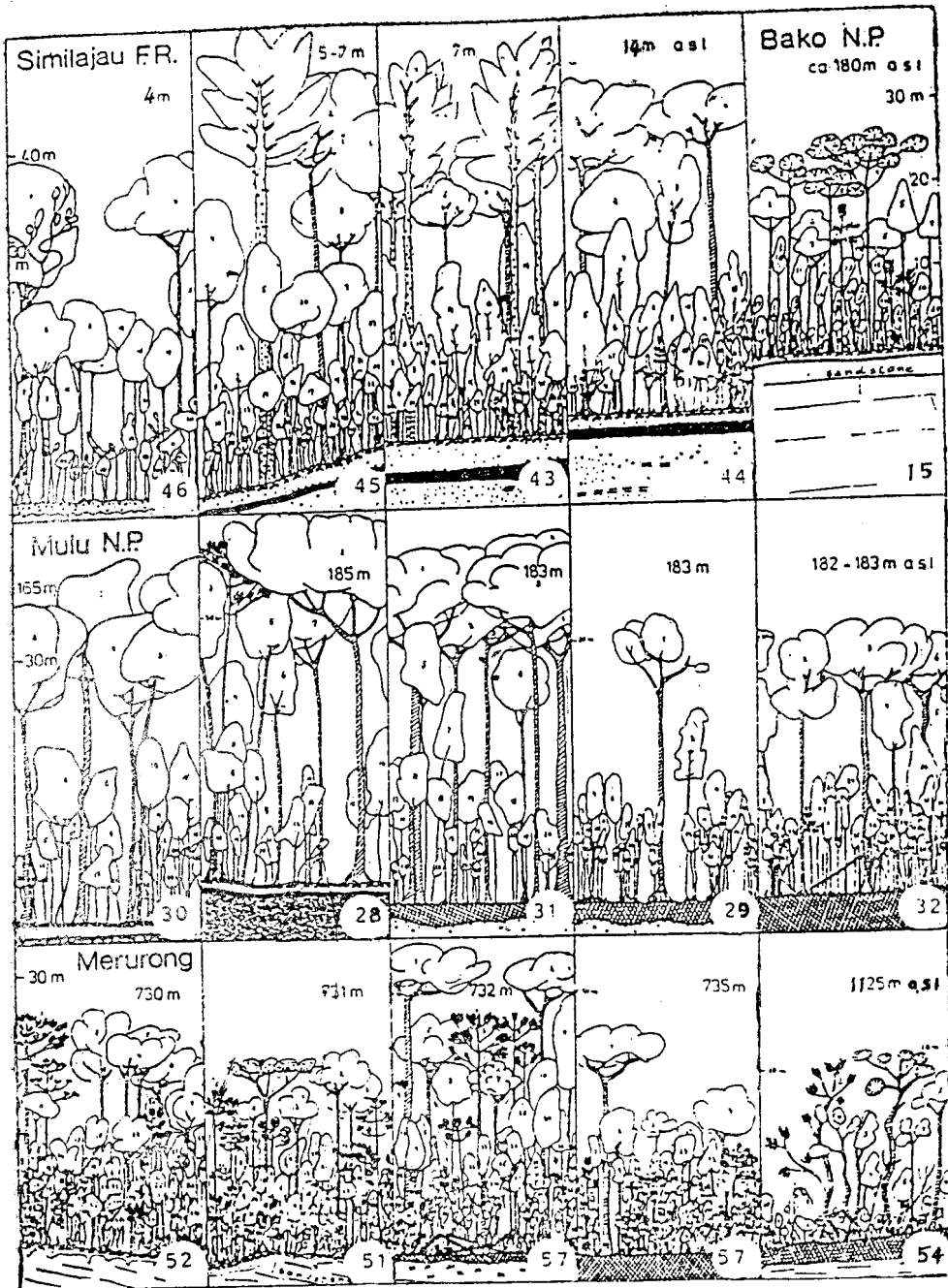


Fig. 5. Profiles of a series of sample forest stands:
 (a) coastal, Agathis dammara (45-43) and Shorea albida (45-44) terrace catena (Similajau Forest Reserve, Bintulu, Sarawak), a strongly sclerophyll stand on a coastal sandstone plateau (Bako National Park) with dominant Dacrydium beccarii;
 (b) Melinau terraces (Mulu N. P.) with Shorea albida

- and Casuarina nobilis initiating peat formation;
- (c) Upper lowland to submontane sandstone plateau (Merurong Plateau) with Casuarina nobilis, Dacrydium spp., Shorea albida, S. monticola.

Caatinga forest to low bana woodland in the MAB Amazon Ecosystem Study area at San Carlos de Rio Negro, Venezuela (BRUENIG et al., 1979; KURZ, 1982). The relationships to rates of production, decay and decomposition have yet to be investigated, but BRUENIG hypothesized that energy-related adaptation of form might be involved. The relatively ample sclerophyll leafage of the generally flatter crowns can take advantage of periods favourable to growth, and at the same time maintain itself well during unfavourable periods of low illumination, in damp, foggy conditions with high indirect solar radiation, and in windy, bright and dry periods. The relative to the wood biomass less ample mesophyll leafage of the more semispherical crowns on more favourable sites could be explained as avoiding stress and excessive transpiration from the high heat-load on the larger leaves, but maintain high performance under favourable growing conditions. However, so far experimental evidence is lacking.

Common associates at all altitudes are tree species of Myrtaceae, Sapotaceae, Guttiferae, Euphorbiaceae, Lauraceae and Fagaceae. Ericaceae (Vaccinium, Diplocosia, Rhododendron) occur preferably at higher altitude, but also on certain sites, especially exposed to light, at low altitude.

Note the change in tree stature and biomass density which is not related to soil fertility. In Similajau, S. P. 46 on a fairly nutrient-rich, undeveloped holocene terrace soil, tree height and biomass is less than on the flanks of the tertiary terrace with much poorer soil and single- or two-species dominance. Similarly, in Mulu N. P., the taller forest and highest biomass is not on the less nutrient-deficient lower terrace level, but in S. P. 28 and 31 with beginning peat formation and single-species dominance. The same feature is repeated on the Merurong Plateau.

4. POSSIBLE CAUSES FOR THE LOWLAND-MONTANE FOREST AFFINITY

GRUBB (1977) after reviewing the meagre information and based on his own results in Jamaica and New Guinea hypothesized that the more important ecological factors determining the distribution and productivity of forests on wet tropical mountains are:

- air temperature and solar radiation climate;
- nutrient scarcity, especially of nitrogen and phosphorus. Wind would only rarely and locally be of major impact. Al-

so, leaf production would relatively increase and wood matter production decrease with altitude.

The results of a more recent investigation on 4 sites on Gunung Mulu, Mulu N. P., differ partly and in some respects from GRUBB's generalizations (PROCTOR et al. 1983a-c). They found differences between "windy", i.e. exposed, and sheltered sites similarly to MARTIN (1977). The nature of these differences accords with those reported by BRUENIG (1966) from Kerangas forests in the lowlands. Also, the leaf litter production on Gunung Mulu was relatively low in the upper montane forest plot at 1860 m, and the nutrient status of the upper montane forest plots at 1310 m and at 1860 m was in many respects superior to that of the much more luscious lowland Mixed Dipterocarp forest of much larger stature. They exclude fire as a major influence on Mulu, but the find of charcoal in a kerangas soil pit on the Melinau terraces (BRUENIG, 1966) and the relatively frequent fires in the sclerophyll forest on limestone in the area should caution not to exclude episodic fires as ecological factors in Kerangas and more exposed montane forests. The evidence on soil and plant mineral contents, nutrient supply, cycling and demands is yet inconclusive and no clear-cut answer is yet possible with respect to major and minor limiting factors in Kerangas and Montane forests.

TANNER (1980) concludes from results of his work in Jamaican montane rainforest, that lack of water is not limiting the growth of the forests, and that the large differences in structure and composition between the studied 4 forest types are unlikely to be due primarily to differences in water relations. Similarly, differences between these impoverished upper montane rainforests in Jamaica and the much more luscious lower montane rainforest in New Guinea are not likely to be due to water stress (either too much or too little) in the impoverished Jamaican upper montane rainforest. TANNER explains the greater longevity of leaves in the poorer upper montane forest by the possibility that, "perhaps, in a situation where minerals are in short supply, leaves are retained by trees for longer periods, even though they are becoming less efficient at photosynthesis, whereas in a situation with a better mineral supply the leaves are shed sooner and replaced more easily (in terms of minerals) with more efficient leaves".

BRUENIG estimates water use and depletion from calculations of plant-available soil water, water storage in the biomass, 30-days sliding totals of rainfall, saturation pressure deficits, vegetation stature and corresponding rates of evapotranspiration (BRUENIG, 1973). His conclusion was, that more or less severe drought conditions will occur episodically and sporadically on all sites, but particularly and more often on soils which are shallow, have a low field capacity, or a deep but only partly rooted (e.g. giant podzols). BAILLIE (1972) confirmed

that drought conditions may occur near the coast on shallow soils. History of droughts in Borneo and the severe and widespread 1982/83 droughts in many parts of Southeast Asia confirmed that episodic droughts occur, may effect large tracts of land, and have a profound ecological effect on trees and forests even on deep, loamy to clayey soils and inland sites.

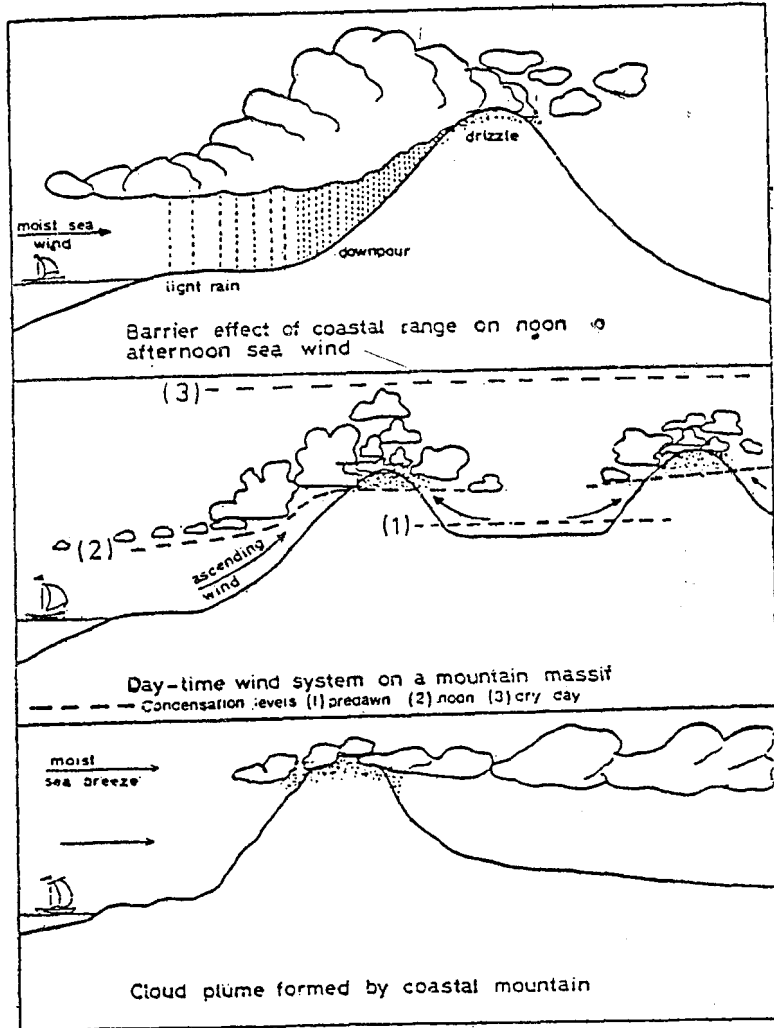


Fig. 6. Effect of a broad coastal mountain range (top), a complex mountain massif with broad valleys and plateaux (middle) and of an isolated coastal peak on cloud formation, condensation levels and precipitation.

BRUENIG's interpretation of the ecological significance of sclerophylly in lowland and submontane kerangas and kerapah and in lower montane moss forest accords with WALTER's (1973) state-