# Leaf Morphological Distribution in 250 Tree Species in a Lowland Dipterocarp Tropical Rain Forest, Sarawak, Malaysia –Comparison of Homobaric and Heterobaric Leaves

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## Introduction

Plant leaves show a range of morphological differences among species, including in their shape, size, and structure (Esau 1960). One important characteristic relates to the presence or absence of bundle-sheath extensions (BSEs) in the leaf (Wylie 1952): heterobaric leaves have BSEs, whereas homobaric leaves do not. BSEs are formed by parenchyma or sclerenchyma cells of the vascular bundle sheath, which extend to the epidermis on both sides of the leaf in heterobaric leaves. As a result, the mesophyll of heterobaric leaves is separated into many small "bundle-sheath extension compartments" by the BSEs (Terashima 1992). In contrast, homobaric leaves lack the BSEs and their internal structure is relatively homogeneous. These leaf types differ not only in their structural traits but also in their mechanical and functional characteristics. For example, BSEs in heterobaric leaves may provide mechanical support to the leaf blade (Wylie 1952), may act as a water conduit, or may cause non-uniform photosynthesis (Terashima 1992). Homobaric leaves, in contrast, exhibit larger lateral movements of gases in the leaf than is the case in heterobaric leaves (Pieruschka et al. 2006).

These morphological and functional differences may relate to a tree's growth environment and life form. Some authors have suggested that trees with heterobaric leaves will preferentially be found in deciduous forests, which have dry or cold seasons (Wylie 1952). In contrast, the proportion of trees with homobaric leaves may increase in wet or warm regions, which are usually dominated by evergreen species. This hypothesis is supported by the observation that many more evergreen tree species have homobaric leaves than is the case for deciduous tree species (Wylie 1952). Consequently, in the tropical rain forest, most tree species would be expected to have homobaric leaves, since the forest is humid throughout the year and consists mainly of evergreen trees.

In this study, we hypothesized that leaf type would be correlated with the growth environment or life form rather than with the forest biome, even in a tropical rain forest where most trees have evergreen leaves. The spatial distribution of microenvironmental factors such as light intensity, temperature, and relative humidity varies significantly even within a humid tropical rain forest. In particular, the upper canopy of the forest experiences significant desiccating conditions because of the high light intensities, high temperature, low humidity, and high wind speed, whereas the interior of the tropical rain forest is light-deficient, cooler (as a result of shading), and humid, and has lower wind speeds. Canopy gaps are drier and experience higher irradiance than the forest floor under a closed canopy. As a result of the frequent occurrence of water stress in the canopy and canopy gaps, heterobaric leaves may offer an adaptive advantage even in tropical rain forests. On the other hand, trees with homobaric leaves should be more abundant in forest understory species because of their more humid environment. If the proportion of species with each leaf type varies with the location in such heterogeneous forest environments, the distribution of the two types of leaves may influence stand-level photosynthesis and transpiration traits, which have been reported to differ between leaf types (Terashima 1992). However, only limited information is available on the distribution pattern of the two leaf types and their responses to different growth conditions. In the present work, we investigated the distribution of heterobaric and homobaric leaf types among 250 tree species in 45 families, with different life forms, in a tropical rain forest. In particular, we focused on the relationship between each leaf type and the corresponding life form type (e.g., emergent, canopy, sub-canopy, understory, and canopy gap species).

## Materials and Methods

***Study site*** The study was carried out in 2005 in a lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°12′N, 113°50′E; 150 to 250 m a.s.l.). The mean canopy height was about 30 to 40 m; some emergent trees reached heights of 50 to 70 m. The area has a humid tropical climate, with weak seasonal changes in rainfall and temperature. The mean annual precipitation and temperature were 2540 mm and 26.3 °C, respectively.

***Plant material and leaf collection*** We collected the leaves of 434 individuals of 250 tree species from 127 genera in 45 families, from the forest understory to the emergent layer and in canopy gaps. Between two and five fully expanded and apparently nonsenescing leaves of each species were sampled for microscopic observation. Transverse slices were prepared and photographed under a light microscope. Based on these observations, all tree species were classified into heterobaric and homobaric leaf types (Fig. 1). However, some species displayed intermediate morphology. These leaves had BSEs only around the large veins, and the bundle sheath extension compartments were consequently very large compared with those in heterobaric leaves. In this study, these species were categorized as having homobaric leaves.

All tree species that we studied fell into five categories based on their mature tree height and their distribution bias (canopy gap vs. shaded). The height of mature trees of each species was determined by observation or obtained from the research literature (e.g., Sakai et al. 1999). The tree species were classified into four categories (Table 1) based on their mature height: forest understory (<12.5 m), sub-canopy (12.5 to 27.5 m), canopy (27.5 to 42.5 m), and emergent (>42.5 m). Tree species that grow mainly in canopy gaps were classified in a fifth category (canopy gap species), regardless of their height.

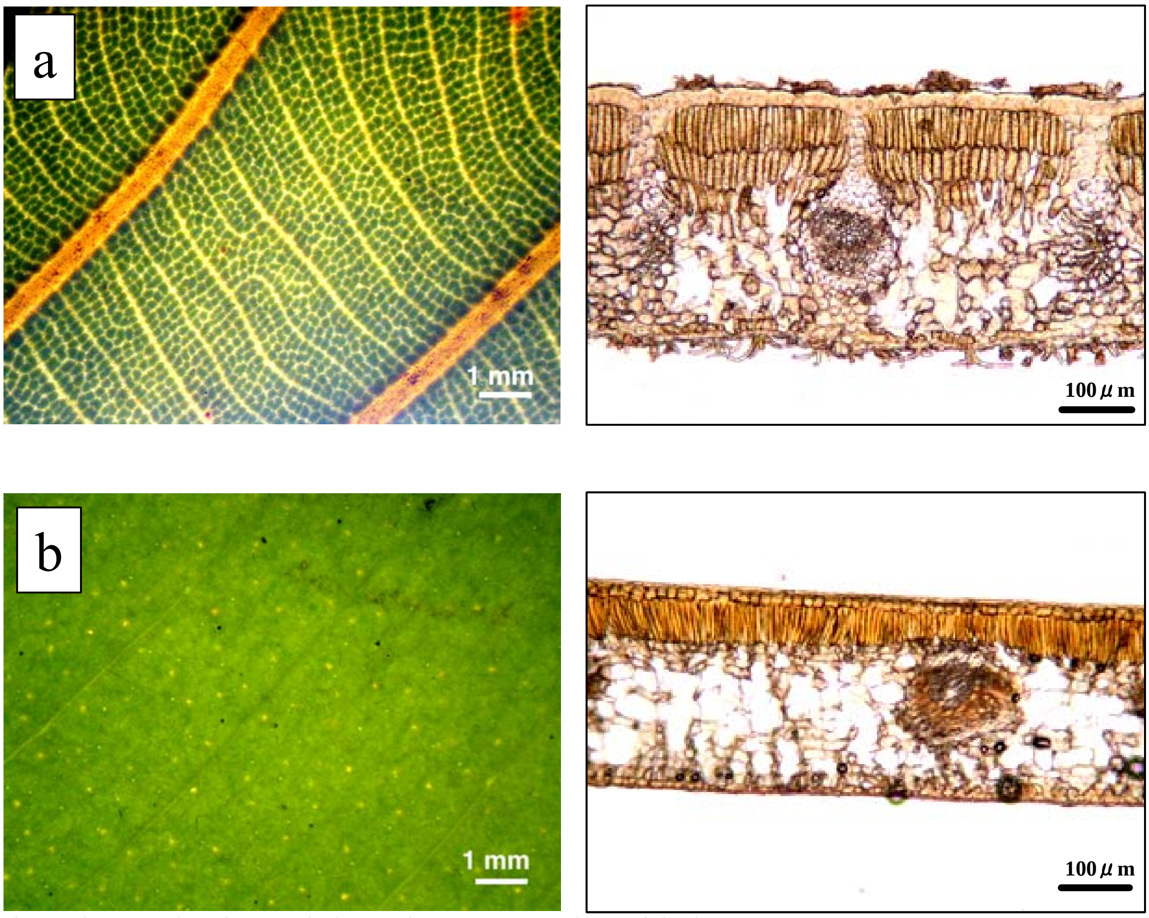


**Fig. 1** Photographs of transmission and transverse sections of the leaves.
a: heterobaric leaf (*Lithocarpus luteus*), b: homobaric leaf (*Eugenia subrufa*)

## Results

In total, 99 species (40% of the total) in 21 families displayed heterobaric leaves, and 151 species (60%) in 36 families had homobaric leaves (Table 1). The proportion of species with each leaf type differed significantly among life form categories ($P < 0.0001$, $\chi^2$ test). The proportion of trees with heterobaric leaves was only 6% for understory species and 17% for sub-canopy species. The proportion increased to 43% for canopy species and reached 96% for emergent species. The proportion in the canopy gap species was also high (62%)

**Table 1** Number of sampled tree species and tree proportion of heterobaric leaf among five life forms

| Life form | No. of heterobaric leaf trees | No. of homobaric leaf trees | Total | Heterobaric leaf ratio (%) |
|---|---|---|---|---|
| Understory | 3 | 46 | 49 | 6.1 |
| Subcanopy | 13 | 65 | 78 | 16.7 |
| Canopy | 23 | 30 | 53 | 43.4 |
| Emergent | 47 | 2 | 49 | 95.9 |
| Canopy gap | 13 | 8 | 21 | 61.9 |
| Total | 99 | 151 | 250 | 39.6 |

We also found a significant relationship between taxonomic group (family) and leaf type ($P < 0.0001$, $df$ =

13, $N$ = 184 species; $\chi^2$ test for 14 families that included more than five species in the family). All species of Dipterocarpaceae, consisting mainly of canopy and emergent trees, were classified as heterobaric (see Kenzo et al. 2007). In contrast, species of Annonaceae and Rubiaceae, which appeared mainly in the forest understory, had only homobaric leaves. However, we found seven families (including the Euphorbiaceae and Sapotaceae) that had both leaf types. Species with different leaf types were found even in the same genus in these families: for example, this was true of genus *Macaranga* in the Euphorbiaceae and genus *Santiria* in the Burseraceae.

## Discussion

The leaf type of a tree species (heterobaric or homobaric) may depend on its life form type in the tropical rain forest. In general, a greater proportion of evergreen tree species than deciduous species tend to have homobaric leaves (Wylie 1952). Nevertheless, upper canopy and gap species, and especially the most emergent species in the tropical rain forest, had heterobaric leaves, even at the small seedling stage (Table 1).

The difference in the distribution of leaf types as a function of mature tree height may be related to the steep microenvironmental gradient along the tree's height that occurs in a forest ecosystem. Under the canopy conditions of a tropical rain forest, tree leaves of emergent and canopy trees suffer strong desiccating conditions as a result of the higher vapor pressure difference (VPD), temperature, radiation, and winds compared with those in the understory layer (Yoda 1978). The presence of BSEs might confer an advantage to heterobaric leaves over homobaric leaves in the high-water-stress canopy environment. BSEs may be responsible for rapid stomatal response to drought signals, such as a reduction of water potential in the mesophyll or a higher concentration of abscisic acid (ABA), as a result of rapid transportation of these signals via the transpiration stream in BSEs (Terashima 1992). BSEs may also support and protect the leaf blade against collapse after severe dehydration or other stresses and may guide sunlight to thicker sun leaves (Nikolopoulos et al. 2002; Terashima 1992). The relatively high proportion of species with heterobaric leaves in the canopy gap and canopy species may also be related to their dry and sunny environment.

Conversely, the understory of a tropical rain forest is more suited to homobaric leaves, which may perform better than heterobaric leaves under shade. Light intensity in the tropical rain forest decreases significantly with decreasing height below the canopy, usually reaching only a few percent of the level of sunlight above the canopy at the forest floor (Yoda 1978). Under such conditions, the leaves of most plants that reproduce in the understory perform better in the shade. A lack of BSEs may improve the leaf's ability to utilize sunflecks because improved lateral $CO_2$ diffusion from shaded to illuminated areas of a homobaric leaf will enhance photosynthesis (Lawson and Morison 2006). Homobaric leaves can also increase their proportion of photosynthetically active leaf area. In a study of BSEs in 31 temperate heterobaric leaf tree species, Nikolopoulos et al. (2002) reported that photosynthetically active leaf area decreased from 91 to 48% as the density of BSEs increased. These characteristics of homobaric leaves could thus contribute to improved photosynthetic efficiency under limited light conditions.

The leaf types (heterobaric or homobaric) were also related to the taxonomic groups (family and genus), which usually reflect differences in life form types or growth habitats at or around maturity. Families that mainly appear in the canopy layer, such as Dipterocarpaceae, tend to have heterobaric leaves. In contrast, families that mainly appear in the forest understory, such as Annonaceae and Rubiaceae, tend to have homobaric leaves (see Kenzo et al. 2007). However, families such as Euphorbiaceae and Sapotaceae, which include tree species with a range of life form types from understory to emergent, included both heterobaric and homobaric species. Furthermore, some genera in these families, such as *Macaranga* (Euphorbiaceae), included species with different leaf types. The leaf type in a single species does not change throughout its growth stages or between individuals (Kenzo et al. 2007). These results suggest that the leaf type in each species depends on the growth habitats or life form types at maturity for each species, and these are, in turn, commonly related to the forest microenvironments at maturity.

In conclusion, we found a clear distribution pattern of the heterobaric and homobaric leaf types with respect to the growth environment and life form type of a species, and with respect to taxonomic groups, in a tropical rainforest. Our results suggest that tropical tree species might have adapted to a spatial gradient at maturity in various physical variables, such as light intensity and VPD, by developing different leaf types (heterobaric or homobaric) that offer different physiological and mechanical advantages.

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