



Title	Differentiation in architecture and demographic properties across forest types and species in tropical lowland Kalimantan
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Citation	北海道大学. 博士(環境科学) 甲第11350号
Issue Date	2014-03-25
DOI	10.14943/doctoral.k11350
Doc URL	http://hdl.handle.net/2115/55482
Type	theses (doctoral)
File Information	Tika_Dewi_Atikah.pdf



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**Differentiation in architecture and demographic properties
across forest types and species in tropical lowland Kalimantan**

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Dissertation submitted to Graduate School of Environmental Science
Hokkaido University
For the Degree of Doctor of Philosophy in Environmental Science

March 2014

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Abstract

Lowland forests in Kalimantan are the most extreme on earth in terms of their vast biomass and tree species diversity. In this region, three forest types are recognized in relation to soil conditions: i.e., heath forest, peat swamp forest, and mixed dipterocarp forest. These forests are unique in terms of physiognomy, canopy architecture, and tree species composition. Heath and peat swamp forests occur on flat topography on nutrient-poor, acidic soils, whereas mixed dipterocarp forest occurs on hilly topography on relatively nutrient-rich alluvial loam soil. These forests are experiencing progressive conversion to palm oil and rubber plantations, and it is essential to evaluate these endangered ecosystems in order to achieve sustainable management. This thesis examines the architectural and functional traits of tree saplings that contribute to regeneration, and the demographic properties of tree populations and their consequences for tree size structure across the three forest types in lowland Kalimantan.

Saplings (150-310 cm tall) of species that represent each forest type were selected under the canopy of developed forest stands. Among these, there was one species found in all forest types and two species in both heath and peat swamp forests. Significant differences in crown allometries were found among forest types and species. Saplings in mixed dipterocarp forest had thicker stems and wider crowns at the same sapling height compared with other forests. They had higher

specific leaf area, higher mass-based leaf nitrogen content and lower wood density. Heath forest saplings showed the lowest leaf nitrogen content and the highest wood density. Species with cross-forest type distribution showed plastic changes in sapling traits, which were similar to inter-specific differences among forest types. The results suggested that saplings showed morphological responses to nutritional and water conditions in the different forest types.

To characterize the dynamics of peat swamp forest, five forest plots of 50 m × 50 m of selective-logged peat swamp forest in Sebangau basin in Central Kalimantan were monitored over a 12-year period. Based on the estimated growth, mortality, and recruitment rates, observed tree size distribution was compared with demographically projected stable size distributions at the levels of plots and species. The deviation between observed and projected size distribution suggested that the forest is still undergoing recovery. Large-statured species tended to have low growth rate, mortality, and recruitment rate, whereas short species showed the opposite demographic properties.

Demographic projection of stable tree size distribution was carried out for the three forest types, based on the censuses of five 1-ha plots in West and Central Kalimantan. Tree-size dependent growth rate and mortality varied across forest types. Heath forest with a dense understory of small trees showed high growth rate and low mortality for small-sized trees, and also high recruitment rate. By contrast, high growth rate and low mortality for large-sized canopy trees, and low recruitment rate characterized mixed dipterocarp forest with a tall and dense canopy layer. Peat

swamp forest showed intermediate demographic properties that fell between the other two. High vigor and productivity of understory trees in heath forest on poor soil were likely due to high light availability underneath the relatively thin canopy layer.

This thesis quantifies the differences in architectural and demographic properties across forest types in lowland Kalimantan, which will help in the prediction of forest dynamics for better conservation and management.

Chapter I

General introduction

Borneo, the third largest island in the world, hosts the richest flora in terms of species richness and diversity, with possibly 10,000 to 15,000 species of flowering plants, including 3000 tree species. The flora of Borneo is 40 times larger than the recorded flora for the whole African Continent (Mackinnon et al. 1996). Most of these species are found in lowland forests (Whitmore 1990). Together with the high alpha diversity within habitat or forest type, beta diversity in relation to habitat types, edaphic conditions and geographic regions contribute to the species diversity of the island (Ashton and Hall 1992, Slik et al. 2009).

Borneo's lowland forests are established on various geomorphologic substrates. Heath forests are found on the coastline and inland, mostly on sandstone plateaus. In Sabah, Brunei, and Sarawak, located in northern and northeastern Borneo, heath forests are usually found on dip topography in hilly landscapes, where sandstone beds lie close to the ground surface (Whitmore 1975). In addition, in Kalimantan, representing western, southern, and eastern Borneo, heath forest is distributed diagonally through the province of Central Kalimantan to East Kalimantan mainly on flat topography (Mckinnon 1996).

Mixed dipterocarp forests are found on hilly topography throughout Borneo with some geographic variation within Borneo in terms of composition and

diversity of tree species (Slik et al. 2009). Dipterocarpaceae and Euphorbiaceae are dominant families, and genera such as *Shorea*, *Syzygium*, *Diospyros*, *Madhuca*, and *Dipterocarpus* predominate in this forest type.

Peat land covers 5.7 million ha in Kalimantan, Indonesian Borneo, with varied depth of peat from shallow (< 50 cm) to extremely deep (800-1200 cm) peat depth (Anonymous 2011a, b). Variation in tree floristic composition is also found in peat swamp forests. The dominant species, which sometimes forms mono-dominant stands in Sarawak, is *Shorea albida*, whereas that in southern Borneo, typically in Central Kalimantan, is *Shorea balangeran*. The same biogeographic history as in mixed dipterocarp forest is likely to contribute to the contrasting floristic composition between northern and southern Borneo.

Different hydrologic and nutritional substrate conditions characterize these three forest types of Borneo lowland forests. Heath forest in southern Borneo typically develops on sandy material originating from granite of the central mountain range, and it is characterized by a podzolic white quartz sand layer with a coarse texture, low water holding capacity, and low soil nitrogen content (Mackinnon et al. 1996, Richards 1996). Peat swamp forest develops on peat deposits originating from wood debris, in which decomposition is repressed by the high level of the water table that spatially and temporally fluctuates around the level of the topsoil surface. Peat soil is characterized by low availability of nutrients and acidic condition caused by humic acid from wood debris, and occasionally by sea-water-origin sulfate in coastal regions (Shepherd et al. 1997, Haraguchi et al. 2000). Similar acidic, brackish water

is also typical in heath forest. In contrast, soil in mixed dipterocarp forest distributed on hilly topography without waterlogged conditions is characterized by sticky red, yellow loam (alluvial koolisols) with high nutrient content compared with the other forest types (Laman and Weiblen 1998, Anonymous 2011a).

Among the three forest types, heath forest develops a short-statured canopy 30-40 m in height, relatively low tree species diversity, and a two (rather than three) storied canopy, low biomass and leaf surface area (Richards 1996, Miyamoto et al. 2003). The canopy structure of peat swamp forest from the edge to the center of a typical peat dome is characterized by decreasing top height, and stem diameter of canopy trees. At the edge of the peat swamp, tree height can reach 50-60 m (Whitmore 1975, Mackinnon et al. 1996). Mixed dipterocarp forest has the highest tree species diversity and the tallest canopy with a scatter of emergent crowns, reaching over 70 m at the present census site in Serimbu forest in West Kalimantan (Kohyama et al. 2003), above a relatively closed canopy layer and also developed subcanopy/understory layers (Whitmore 1975, Richards 1996). Most of the tree species show properties unique to each of these forest types at some stages of their life history (Nishimura and Suzuki 2001, Poorter et al. 2003, Miyamoto et al. 2007, Poorter and Bongers 2006).

The present study examined trees at sapling stage and larger-statured stages. Saplings are an important stage for the successful regeneration of the population, and it is known that seedlings and saplings show morphological properties in response to environmental conditions (Kohyama and Hotta 1990,

Turner et al. 1994, Nishimura and Suzuki 2001); however, sapling performance in terms of architecture and functional traits in these forest types are still unknown.

Meanwhile, at the community level, processes of population dynamics are associated with changes in forest structure and characterize the behavior of forest stands in response to environmental conditions. How trees grow, survive, and recruit in the three forest types, and how these demographic properties are different across forest types are fundamental questions. Growth and mortality of species can vary with resource availability (Chapin 1980). Generally, in severe environmental conditions species have low growth rate and high mortality compared with moderate conditions (Chapin 1980, Valladares et al. 2000). In a Panamanian forest, Wright et al. (2010) showed that the trade-off between growth and mortality is larger in small-sized trees than in large-sized trees, and which is caused by larger variation in light conditions in the forest understory. Similarly, Iida et al. (2014) showed for Malaysia rainforest that the association of fast growth and high mortality was found in the small-size class because of adaptation to variable understory conditions. It is natural to ask how trees respond to variation in edaphic conditions in lowland Borneo. To answer this question, I examined the demographic properties of tree populations in nutrient-deficient and waterlogged conditions and their consequences in tree size structure in each forest type.

In order to better understand the behavior of forest stands based on the architectural and demographic properties of trees, I carried out this forest ecological study in three types of forest in lowland Kalimantan, Indonesia, namely heath, peat

swamp, and mixed dipterocarp forests.

General objectives

To understand the characteristics of lowland forest of Kalimantan, sapling architecture and demographic properties of representative tree species and community-wide forest structure were examined in the three forest types of heath, peat swamp, and mixed dipterocarp forests. The objectives in this dissertation were (1) to quantify inter-specific and across-forest-type variations in sapling architecture and functional traits together with intra-specific response of generalist species to forest type; (2) to characterize abundant species and forest stands of a peat swamp forest using demographic properties based on long-term census records; and (3) to compare tree demographic properties among heath, peat swamp, and mixed dipterocarp forests in relation to their stand structure. Chapter II describes study sites and methods of field research. Chapter III demonstrates how sapling architecture varies across forest types and species. Inter-specific variation in allometry and functional traits of leaves and stem wood was quantified, and also whether or not plastic responses occurred in generalist species. Chapter IV examines tree demographic properties and community structural properties of a peat swamp forest in a developed peat dome of Sebangau basin, Central Kalimantan, by analyzing the records of 12 years of stand dynamics. Chapter V quantitatively compares tree demography among three types of lowland forests in Central and West Kalimantan. Finally, in Chapter VI the results are synthesized according to the present research

objectives; a particular focus is on the reasons for the high abundance of small-sized understory trees in heath forest, suggesting that this layer is maintained by high turnover rate, rather than long residence time in nutrient-poor conditions.

Chapter II

Study area

Description of the study area

The three forest types, i.e. heath, peat swamp, and mixed dipterocarp forests, cover the lowland of Kalimantan, Indonesia. These forests have different characteristics in terms of structure, floristic composition, and physical habitat properties (Mackinnon et al. 1996; Richards 1996).

Study area

The census was conducted in mixed dipterocarp forest in Serimbu, West Kalimantan in November 1992 (Kohyama et al. 2003, T.S. Kohyama unpublished data) (Figure 2.1). Another census was conducted at heath and peat swamp forests at Lahei in Central Kalimantan (Miyamoto et al. 2003), and the third census was carried out in peat swamp forests in Sebangau basin in Central Kalimantan, the last census was of heath and peat swamp forests at Bawan in Central Kalimantan in 2011 and 2012 (Figure 2.1).

The mixed dipterocarp forest was located near Serimbu village, Landak district at 04°5'N110°06'E. The annual mean temperature in Pontianak (capital city of West Kalimantan) is 26.3°C and annual precipitation at Serimbu is 4470 mm year⁻¹ (Suzuki et al. 1997).

The peat swamp forest in the western basin of the Sebangau river was located at 02°32'366" S and 113 °90'274" E – 02 °34'344" E and 113 °88'796" E, about 10 m above sea level. This site belongs to Kereng Bangkirai village, Sebangau sub-district, Palangkaraya district about 20 km southwest of Palangkaraya. The depth of the peat layer in this area varies from 2 m to 10 m. Selective logging had been carried out for approximately the last 30 years (Mirmanto 2010). The annual precipitation in Palangkaraya (capital city of Central Kalimantan) is 4361 mm year⁻¹ with mean annual temperature of 27.5°C.

Another peat swamp forest was located at Bawan village, Banama Tinggang sub-district, Pulang Pisau district about 86 km northeast of Palangkaraya. In the same area, heath forest was also monitored with a shallow humus layer in the same administrative location. The elevations of these forests were approximately 25 m above sea level. The peat layer in this area was 0.5-2 m deep. This area with a thin peat layer was dominated by heath forest, but also had some patches of peat swamp scattered over the area. These peat swamp forests have remained relatively intact compared with the matrix of heath forest, which in contrast has been disturbed frequently by local illegal logging activities.

The Lahei site was situated at 1°55'15" S and 114°10'0" E about 20 m above sea level. The area belongs to Dusun Babungus of Lahei village about 40 km northeast of Palangkaraya. In this area, there are two types of forest: heath and peat forests. A 1-ha plot, called P1, was established in heath forest (Miyamoto et al. 2003, Rahajoe and Kohyama 2003) and another 1-ha plot, P2, was set in peat swamp forest

(Rahajoe and Kohyama 2003). P1 was located about 1.2 km to the west of P2 and several meters higher in altitude.

According to the Schmidt and Ferguson's classification (Whitmore 1975) Kalimantan is type A with mean annual rainfall of about 2900 mm. Mean monthly rainfall is > 300 mm in most months (Figure 2.2).



Figure 2.1 Map of Kalimantan, Indonesian Borneo, showing the research locations: Bawan, Lahei, Sebangau, and Serimbu.

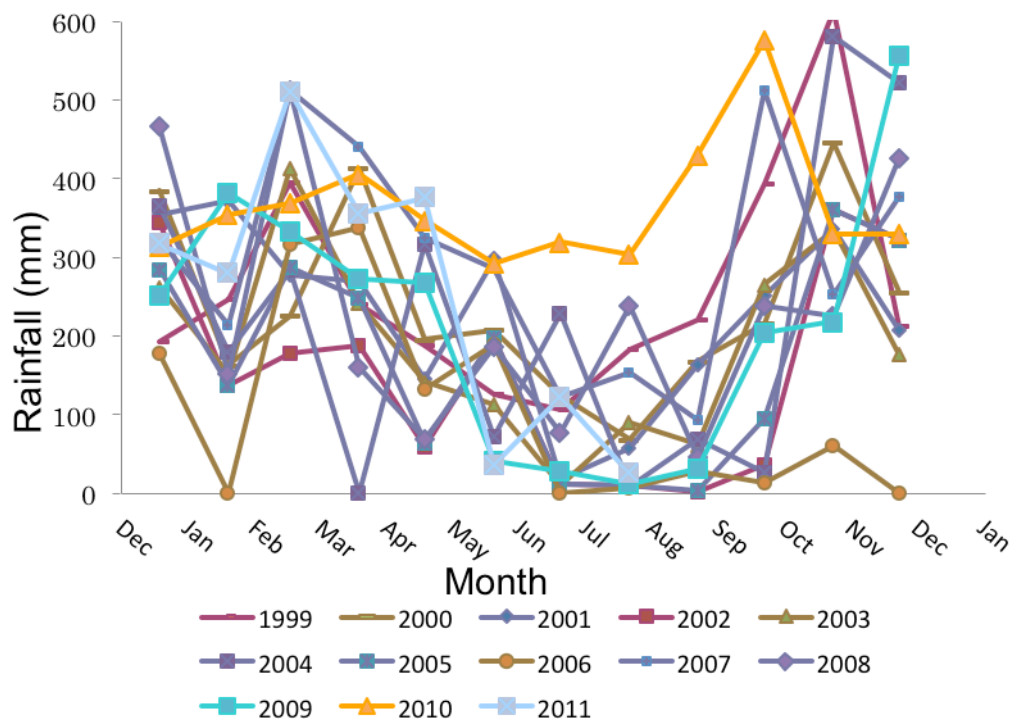


Figure 2.2 Rainfall in Palangkaraya recorded from 1999 to 2011.

Chapter III

Differentiation in architectural properties and functional traits of forest-floor saplings among heath, peat swamp, and mixed dipterocarp forests

Introduction

In lowland Kalimantan, three distinctive forest types; i.e. heath forest, peat swamp forest, and mixed dipterocarp forest, are distributed depending on topographic and edaphic conditions. As described in the general introduction, these three forest types have different characteristics in terms of forest structure, soil development, and water conditions. Trees in heath forest usually develop small-sized, thick, scleromorphic leaves that are relatively tough and hard (Richards 1996). Leaves from heath forest trees show low specific leaf area (SLA) with low mass-based nitrogen (Turner et al. 2000) and low phosphorus content (Moran et al. 2000). Chapin (1980), Jordan (1982), and Turner (1994) mention that sclerophylly is associated with long lifespan of leaves. Under nutrient-deficient conditions, the increase in leaf longevity generally contributes to maintain leaf nutrients for a long period (Reich et al. 1992). Poorter and Bongers (2006) reported that species with short leaf lifespan tended to have high SLA and high nitrogen concentration per unit leaf area. As a consequence, they have high assimilation rates per leaf area (Reich et al. 1992).

The sapling stage is an important part of the life history of trees. In this

stage, trees can show different morphological properties from those in later stages. Sapling properties can vary in response to forest environment, and in relation to inter-specific differentiation in regeneration strategy (Kohyama 1987, Kohyama and Hotta 1990).

Morphological properties of tree crowns are usually demonstrated with allometric relationships, i.e. power functions between tree crown dimensions. Allometric studies of tree architecture in these forest types of Indonesian lowland forests have been carried out previously (Kohyama and Hotta 1990, Nishimura and Suzuki 2001, Miyamoto et al. 2007, Kohyama et al. 2003). Nishimura and Suzuki (2001) examined the above- and below-ground morphology of seedlings (12–19 cm tall) in heath and peat swamp forests in Central Kalimantan. Whereas, Miyamoto et al. (2007) reported that trees ≥ 5 cm in stem diameter in heath forest tended to have slender stem shapes and small crown sizes up to about 10 m tall compared with those in mixed dipterocarp forests, but there is no information on sapling architecture in these forest types. Growth in stem diameter and height is correlated with soil fertility (Ashton and Hall 1992). On fertile soil such as that in mixed dipterocarp forest, subcanopy tree species are more abundant and the forest captures a large proportion of light in the subcanopy layer (Coomes et al. 2009).

Despite the above studies, morphological responses of sapling to such conditions as limited water, heat load, and nutrient deficiency have not been examined so far. It could be expected that saplings on fertile soil will have thicker stems with wider crowns at the same height as well as higher SLA and nitrogen

content of leaves than species on infertile soil, as represented by heath forest. Species in peat swamp forest are expected to show intermediate tree-architecture properties and functional traits compared with mixed dipterocarp and heath forests. Besides inter-specific differentiation across forest types, inter-specific variation in allometric and functional traits at sapling stage can also be expected, such as within-forest differentiation between pessimistic strategies for better persistence in deep shade and an optimistic strategy showing an expected change towards better light conditions in the near future (Kohyama 1987).

In this study, I examined these predictions across forest types, paying attention to the degree of inter-specific variation within each forest type by analyzing crown allometry and other morphological-functional traits in the sapling stage. The architecture of saplings of abundant species was analyzed in the three forest types in Central and West Kalimantan, Indonesia, where full forest-level tree community structure analysis was also carried out based on an ordinary census of trees larger than 5 cm in stem diameter, at the scale of 1-ha plots.

A clear separation in species assembly was observed across forest types, with the exception of overlap of a few species that provided an opportunity to examine possible intra-specific variation in response to environments. Therefore, attention was paid to the question of whether or not within-species plastic response in sapling traits to forest types was related to community-level response to forest types via inter-specific variation. The present results were addressed in the context of the whole life history of tree species over forest types of Indonesian lowland forests.

Materials and methods

Study sites

This study was conducted in tropical lowland forests in Kalimantan, Indonesia. The site for typical mixed dipterocarp forest was set on Berui mountain, Serimbu village, Air Besar subdistrict, Landak district, West Kalimantan (0°45'N 110°06'E) in November 1992, where tree community structure and dynamics have been examined using a census of two 1-ha plots (Kohyama et al. 2003). Sapling censuses were set up around these plots, with an elevation of around 250 m above sea level. The sites for heath and peat swamp forests were set in Bawan village, Pulang Pisau district in February 2011, located about 86 km northeast from Palangkaraya, the Provincial Capital of Central Kalimantan. These sites are located at 01°35'S and 113°59'E (heath forest), and 01°36'S and 114°00'E (peat swamp forest). The elevation of these sites is approximately 25 m above sea level. Most of these sites are covered by heath forest, whereas some patches of peat swamp forest are scattered around. Peat swamp forest has been kept relatively intact compared with heath forest, which had experienced frequent disturbance by illegal logging.

The site of the mixed dipterocarp forest was characterized as follows. The annual mean temperature at Pontianak (Provincial Capital of West Kalimantan) is 26.3°C and annual precipitation at Serimbu village is 4470 mm year⁻¹ (Suzuki et al. 1997). For heath and peat swamp forests, the annual precipitation in Palangkaraya is 4361 mm year⁻¹ with mean annual temperature of 27.5°C (Anonymous 2011b).

Sapling dimensions

Saplings of 150-310 cm top height of 45 tree species by forest-type, which represent the tree community of each forest type around the plots (Table 3.1), were selected under the closed canopy of mature stands. Four to five individual saplings without any visible sign of breakage or re-sprouting were selected for each species. The total number of samples was 200 individuals. Among the 45 species-by-type that were examined (10 species from heath forest, 10 species from peat swamp forest, and 25 species from mixed dipterocarp forest), one overlapping species, *Neoscortechinia kingii*, occurred in all locations, and two species, *Calophyllum calcicola* and *Shorea teysmanniana*, were sampled both in heath and peat forests; therefore, the net number of species was 41 (Table 3.1).

The following dimensions were measured (Table 3.2): total height of saplings above the ground surface, height of the lowest foliage, crown width (the geometric mean of two perpendicular horizontal crown widths including the maximum one), and stem diameter at 1/10 of top height (geometric mean of two perpendicular diameters). All measurements were made using a tape measure, with measurements to the nearest 1 mm, except for stem diameters, which were measured using digital calipers to the nearest 0.1 mm.

To quantify sapling functional traits, stem wood was sampled at pole stage and the lamina of leaves from each sapling sample. Two to five leaves were collected per sample to measure lamina area and nitrogen content per dry mass of leaves (or leaflets in the case of compound-leaved species), from the mid portion of a leafy

branch (located in the mid portion of the leafy crown). Wet mass of lamina samples was measured using a small portable electric balance in the field, and oven-dried mass and leaf nitrogen content per leaf dry mass, or nitrogen per mass of lamina samples, in the plant ecology laboratory of Herbarium Bogoriense, West Java, after samples were air dried in the field. The area of fresh lamina was determined by tracing the leaf in the field and scanning the image in the Plant Ecology Laboratory, Hokkaido University using ImageJ 1.37 software (<http://rsbweb.nih.gov/ij/>). SLA was obtained as the quotient of lamina area over leaf oven-dried mass of samples for each individual. Water content of the lamina was defined as $[\text{fresh mass} - \text{dry mass}]/[\text{dry mass}]$. To represent each individual, the arithmetic mean of leaf samples was calculated.

Wood density

Wood density of the sampled species was estimated from independent sampling of larger saplings. Samples for 25 species from mixed dipterocarp forest were collected at the same site as sapling measurements in Gunung Berui, of which the details have been reported by Suzuki (1999), whereas those for each of the 10 species from heath and peat swamp forests were obtained in January 2012 at the same site as sapling measurements in Desa Bawan. One to four individuals with a stem diameter of about 5 cm at stem base (ca. 5 to 7 m top height) were cut at the stem base; a stem disk sample of 2 cm length was obtained from the base position. Wood density was obtained from the oven-dried mass of sampled stems divided by the fresh volume,

where the fresh volume was determined by the procedure of volume replacement by water (Suzuki 1999). Volume and fresh mass of wood samples were determined in the field, whereas the oven-dried mass was obtained in the plant ecology lab of Herbarium Bogoriense. Species by forest-type trait measures were determined as the arithmetic mean of each individual sample.

Data analysis

Allometric relationships were analyzed between sapling dimensions to quantify the difference in sapling architecture among three forest types (species aggregated) and among 45 species-by-forest types. Three allometries were examined: top height versus stem diameter, height versus crown width, and height versus crown depth, (where crown depth was top height minus the height of the lowest foliage; Kohyama and Hotta 1990). Top height, crown width, and crown depth were log transformed before linear regression. The standardized major axis method was used for analysis across forest and inter-specific comparison of regression lines, and ANCOVA-type analysis was carried out using SMATR (Warton et al. 2012) on R 2.15.2 (R Development Core Team 2012). Major axis regression was used because architectural dimensions for allometric analysis are inter-dependent, and also because the purpose of this analysis was not to estimate one dimension from another but to characterize their inter-relationships. Functional traits were compared among forest types using Kruskal–Wallis test. Multivariate analysis of functional traits and architecture properties was analyzed using ordinary principal components analysis

(PCA).

Results

Three allometric properties were quantified that characterized the crown architecture of saplings across forest types and across species. The three allometric relationships did not show significant differences ($P > 0.05$) in allometric coefficients (i.e. the slope of log-log linear regression) among forest types (Table 3.3). The allometric coefficient was similar for each allometric relationship among species-by-site in allometric coefficients without significant differences (Table 3.4). The exception was for the stem diameter versus height relationship for 13 species (Table 3.4). For the convenience of quantifying species allometric traits for PCA, the model was applied with common allometric coefficients (Kohyama and Hotta 1990). The allometric constants (i.e. the intercepts of log-log linear regression) were markedly under the common allometric coefficient variations among forest types and among species (Figure 3.1, Tables 3.3 and 3.4).

At any given height, saplings in mixed dipterocarp forest had thicker stems and wider crowns than other forest types, whereas saplings in heath forest had the slenderest stems, but there was no difference between heath and peat swamp forests in terms of crown width at a given sapling height. Allometries between height and crown depth dimensions did not show differences among the three forest types for allometric constants (Table 3.3). At a given height, species of mixed dipterocarp forest had thicker stems (most emphasized in *Diospyros* sp. '*trinerve*') as well as

wider crowns (cf. *Shorea pauciflora*), whereas species from heath forest showed the slenderest stems (cf. *Hopea ferruginea*) among all species.

SLA of saplings was higher in mixed dipterocarp forest and peat swamp forest than heath forest (Table 3.5). In contrast, leaf nitrogen content per leaf dry mass, or N per mass, showed significant differences among the three forest types. The highest leaf nitrogen per mass was found in mixed dipterocarp forest followed by peat swamp forest, and the lowest was in heath forest (Figure 3.2a, Table 3.5). On the other hand, the water content of leaf lamina was significantly higher in peat swamp forest, whereas there was no significant difference between mixed dipterocarp forest and heath forest (Table 3.5).

In terms of stem traits, heath forest had higher wood density and mixed dipterocarp forest had lower wood density (Figure 3.2b, Table 3.5). Wood water content showed no difference across forest types (Table 3.5), but stems of wetland forests showed higher water content (Figure 3.2b)

Results of PCA analysis among 45 species by forest type with allometric constant terms of three allometric functions, leaf functional traits (SLA, nitrogen per mass and water content), and wood functional traits (wood density and water content) showed that the first principle component (explaining 36% of the total variance) was negatively correlated with stem diameter and crown width at a given height, SLA, and foliar nitrogen per mass, and was positively correlated with wood density. The second principle component (explaining 19% of the total variance) was negatively correlated with crown depth at a given height and was positively

correlated with water content in leaf lamina and stem wood (Figure 3.3a). On the plane of the first two principle components, heath forest was categorized by high wood density and peat swamp forest was categorized by higher water content (Figure 3.3b). Mixed dipterocarp forest was characterized by high SLA, foliar nitrogen per mass, stem diameter, and crown width relative to sapling height (Figure 3.3b).

The difference in crown architecture and functional traits among species within forest type is also demonstrated in Figure 3.3b. There was a wider inter-specific variation in peat swamp forest than in heath forest. Two species in peat swamp forest, *Syzygium castaneum* and *Xanthophyllum ellipticum*, showed different trends from other species and dominated, as emphasized by high wood density (Figure 3.3b). Whereas in heath forest, *Stemonurus secundiflorus* showed higher leaf water content than other species (Figure 3.3b), because *S. secundiflorus* was found in relatively wet sites in heath forest.

For species with cross-forest-type distribution *N. kingii* in mixed dipterocarp forest had thicker stems, wider crown width, higher SLA, and higher nitrogen per mass than those of the other two forest types (Figure 3.3b). *N. kingii* in heath forest showed the smallest SLA, and the slenderest stems had the lowest leaf water content compared with those in mixed dipterocarp and peat swamp forests. The two species in common between heath and peat swamp forests, *C. calcicola* and *S. teysmanniana*, showed smaller SLA, lower nitrogen per mass, and lower water content in heath forest than in peat swamp forest (Figure 3.3b).

Discussion

In this study, crown architecture and functional traits of leaves and stem wood were compared across three forest types of tropical lowland forests in Kalimantan. As expected, it was found that morphological properties at the sapling stage varied among forest types and among coexisting species within the forest tree community. A few species that occurred across forest types showed plastic changes in morphological performance, and these intra-specific changes were in accordance with the observed community-level differences among forest types. The adaptive significance of the detected variation in crown architecture and functional properties at sapling stage among forest types and among coexisting species within forest type are discussed below, with particular attention to comparison with current knowledge on other ontogenetic stages.

Examined saplings showed inter-specific differentiation of constant terms but not allometric coefficients or the power term of the power functions between tree dimensions (top height, basal stem diameter, crown width, and crown depth). The same tendency has been reported in previous studies on tropical rain forests (King 1990, Kohyama and Hotta 1990) and in Japanese warm-temperate rain forest (Kohyama 1987). Furthermore, the same tendency, i.e. allometric constant differentiation with common allometric coefficients, was found among forest types. Turner et al. (1995) compared allometric relationships of understory saplings between tropical rain forest, tropical mangrove forest, and warm-temperate rain forest, and they suggested similar patterns to the present study. When the log-log

linear relationship of allometry between dimensions is differentiated with respect to time, the difference in the allometric constant disappears and the allometric coefficient represents the ratio between the relative growth rates of the two dimensions. Therefore, it is suggested that inter-specific, as well as across-forest variation, tends to be determined only by the small-sized individuals (as the integration constant). In other words, there is a strong morphological constraint for tree saplings to share a general rule of keeping the ratio between relative growth rates of dimensions unchanged through size increment, regardless of species and forest types. Saplings analyzed in the present study showed similar performance to larger trees (up to 10 m tall) in height versus stem diameter relationship (Miyamoto et al. 2007). Stem diameter at the same tree height was consistently larger in mixed dipterocarp forest than in heath forest in understory up to about 10 m. In contrast, stem diameter tended to be smaller in mixed dipterocarp forest with a large exposed canopy and emergent trees. Saplings in mixed dipterocarp forest were also characterized by wide crowns for foraging light resources over a wide area. Sterck et al. (1999) suggested that wide crowns were advantageous for survival in the understory because of higher foraging efficiency. King (1990) mentioned that saplings with wide crowns showed thick stems and vice versa.

Compared with heath and peat swamp forests, most of the species in mixed dipterocarp forest had larger SLA as an adaptive response for light capturing and carbon gain in light-limited conditions. Leaves in heath forest tended to have smaller SLA compared with those in peat swamp and mixed dipterocarp forests

(Table 3.5), with a significant difference only detected between leaves in mixed dipterocarp and heath forests. This result was consistent with the SLA of seedling leaves (Nishimura and Suzuki 2001) and tree leaves (Turner et al. 2000, Rahajoe and Kohyama 2003, Miyamoto et al. 2007). A cross-stage common tendency for small SLA in heath and peat swamp forests can be suggested to be an adaptive response to low nutrient conditions or adaptation to reduce water loss (Medina et al. 1990, Richards 1996). Leaf nitrogen content per mass showed a significant difference across forest types (Table 3.5). Turner (1994) showed that nitrogen content in heath forest was lower than that in mixed dipterocarp forest. Low SLA and low nitrogen per mass were associated with high leaf longevity (Reich et al. 1991, 1992). Saplings with high longevity need to expend construction costs for protection against herbivores, pathogens, and physical damage (Turner 1994) and for the sake of saving limited resources (Shiodera et al. 2008).

The water content of leaves and stem wood showed variations among forest type and species (Figure 3.2b, Table 3.5). Saplings in peat swamp forest showed higher water content, especially in leaves, compared with those in mixed dipterocarp and heath forests. Waterlogged conditions with high pH due to humic acid cause high leaf water potential, which causes reduced transpiration rate (Jackson et al. 1977). In peat swamp forest, waterlogged soil with acidic water induces physiological responses in saplings to reduce transpiration (Chapin 1991). Waterlogged conditions are also associated with thick laminae and stomata closure (Meinzer et al. 1992).

Wood density at pole stage showed variation across forest types (Figure 2b). It was found that among the three forest types, wood density in heath forest was the highest, which is in accordance with the findings of Slik et al. (2009). Wood density was correlated with stem performance (King et al. 2006, Iida et al. 2012). Tree species with high wood density tend to have the slenderest stems, and vice versa.

Furthermore, this study found intra-specific variation in species distributed between forest types. *N. kingii*, *C. calcicola*, and *S. teysmanniana* showed morphological variations in response to forest conditions. The plastic response in architecture was also reported at seedling stage (Nishimura and Suzuki 2001). They showed that seedlings of *Canarium* sp. in peat swamp forest develop a lateral root system to escape from submergence in anaerobic conditions, whereas seedlings of the same species in heath forest develop a deep root system to absorb water.

The findings from this study suggest that saplings show morphological differences across forest types that are characterized by hydrologic and nutritional conditions, providing a possible hypothesis for the community-wide response to different environments. Habitat-specialist species shared common architectural and functional performance to the forest type, and habitat-generalist species showed corresponding plastic changes in response to forest types.

Table 3.1 Population properties of tree density and basal area for trees ≥ 5 cm stem diameter at breast height of examined species in three forest types in lowland Kalimantan.

Species	Family	Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)
Heath forest				
<i>Calophyllum calcicola</i> P.F. Stevens	Clusiaceae	Cch	456	2.96
<i>Hopea ferruginea</i> Parijs	Dipterocarpaceae	Hf	211	1.39
<i>Ternstroemia aneura</i> Miq.	Theaceae	Ta	162	1.68
<i>Mangifera swintonioides</i> Kosterm.	Anacardiaceae	Ms	78	0.03
<i>Neoscortechinia kingii</i> Pax & K. Hoffm.	Euphorbiaceae	Nkh	58	1.18
<i>Shorea rugosa</i> F. Heim	Dipterocarpaceae	Sr	58	2.71
<i>Stemonurus secundiflorus</i> Blume	Icacinaceae	Ss	51	0.70
<i>Shorea atrinervosa</i> Symington	Dipterocarpaceae	Sa	48	0.30
<i>Tristaniopsis merguensis</i> (Griff.) Peter G. Wilson & J. T. Water house	Myrtaceae	Tm	38	0.74
<i>Shorea teysmanniana</i> Dyer ex Brandis	Dipterocarpaceae	Sth	7	0.17
Peat swamp forest				
<i>Calophyllum calcicola</i> P.F. Stevens	Clusiaceae	Ccp	427	5.85
<i>Palaquium leiocarpum</i> Boerl.	Sapotaceae	Pl	192	2.28
<i>Palaquium ridleyi</i> King & Gamble	Sapotaceae	Pr	162	2.56

Table 1. (Continued)

Species	Family	Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)
<i>Garcinia vidua</i> Ridl.	Clusiaceae	Gv	162	1.43
<i>Xanthophyllum ellipticum</i> Korth. Ex Miq.	Polygalaceae	Xe	89	1.10
<i>Dactylocladus stenostachys</i> Oliv.	Melastomataceae	Ds	76	1.20
<i>Shorea teysmanniana</i> Dyer. ex Brandis.	Dipterocarpaceae	Stp	71	2.44
<i>Syzygium castaneum</i> (Merr.) Merr. & L.M.Perry	Myrtaceae	Sca	49	0.71
<i>Horsfieldia crassifolia</i> Warb.	Myristicaceae	Hc	47	0.21
<i>Neoscortechinia kingii</i> Pax & K. Hoffm.	Euphorbiaceae	Nkp	4	0.03
Mixed dipterocarp forest				
<i>Dryobalanops beccarii</i> Dyer	Dipterocarpaceae	Db	23.5	8.30
<i>Pimelodendron griffithianum</i> (M. A.) Benth.	Euphorbiaceae	Pg	17.5	0.44
<i>Strombosia ceylanica</i> Gardner	Olacaceae	Sc	16	0.45
<i>Hopea</i> cf. <i>dryobalanoides</i> Miq.	Dipterocarpaceae	Hd	13	0.55
<i>Amyxa pluricornis</i> (Radlk.) Domke	Thymelaeaceae	Ap	11	0.27
<i>Chionanthus</i> cf. <i>cuspidatus</i> Blume	Oleaceae	Cc	11	0.21
<i>Mallotus penangensis</i> Müll. Arg.	Euphorbiaceae	Mp	10.5	0.12
<i>Elateriospermum tapos</i> Blume	Euphorbiaceae	Et	9	0.50
<i>Shorea quadrinervis</i> Slooten	Dipterocarpaceae	Sq	9	0.76

Table 1. (Continued)

Species	Family	Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)
<i>Shorea parvifolia</i> Dyer	Dipterocarpaceae	Sp	9	0.65
<i>Neoscortechinia kingii</i> (Hook. F.) Pax. & Hoffm.	Euphorbiaceae	Nk	8.5	0.20
<i>Scaphium macropodium</i> Beumee ex K. Heyne	Sterculiaceae	Sm	7.5	0.38
<i>Macaranga brevipetiolata</i> Airy Shaw	Euphorbiaceae	Mb	7	0.08
<i>Shorea multiflora</i> (Burck) Symington	Dipterocarpaceae	Smu	7	0.48
<i>Shorea pauciflora</i> King	Dipterocarpaceae	Spa	5.5	0.95
<i>Fordia splendidissima</i> (Blume ex Miq. J. R. M.) Buijsen subsp.	Leguminaceae	FsS	5	0.04
<i>Splendidissima</i> (Miq. J. R. M.) Buijsen				
<i>Canarium littorale</i> Blume	Burseraceae	Cl	4.5	0.09
<i>Shorea parvistipulata</i> F. Heim	Dipterocarpaceae	Spr	4.5	1.55
<i>Palaquium oxleyanum</i> Pierre	Sapotaceae	Po	4.5	0.37
<i>Aglaia forbesii</i> King	Meliaceae	Af	3.5	0.08
<i>Knema stenophylla</i> (Warb.) J. Sinclair subsp. <i>Longipedicellata</i> (J. Sinclair) W. J. de Wilde	Myristicaceae	KsL	3	0.14
<i>Shorea mecistopterix</i> Ridl.	Dipterocarpaceae	Sme	1.5	0.13
<i>Eusideroxylon zwageri</i> Teijsm. & Binn.	Lauraceae	Ez	1.5	0.03
<i>Diospyros</i> sp. 'trinerve'	Ebenaceae	Dt	1	0.01

Table 3.2 Architectural dimensions and functional traits of tree saplings.

Dimensions and traits	Symbols	Units
Top height	H	cm
Stem basal diameter	D	cm
Crown width	Cw	cm
Crown depth	Cd	cm
Specific leaf area	SLA	cm ² g ⁻¹
Leaf nitrogen content per mass	N per mass	mg g ⁻¹
Water content of leaf lamina	Wl	g g ⁻¹
Wood density	Wd	g cm ⁻³
Wood water content	Wc	g g ⁻¹

Table 3.3 Difference among forest types in allometric relationships, $\ln y = \alpha \ln x + \beta$, between selected pairs (x, y) of sapling dimensions.

Significant differences among traits are indicated by different superscript letters at $P < 0.05$, and ^{NS} for not significant at $P > 0.05$.

Dimensions x - y	Specific α			Common α	Specific β		
	Heath	Peat swamp	Mixed dipterocarp		Heath	Peat swamp	Mixed dipterocarp
Height–Stem diameter	1.433 ^{NS}	1.47 ^{NS}	1.46 ^{NS}	1.45	–3.41 ^a	–3.35 ^b	–3.25 ^c
Height–Crown width	1.88 ^{NS}	1.73 ^{NS}	1.52 ^{NS}	1.66	–2.05 ^a	–2.03 ^a	–1.80 ^b
Height–Crown depth	3.08 ^{NS}	3.17 ^{NS}	3.03 ^{NS}	3.07	–5.22 ^a	–5.23 ^a	–5.20 ^a

Table 3.4 Inter-specific difference in allometric relationships, $\ln y = \alpha \ln x + \beta$, between selected pairs (x, y) of sapling dimensions with the common α values of 1.1 (Height–Stem diameter), 1.25 (Height–Crown width), and 2.7 (Height–Crown depth).

$x - y$	Height–Stem diameter		Height–Crown width		Height–Crown depth	
Code	Specific α	Specific β	Specific α	Specific β	Specific α	Specific β
Heath forest						
Cch	0.89*	–2.63	1.74	–1.15	0.92	–4.21
Hf	0.94*	–2.71	0.98	–0.96	2.25	–4.33
Ms	0.91	–2.63	–0.56	–1.12	–3.60	–4.56
Nkh	1.04*	–2.52	1.34	–1.09	3.19	–4.48
Sa	1.34	–2.65	4.08	–1.13	2.87	–4.35
Sr	0.98	–2.58	–1.57	–1.02	4.67	–4.37
Sth	0.96*	–2.68	0.97	–1.07	1.86	–4.43
Ss	1.17	–2.56	1.72	–1.24	–3.12	–4.51
Ta	1.30*	–2.53	0.70	–1.10	0.77	–4.40
Sm	1.65	–2.65	2.07	–1.10	2.44	–3.97
Peat swamp forest						
Ccp	1.05*	–2.63	1.57*	–1.15	2.67*	–4.16
Ds	0.65	–2.50	–2.05	–1.16	6.22	–4.26
Gv	1.55*	–2.56	2.23	–1.06	3.55	–4.38

Table 3.4 (Continued)

$x - y$	Height–Stem diameter		Height–Crown width		Height–Crown depth	
Code	Specific α	Specific β	Specific α	Specific β	Specific α	Specific β
Hc	0.45	–2.45	0.87	–0.98	3.63	–4.74
Nkp	1.56	–2.49	0.87	–1.12	1.97	–4.38
Pr	0.40	–2.44	0.90	–1.27	3.75	–4.59
Pl	1.42	–2.57	1.19	–1.00	–4.27	–4.55
Stp	1.03	–2.55	1.12	–0.94	4.09*	–4.23
Sca	1.20*	–2.56	–2.48	–1.14	2.43	–4.28
Xe	0.44	–2.63	0.88*	–0.99	3.83*	–4.26
Mixed dipterocarp forest						
Af	0.75	–2.39	2.19	–0.74	4.95	–4.32
Ap	1.02*	–2.47	0.51	–0.86	1.17	–4.23
Cl	1.25	–2.42	1.19	–0.96	1.13	–4.49
Cc	1.40*	–2.48	0.79	–0.92	1.87	–4.40
Dc	3.32	–2.40	1.83	–0.95	10.06	–4.44
Dt	1.67	–2.35	1.60	–0.88	1.66	–4.35
Db	1.23	–2.42	0.84	–0.82	0.54	–4.32
Eb	1.04*	–2.49	1.81	–0.82	2.94*	–4.16
Ez	1.29*	–2.40	1.06	–0.77	2.29	–4.26

Table 3.4 (Continued)

$x - y$ Code	Height–Stem diameter		Height–Crown width		Height–Crown depth	
	Specific α	Specific β	Specific α	Specific β	Specific α	Specific β
FsS	1.04	–2.42	1.49	–0.99	4.25	–4.33
Hd	1.71	–2.43	3.93	–0.85	–6.24	–4.30
KsL	1.75	–2.37	2.63	–0.91	3.65	–4.32
Mb	1.93	–2.48	–1.96	–0.95	3.46	–4.39
Mp	1.87	–2.45	1.75	–0.92	1.65	–4.15
Nk	1.33	–2.45	1.83	–0.87	–1.29	–4.23
Po	1.03	–2.46	1.11	–0.89	1.15	–4.24
Pg	2.48	–2.51	3.44	–1.01	11.62	–4.43
Sm	0.78	–2.39	0.59	–0.92	0.95	–4.49
Sme	0.99	–2.37	0.33	–0.94	–1.97	–4.41
Smu	0.64*	–2.49	1.31	–0.88	2.37*	–4.33
Sp	1.41	–2.42	2.35*	–0.76	5.03	–4.37
Spr	0.82	–2.45	1.28	–0.89	4.05	–4.39
Spa	0.95	–2.42	1.19*	–0.73	1.74	–4.33
Sq	1.21	–2.50	1.79*	–0.8	–1.34	–4.59
Sc	2.40	–2.37	–3.83	–0.88	–4.92	–4.45

F Assuming equivalent α across species and forests.

* Significant difference at $P < 0.05$.

Table 3.5 Mean \pm standard deviation of species-specific functional traits for each forest type.

Functional traits	Heath		Peat swamp		Mixed dipterocarp	
SLA ($\text{cm}^2 \text{g}^{-1}$)	102	$\pm 37^a$	139	$\pm 37^{ab}$	161	$\pm 27^b$
Leaf nitrogen content (mg g^{-1})	10.9	$\pm 2.3^a$	13.1	$\pm 2.0^b$	18.6	$\pm 3.5^c$
Leaf water content (g g^{-1})	0.349 ± 0.063^a		0.475 ± 0.081^b		0.414 ± 0.677^a	
Wood density (g cm^{-3})	0.702 ± 0.101^a		0.667 ± 0.186^{ab}		0.578 ± 0.126^b	
Wood water content (g g^{-1})	0.481 ± 0.110^a		0.502 ± 0.150^a		0.403 ± 0.065^a	

Significant differences between forest types are indicated with different superscript letters ($P < 0.05$, Kruskal–Wallis test).

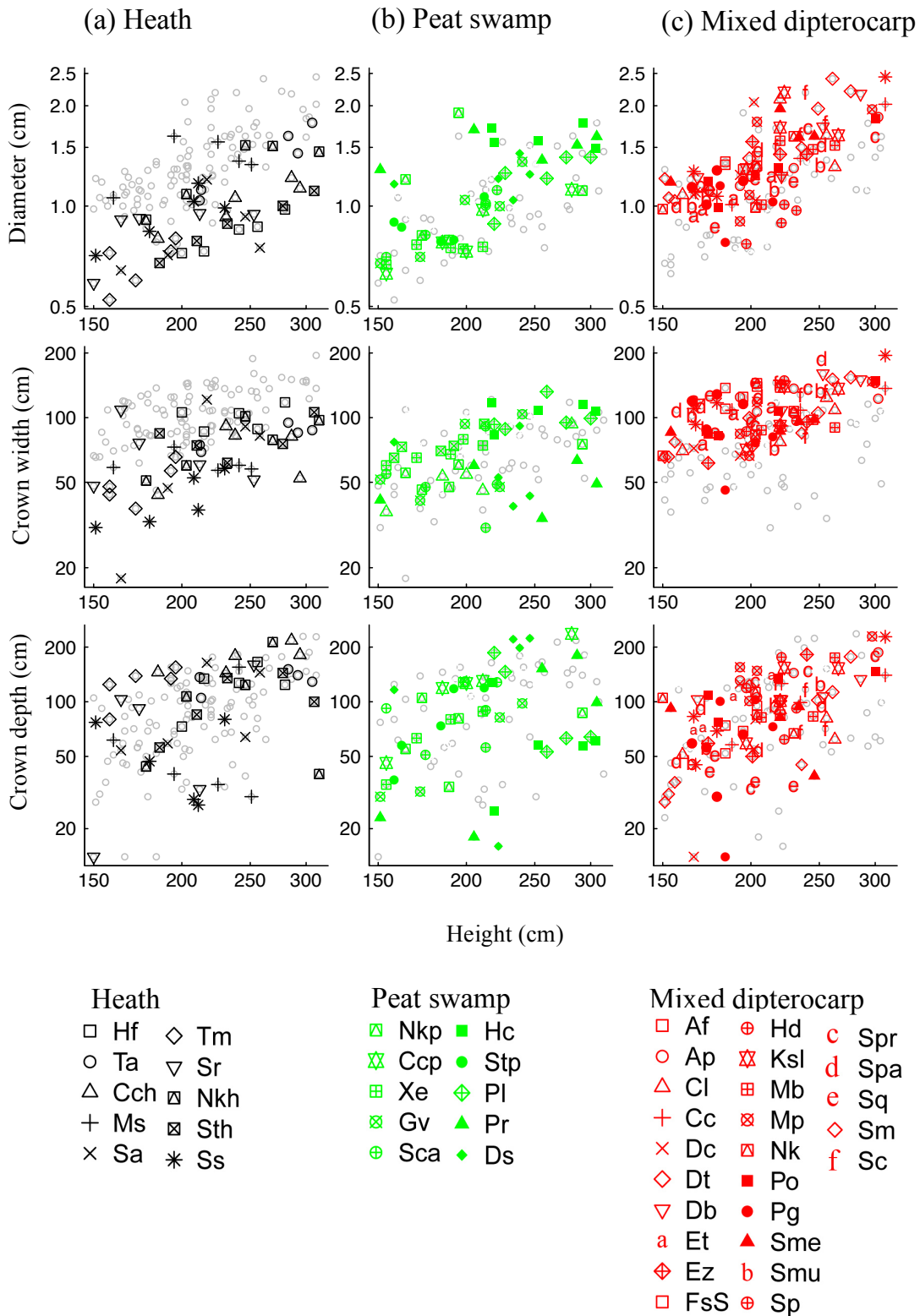


Figure 3.1 Observed relationships among tree sapling dimensions for allometric analysis. All axes are log-scaled. Species in the forest of interest are in black symbols, whereas those in others are in grey. Symbols correspond to the species within each forest type.

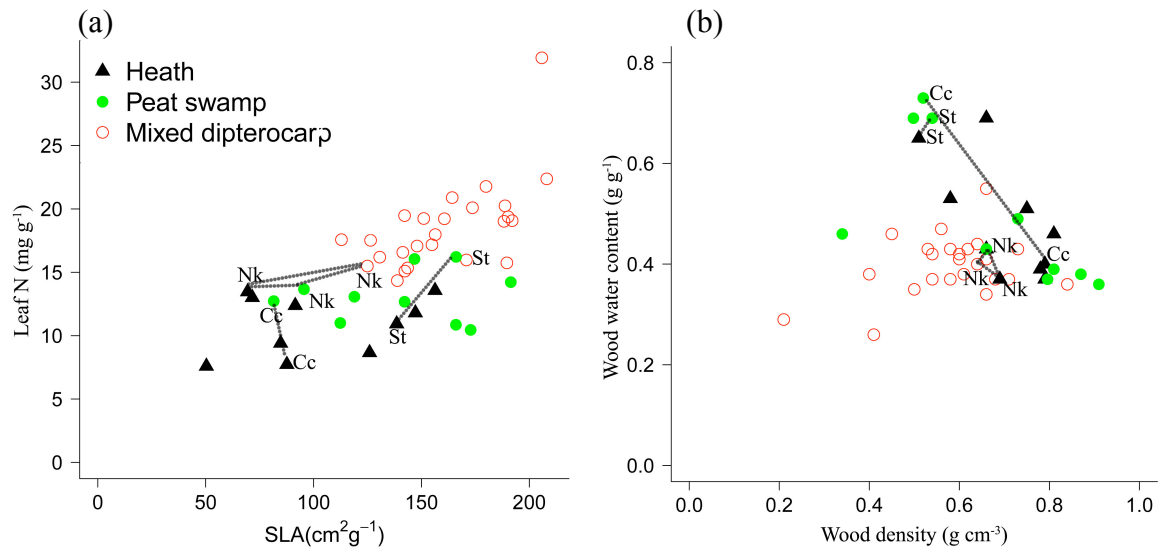


Figure 3.2 Distribution of species for functional traits in (a) leaves and (b) stem wood. The three forest types are shown with different symbols, and shared species across forest types (Nk, *Neoscortechinia kingii*; Cc, *Calophyllum calcicola*; St, *Shorea teysmanniana*) are connected by dashed lines.

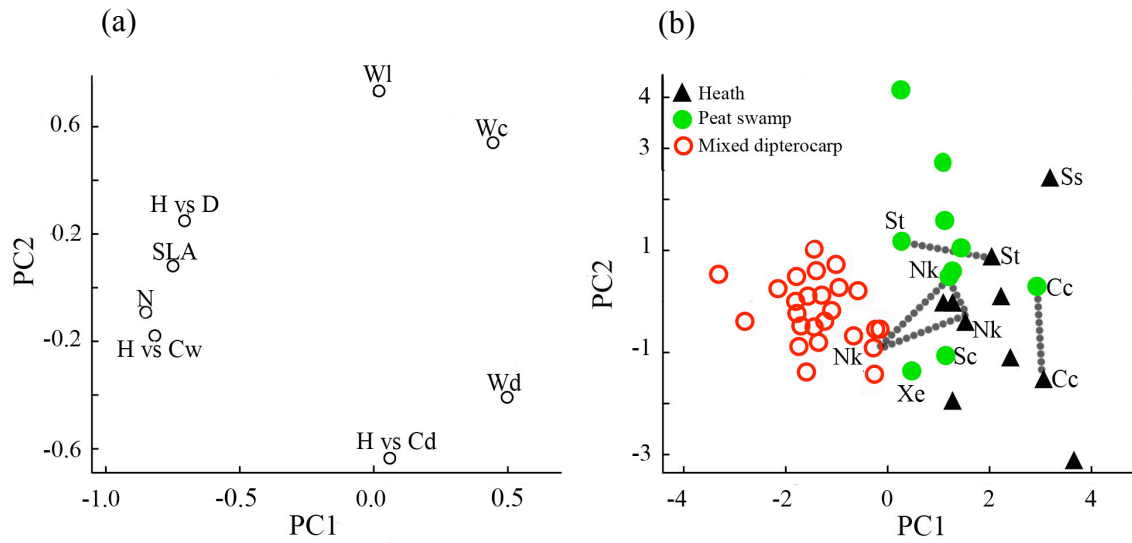


Figure. 3.3 Results of principal components analysis for saplings of 45 species by forest type based on the allometric constants and functional traits (symbols as in Table 3.2). Nk, *Neoscortechinia kingii*; Cc, *Calophyllum calcicola*; St, *Shorea teysmanniana*; Sc, *Syzygium castaneum*.; Xe, *Xanthophyllum ellipticum*; Ss, *Stemonurus secundiflorus*. (a). Factor loadings for two major components, (b). Principal component scores of 45 species for the two major components. Dashed lines show shared species across forest types (Nk, Cc and St).

Chapter IV

Tree demography over 12 years in a peat swamp forest

Introduction

Tropical peat swamp forests are characterized by huge deposits of peat originating from wood debris, often with waterlogged conditions with high water acidity caused by humic acids and nutrient deficiency (Nishimua et al. 2007, Posa et al. 2011). They are spatially heterogeneous in physiognomy and species composition, and have a fragile ecosystem under the influence of anthropogenic pressure (Mirmanto 2010). However, our knowledge about how tree species populations are maintained in the tree community of peat swamp forests in terms of growth, mortality, and recruitment rates is still limited. Many studies have been conducted to characterize tropical peat swamp forest, not only based on species composition and tree size distribution but also on growth and mortality. However, most studies were conducted based on repeated censuses with short time intervals, which may not be sufficient to quantify the demographic properties of tree species and forest stands due to large fluctuations in annual precipitation caused by ENSO effects.

So far, research in tree demographic properties based on long-term censuses has been very limited with regard to peat swamp forest of Kalimantan Indonesia, regardless of the fact that peat land in Kalimantan is a major store of organic carbon (Jaenicke et al. 2008). Growth, mortality, and recruitment in

permanent long-term research plots are important for describing the population dynamics of tree species in tropical forests. This study examined records over twelve years for changes in tree populations in a peat swamp forest to characterize tree species populations and forest stands in terms of demographic properties to understand the dynamics of tree community structure.

Maximum tree size, which characterizes the range of tree size distribution, has been related to the dynamic properties of growth and mortality rate (Aiba and Kohyama 1997, Kohyama et al. 2003, Poorter et al. 2003, King et al. 2006, Iida et al. 2014). By examining 14 abundant tropical tree species, Aiba and Kohyama (1997) characterized inter-specific variation in a tree community of warm-temperate rain forest on Yakushima Island and found a trade-off between high growth rate and low recruitment rate per species basal area for tall species and *vice versa* for short species. Whereas, in a mixed dipterocarp forest of West Kalimantan, Kohyama et al. (2003) found that inter-specific differences in tree size were dependent on relative growth rate related to the adult stature, or maximum size of species, which means that tall-statured species grow faster than short species. The effect of adult stature is also found in recruitment rate (Kohyama et al. 2003). Iida et al. (2014) found for a mixed dipterocarp forest in Peninsular Malaysia that large-statured species grow faster than small-statured species, and the trade-off between growth and mortality was most evident for trees in small size classes. It remains unknown how the tree community of peat swamp forest is characterized by the demographic properties of species populations.

Tree size distribution reflects the demographic and dynamic properties of species populations. Condit et al. (1998) showed for Panamanian rainforest that growth rate of small-sized trees was much more than the rate of population increase. This explains the observed tree size distribution, with species with higher growth rate in small-sized trees showing less positively skewed size distribution than those with lower growth rate. Kohyama et al. (2003) showed that the observed size-dependent growth rate and recruitment rate of populations sufficiently explained the observed tree size distributions of abundant species, with the assumption of steady-state populations. Stand-level tree size distribution of rain forests shows a marked excess of small-sized trees relative to large-sized trees, and this is often recognized as evidence of stable maintenance of structure with balanced recruitment, growth and mortality (Muller-Landau et al. 2006). It is worth characterizing stand-level size structure by means of demographic properties in peat swamp forests.

In this chapter, I examine tree size distribution of peat swap forest at levels of forest stands and abundant tree species, in the Sebangau basin of Central Kalimantan, through the monitoring of the changes in tree populations over a 12-year period in permanent plots. The distribution of stem diameter, basal area, tree density and demographic properties of 31 abundant tree species were quantified, and a comparison was made of observed and projected equilibrium tree-size distributions to answer whether peat swamp forest in Sebangau has reached equilibrium conditions or is still in the process of recovery since logging activities a decade ago. In addition, it was examined how populations of abundant species are maintained or

changed in the tree community of Sebangau forest along with peat depth and distance from the river.

Materials and methods

Data collection

The research area is set in the western basin of the Sebangau River at Sebangau Natural Laboratory of Peat Swamp Forest (Figure 2.1). Five plots of 50 m × 50 m were established in a relatively undisturbed forest along the gradient of peat depth of a massive peat dome, with 0.5–1 km separation (Mirmanto et al. 2003, Mirmanto 2010). The depth of the peat layer increased toward the center of peat dome, and away from the Sebangau River, ranging from 2.5 m in plot S1 to 5.7 m in plot S6 (Table 4.2). Each plot was divided into 25 subplots of 10 m × 10 m. All trees of which stem girth at breast height was ≥ 15 cm were tagged, and their girth measured to the nearest 0.1 cm using a steel tape measure with a width of 1 cm. Local name and scientific name of tree species were assigned; voucher herbaria specimens are stored in Herbarium Bogoriense for future evaluation.

Data analysis

Data of censuses carried out from 1999 to 2011 were employed to examine demographic properties. The upper tree size in terms of 95-percentile of stem

diameter (cm) at breast height (dbh, i.e. stem girth divided by π), basal area per land area (BA , $\text{cm}^2 \text{ m}^{-2}$), and tree density (n , ha^{-1}) at the first census in 1999. Sample size of trees per species population varied from 20 to 318 (Table 4.1).

For quantifying the mean growth rate of a tree that survived the census period of 12 years, G (cm/year), the empirical model of dbh dependence of Kohyama et al. (2003) was employed:

$$G = aD \exp(-bD)$$

thus

$$\ln G - \ln D = \ln a - bD \quad (\text{eqn 4-1})$$

where D is dbh (cm) from the first census, a is the parameter corresponding to the relative growth rate (year^{-1}) at $D = 0$ cm, and b (cm^{-1}) is the parameter expressing the degree of size-dependent change (typically negative for size-dependent reduction) in growth rate. The model assumes that relative growth rate, G/D , decreases exponentially with increasing dbh, D . Growth rate at a given dbh was assumed to be exponentially distributed around the mean G , based on the observation for mixed dipterocarp forest in West Kalimantan (Kohyama et al. 2003), where negative growth records were replaced by zero growth.

The instantaneous mortality rate, M (year^{-1}) (Sheil and May 1996), was estimated from the observed probability p of death of each tree as to whether it died (0) or survived (1) during the 12 years, such that

$$p = 1 - \exp(-Mt)$$

thus

$$\ln M = \ln[-\ln(1 - p)] - \ln t \quad (\text{eqn 4-2})$$

where $t = 12$ (year) is the time interval of the two censuses. Size-dependence of the models was tested

$$M = c \exp(dD)$$

thus

$$\ln M = \ln c + d D \quad (\text{eqn 4-3})$$

where c and d are model parameters (Iida et al. 2014) from binomially distributed death probability, p , with cloglog link function (cf. eqn 4-2) using the GLM package on R.

To examine the dbh dependence of mean growth rate G and mortality M , in equations 4-1 and 4-3, AIC's (Akaike's Information Criterion values) were compared between dbh-dependent and dbh-independent models.

For the recruitment rate estimation, the procedure of G_f estimate was employed (Kohyama and Takada 1998). The density of trees of which dbh was 5-7 cm (f_0 , ha⁻¹), average absolute growth rate (G_0 , cm/year) and the width of size class of 2 (cm) or the per-area recruitment rate was used, B , at the lower boundary size of 6 cm dbh, i.e. $B = G_0 f_0 / 2$ (ha⁻¹ year⁻¹). Per-capita recruitment rate (ha⁻¹ year⁻¹) was

obtained by dividing B by tree density $n \geq 6$ cm dbh per land area in ha.

The stable dbh distribution of trees, $f(D)$ ($\text{ha}^{-1} \text{cm}^{-1}$) was projected using the solution of the Von Foerster equation under the stable population assumption that $df(D)/dt = r$ where r (year^{-1}) is the time-independent intrinsic rate of population increase (Kohyama et al. 2003):

$$f(D) = \frac{B}{G(D)} \exp\left(-\int_D^{\infty} \frac{M(\hat{D}) + r}{G(\hat{D})} d\hat{D}\right) \quad (\text{eqn 4-4})$$

Equation (4-4), with an assumption of $r=0$, projects the equilibrium population. To define the upper range of size distribution for trees ≥ 6 cm, 95-percentile of stem size (cm) was used. The intrinsic rate of population increase, r (year^{-1}), by $r = B/n - M$, where B/n is per-capita recruitment rate (year^{-1}) was determined, and M is mortality (year^{-1}) as a population average if M is size dependent.

Canonical correlation analysis was carried out to investigate the relationship between demographic properties and tree size-distribution properties using the Vegan package (Oksanen et al. 2013) on R. To test the significance of the observed correlation between canonical vectors, we employed permutation procedure.

Results

The total number of species among 3926 trees ($\text{dbh} \geq 5$ cm) recorded within the five

permanent plots in 1999 was 170. The 31 most-abundant species with ≥ 20 trees were analyzed. These species represented 74% of the total number trees and 69% of the total basal area (Table 4.1).

Stand-level analysis

At the level of forest stands represented by each of the five plots of 50 m \times 50 m, relative growth rate in dbh and mortality were independent of dbh using AIC model selection. Relative growth rate, mortality, and recruitment rate were quite similar across plots regardless of the variation in peat depth. Plot S1 had higher growth rate than the other plots (Table 4.2). Compared with the other plots, plot S1 had the highest mortality because of the effect of experimental removal of all trees in one 10 m \times 10 m subplot (4% in area) for allometric analysis (not shown here), which resulted in high mortality and subsequent high relative growth rate among the five plots.

Figure 4.1 demonstrates the comparison between the observed and projected equilibrium (i.e. the rate of population increase was assumed to be zero), and stable (i.e. with observed rate of population increase) size distributions with equation 4-4. Generally, the projected size distributions varied across forest types. Plots S1 and S4 showed that the rate of population increase was very small, resulting in the agreement of stable and equilibrium distributions, and that observed size distribution fitted well with the projected equilibrium distribution. The agreement between observed size distribution and stable, but not equilibrium, distribution was

found in plot S3. However, in plot S6 the observed size distribution did not fit with either equilibrium or stable size distributions. In plots S2, S3, and S6 the rate of population increase was positive, so that the observed distribution and the projected stable distribution were negatively steeper than the equilibrium distribution. These results implied that most stands of peat swamp forest in Sebangau basin had not yet reached an equilibrium state after artificial disturbance but were still in the process of stand development.

Species level analysis

Based on the model selection, there was no size dependence in relative growth rate as well as mortality across species. Demographic properties varied across species populations (Appendix 2). The comparison among observed, equilibrium, and stable size distributions is illustrated in Figure 4.2 and appendix 3. The projection of size distribution was demonstrated through mean basal area and upper size limit reflecting the observed size distribution. The projection of equilibrium and stable size distributions showed that size distribution varied and spread out among 31 species. None of the species reached the upper limit diameter of simulation with eqn. 4-4 set at 100 cm. This suggested that species composition in Sebangau forest is still changing along with the stand recovery process.

The intrinsic rate of population increase was largely variable across species (Figure 4.3). The tree densities of 12 species decreased, and those of another 19 species increased during the period of the censuses. There was no correlation

between the rate of population increase and either upper size limit, mean basal area, or population density (Figure 4.3a-c). The strong positive, almost linear, correlation between upper size limit and mean basal area (Figure 4.3d) suggested that the shape of size distribution was not variable across species.

The canonical correlation analysis of species based on demographic properties and size distribution properties showed significant association between the two properties (correlation coefficient = 0.537, $P = 0.001$) along the first axis (Figure 4.4). The per-capita recruitment rate and mortality showed high negative correlation with population density and moderate negative correlation with mean basal area and upper size limit. Relative growth rate of tree size was negatively correlated with upper size limit. These findings indicated that large species at adult stature were characterized by low growth rate and slow turnover rate (low mortality and low per-capita recruitment rate).

Larger species were characterized by low relative growth rate in the canopy (i.e. *Xylopia fusca*, *Camptosperma coriaceum*, *Calophyllum biflorum*), and small species were characterized by high growth rate in the understory (*Acronychia porteri*, *Cratoxylum glaucum*).

Discussion

Peat swamp forests exhibit unique characteristics, such as tree size distribution, species composition, and response to disturbance (Iida et al. 2014). This chapter

examines how demographic properties and tree size structure properties characterize the peat swamp forest in Sebangau basin, Central Kalimantan. All measures of tree size distribution especially mean basal area and upper size limit, showed high negative correlations with recruitment and mortality rates, but less with relative growth rate of tree size.

Relative growth rate and mortality were independent of tree size in dbh both at the levels of stand and species. Size distribution was projected from mortality, growth rate, and recruitment rate, with the assumption of stable/equilibrium populations. Because of the size independence of relative growth rate and mortality, the projected distributions were fitted to the power function (Muller-Landau et al. 2006). Agreement between observed and equilibrium distribution was found in two plots of Sebangau forest, indicating that these stands had reached an equilibrium state. Kohyama et al. (2003) mentioned that the agreement of projected size distributions did not indicate that the population was at equilibrium because the effect of mortality can be stronger than the effect of the rate of population increase. In contrast, the disagreement between observed data and projected size distributions in the other three plots as well as in abundant species, suggested a progressive change in stand structure and species composition. Even in old growth forests, Woods (2000) suggested that forest stands are not necessarily in demographic equilibrium.

In this chapter, equilibrium and stable populations were projected to characterize the size distribution of stands and species of peat swamp forest based on

demographic rates for censuses with a 12-year interval. Two out of five stands showed that observed size distributions fitted to demographic projections, whereas the other three were projected to be still increasing in upper size as well as population density. Because the peat swamp forest in Sebangau basin experienced selective logging approximately 30 years ago, the results imply the remaining effect of past human disturbance.

By comparing five plots, it was found that peat depth and distance from the river did not have any effect on growth rate, mortality nor recruitment rate. This implied that the change in size distribution experiences the same pattern across plots, after disturbance by selective logging in a similar period, even though the study by Mirmanto (2010) showed that tree size was smaller in plots closer to the river. The differences between the previous study and the present results might be caused by the exclusion of a plot closest to the river that Mirmanto et al. (2003) examined. The depth and distance from the river only gave a major effect on biomass and species composition (Shepherd et al. 1997, Mirmanto 2010).

At the level of species populations, upper size limit was strongly correlated with mean basal area. These species also showed high population densities. They tended to have demographic properties of low recruitment rate, low mortality, and low growth rate. This is in contrast with Mirmanto (2010), who found that short-statured species at the Sebangau site showed high relative growth rate and mortality. The differences between the two results could be due to the different time period, i.e. 12 years in this study and 1 year studied by Mirmanto (2010). Because

the forest is undergoing secondary succession, the present results suggested that the present canopy-dominant species with slow turnover rate tend to be replaced by others over time.

There was inter-specific differentiation in habitat preference at the Sebangau site in terms of peat depth (Mirmanto et al. 2003; Mirmanto 2010). The present results showed that the change in size distribution was similar across species despite their habitat differentiation. This implies that tree species of peat swamp forest were characterized by similar demographic properties regardless of habitat variation in peat depth.

The present results also suggested that large species show lower recruitment per capita and higher probability of survival, which resulted in high basal area, compared with small species. Sebangau peat swamp forest is characterized by high relative abundance of small-sized trees. This result was accordance with Mirmanto (2011). The low density of large trees in this forest means they have been logged in the past decades. The high density of juvenile trees suggested that enhanced recruitment is still taking place after forest disturbance.

This present results suggest that 12 years is not sufficient for peat swamp forest to reach an equilibrium state, but large-statured species increased their population with fast growth rate, high recruitment rate, and high survival.

Table 4.1 Population properties in tree density and basal area for trees ≥ 5 cm stem diameter at breast height of 31 abundant species in peat swamp forest of Sebangau.

Species	Family	Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)
<i>Acronychia porteri</i> Hook.f.	Rutaceaea	acrpor	49	0.24
<i>Blumeodendron elateriospermum</i> J.J.Sm.	Euphorbiaceae	bluela	62	0.62
<i>Calophyllum biflorum</i> M.R.Hend. & Wyatt-Sm.	Cluciaceae	calbif	55	1.02
<i>Calophyllum inophyllum</i> L.	Cluciaceae	calino	62	0.67
<i>Calophyllum teysmannii</i> Miq.	Cluciaceae	caltey	73	1.09
<i>Camptosperma coriaceum</i> (Jack) Hallier f. ex Steenis	Anacardiaceae	camcor	44	0.88
<i>Cratoxylum glaucum</i> Korth.	Cluciaceae	cragla	37	0.33
<i>Diospyros dajakensis</i> Bakh.	Ebenaceae	diodaj	42	0.51
<i>Dyera costulata</i> Hook.f.	Apocinaceae	dieexi	25	0.50
<i>Garcinia tetrandra</i> Pierre	Cluciaceae	gartet	23	0.24
<i>Gonystylus bancanus</i> (Miq.) Kurz	Thymelaeaceae	gonban	28	1.04

Table 4.1 (Continued)

Species	Family	Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)
<i>Horsfieldia crassifolia</i> Warb.	Myristicaceae	horcra	55	0.68
<i>Lithocarpus elegans</i> (Blume) Hatus. ex Soepadmo	Fagaceae	litele	31	0.23
<i>Lithocarpus leptogyne</i> (Korth.) Soepadmo	Fagaceae	litlep	27	0.25
<i>Litsea resinosa</i> Blume	Lauraceae	litres	29	0.24
<i>Litsea rufo-fusca</i> Kosterm.	Lauraceae	litruf	30	0.23
<i>Madhuca</i> cf. <i>sericea</i> S.Moore	Sapotaceae	madser	25	0.37
<i>Neoscortechinia philippinensis</i> (Merr.) Welzen	Euphorbiaceae	neophi	87	0.92
<i>Palaquium cochleariifolium</i> P.Royen	Sapotaceae	palcoc	36	0.59
<i>Palaquium leiocarpum</i> Boeri	Sapotaceae	pallei	254	3.51
<i>Sandoricum emarginatum</i> Hiern	Meliaceae	sanema	42	0.45
<i>Shorea</i> cf. <i>parvifolia</i> Dyer	Dipterocarpaceae	shopar	39	0.21
<i>Shorea guiso</i> Blume	Dipterocarpaceae	shogui	61	0.81
<i>Stemonurus scorpioides</i> Becc.	Icacinaceae	stesco	33	0.35

Table 4.1 (Continued)

Species	Family	Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)
<i>Syzygium castaneum</i> (Merr.) Merr. & L.M.Perry	Myrtaceae	syzcas	88	1.29
<i>Syzygium clavatum</i> (Korth.) Merr. & L.M.Perry	Myrtaceae	syzcla	41	0.43
<i>Syzygium densinervium</i> (Merr.) Merr.	Myrtaceae	syzden	111	1.99
<i>Tetramerista glabra</i> Miq.	Tetrameristaceae	tetgla	22	0.18
<i>Xanthophyllum palembanicum</i> Miq.	Polygalaceae	xanpal	40	0.73
<i>Xylophia fusca</i> Maingay ex Hook.f. & Thomson	Annonaceae	xylfus	33	0.64

Table 4.2 Differences in relative growth rate, mortality rate, and recruitment rate for each of five plots in Sebangau peat swamp forest, Central Kalimantan. The plot code, distances from the river, peat depth were obtained from Mirmanto et al. (2003).

Plot code	Distance from river (km)	Peat depth (m)	Relative growth rate (year ⁻¹)	Mortality (year ⁻¹)	Recruitment rate (year ⁻¹ per capita)
S1	2.5	2.5	0.043	0.058	0.058
S2	3.0	3.3	0.025	0.033	0.041
S3	3.0	3.8	0.020	0.023	0.039
S4	3.5	4.4	0.022	0.036	0.035
S6	4.0	5.7	0.027	0.025	0.041

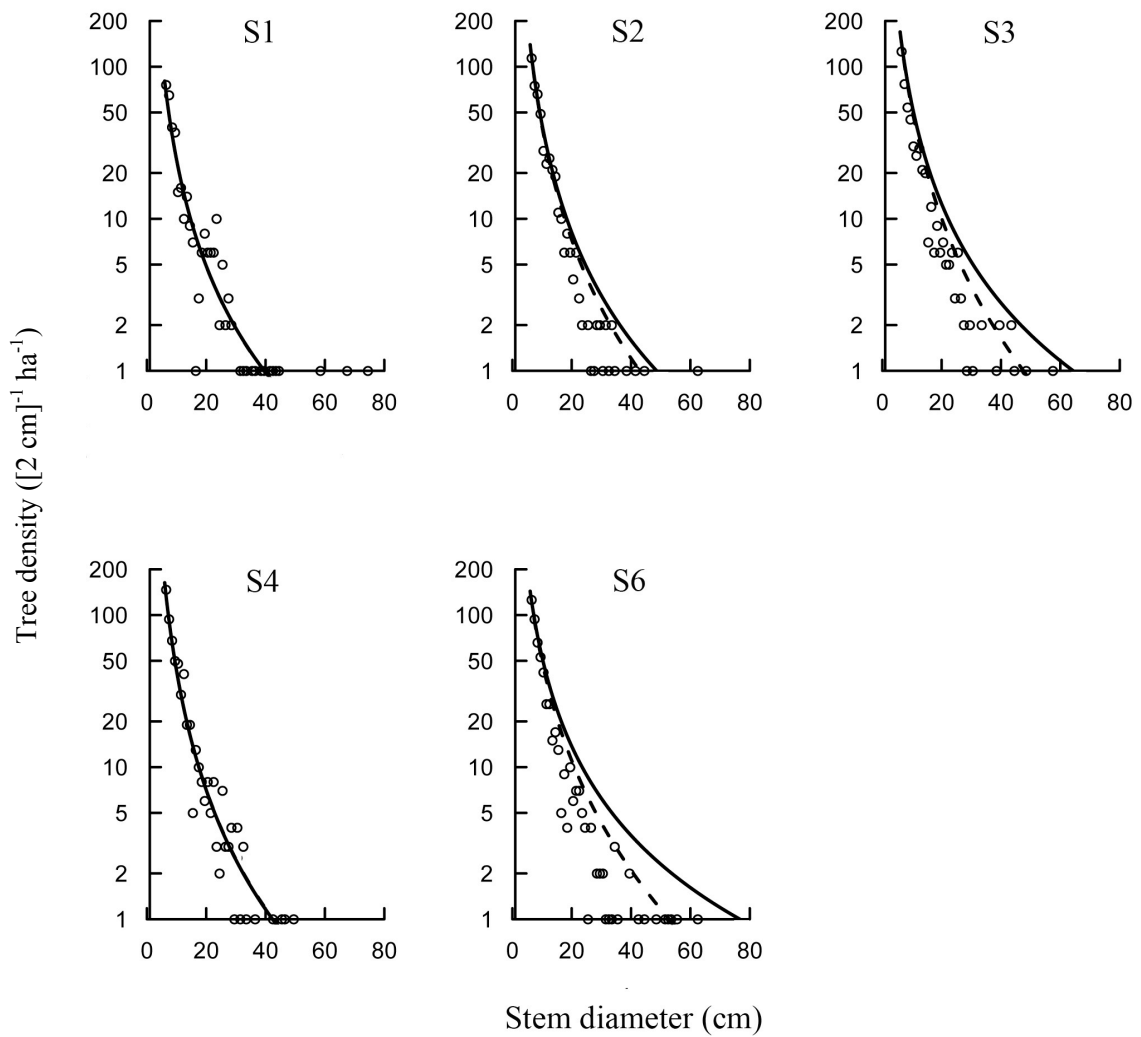


Figure 4.1 Frequency distribution of diameter at breast height (dbh) among plots for trees ≥ 6 cm dbh (number of trees in 2 cm diameter class ha^{-1}). Open circles show the observed distribution in 2011, solid lines show projected equilibrium distribution (assuming the rate of population increase $r = 0$), dashed lines show stable distribution with observed r .

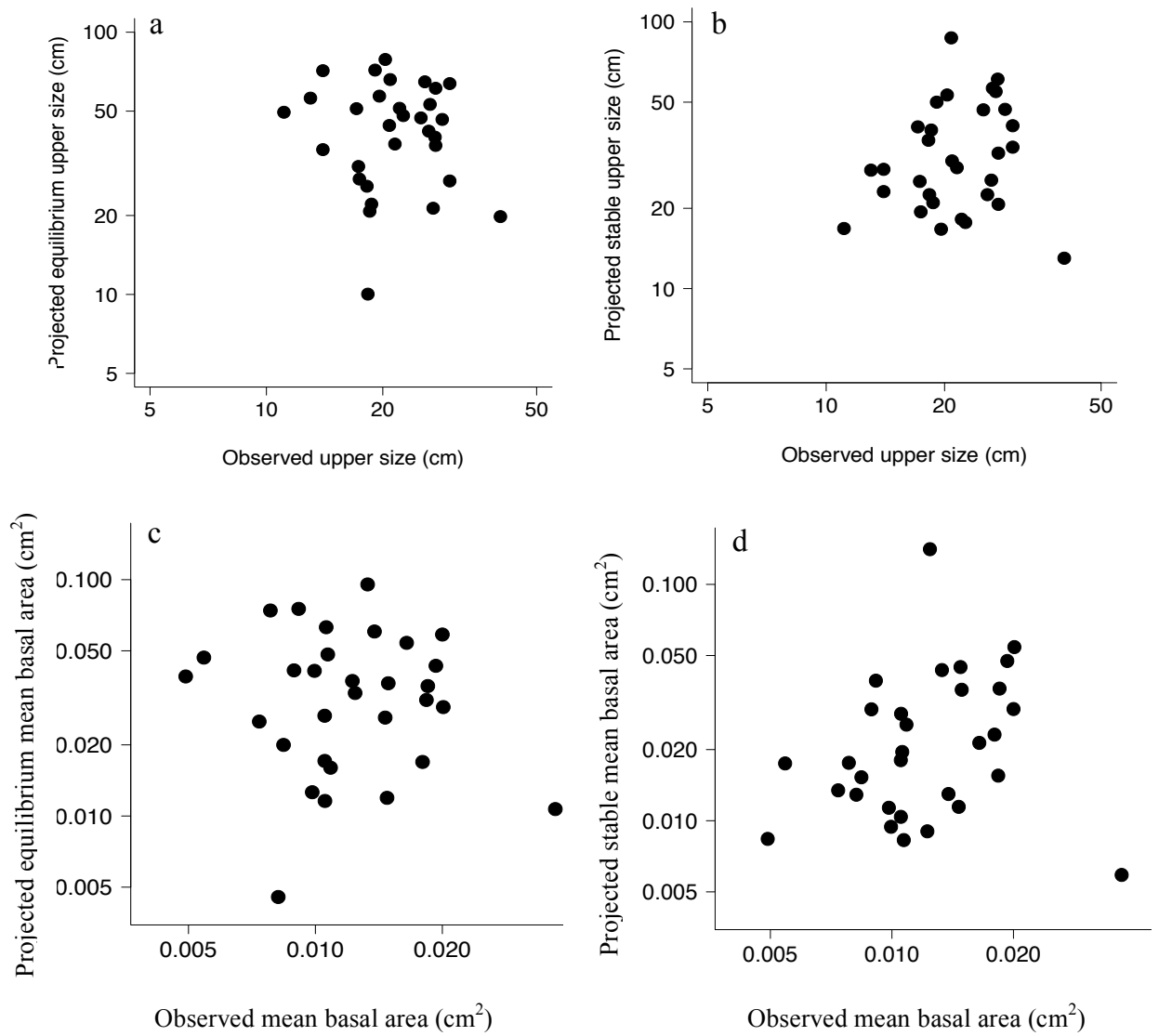


Figure 4.2 Comparison of observed and stable, equilibrium size distribution in Sebangau peat swamp forest, Central Kalimantan. Open circles indicate species of the observed community, and solid circles show species of the permuted community. (a) and (c), projected equilibrium distribution, (b) and (d), projected stable distribution.

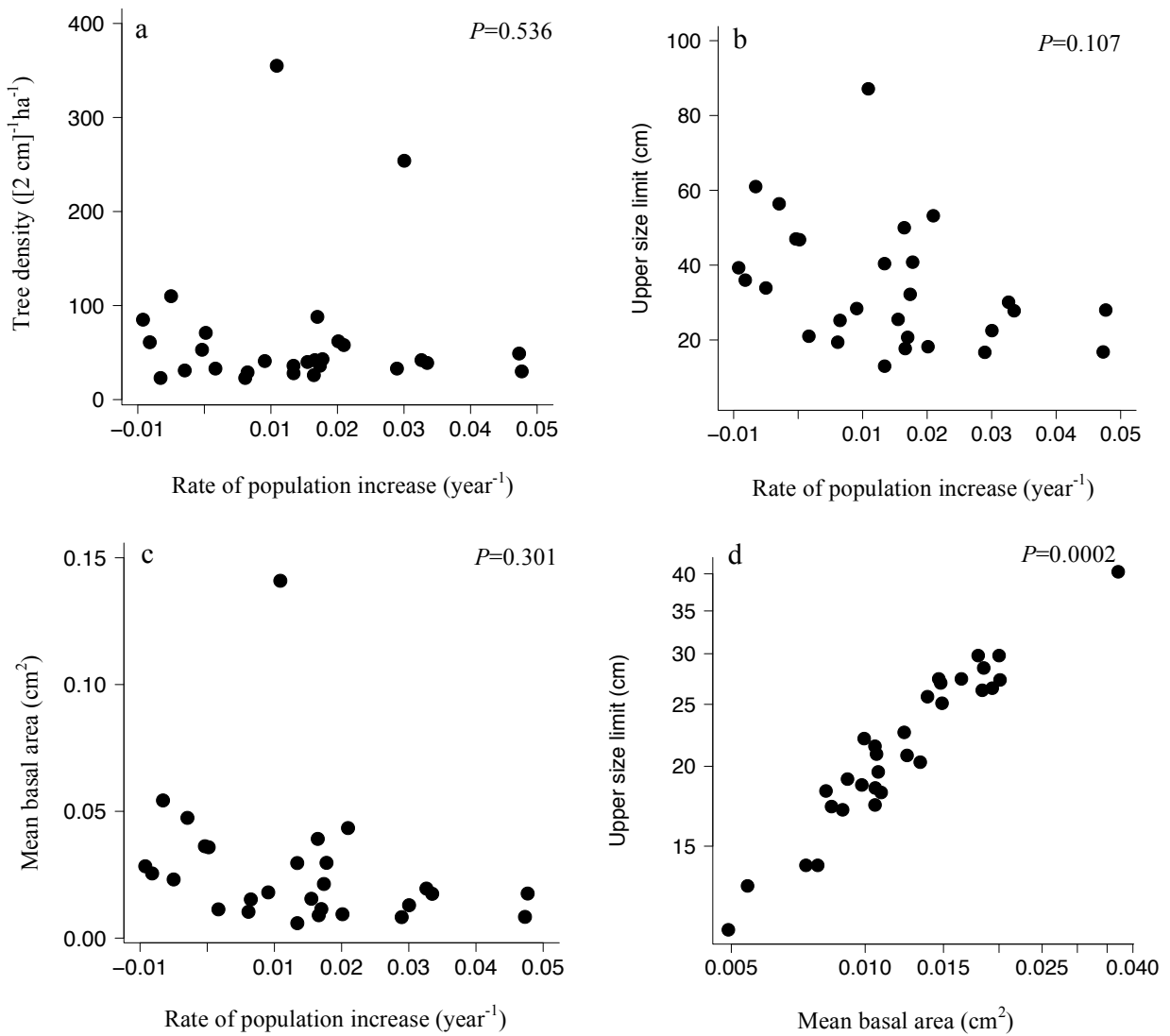


Figure 4.3 Relationship between rate of population increase and density (a), mean basal area (b), and upper size limit (c), and between mean basal area and upper size limit (d).

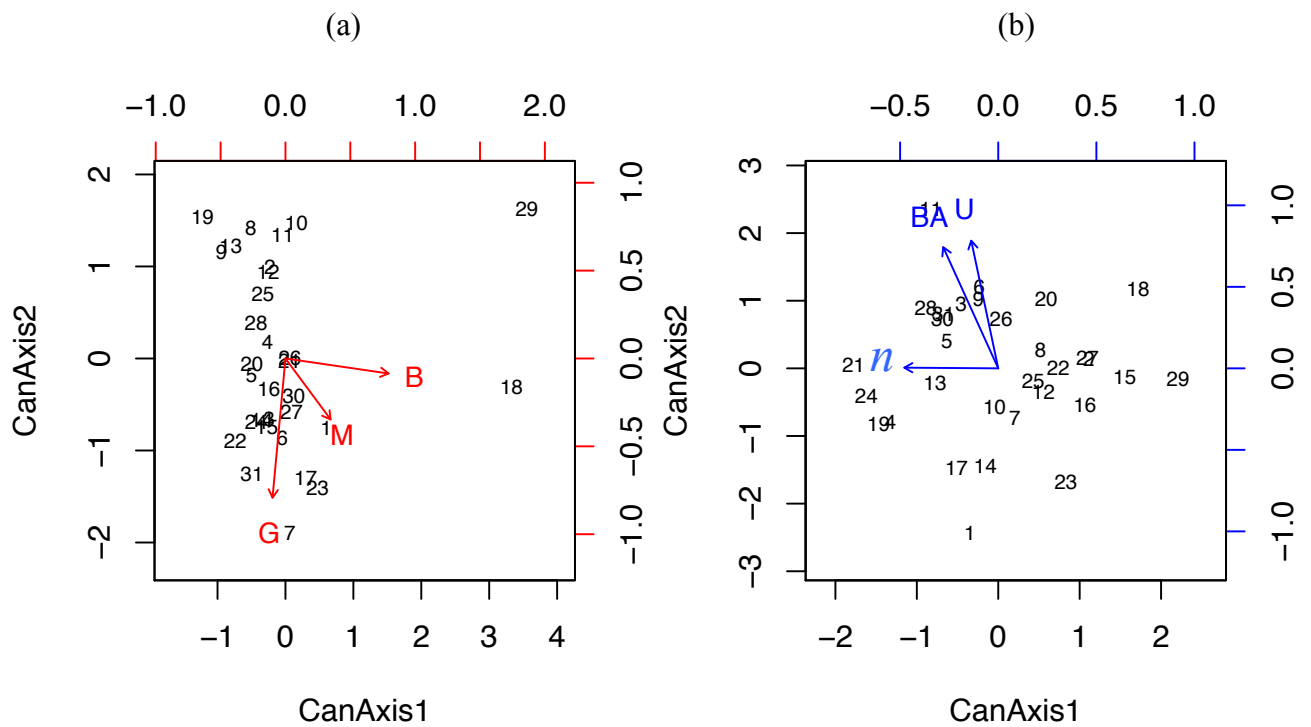


Figure 4.4 Results of canonical correlation analyses between demographic properties and size-distribution properties for 31 abundant tree species in Sebangau peat swamp forest. (a) Standardized demographic properties and species projection of their scores, and (b) standardized size-distribution properties and species projection of their scores. Demographic properties are per-capita recruitment rate B ; average relative growth rate G/D ; average mortality M . Size distribution properties are basal area BA , tree density n , and upper size limit U .

Chapter V

Tree size distribution in heath, peat swamp, and mixed dipterocarp forests

Introduction

Growth rate and mortality of trees can vary with resource availability (Chapin 1980). In nutrient-poor conditions, trees usually exhibit low growth rate and high mortality compared with those in nutrient-rich conditions (Chapin 1980, Valladares et al. 2000). As mentioned in Chapter III, heath forest is characterized by nutrient-deficient conditions compared with peat swamp and mixed dipterocarp forests of Borneo Island. Heath forest shows tree size structures consisting of dense small-sized trees relative to large-sized trees. By contrast, mixed dipterocarp forests are less dense in small-sized trees than heath and peat swamp forests (Whitmore 1975, Miyamoto et al. 2007, Nishimura et al. 2007). Whitmore (1975) suggested that heath forest trees have morphological properties to accommodate nutrient limitation, desiccation, and heat load. So far, the life-history consequences of these environmental stresses remain unclear.

Tree size distribution is often used to indicate forest architecture. If there are large numbers of small-sized trees relative to large-sized canopy trees, a forest can be maintained stably, whereas if there are relatively few small-sized trees relative to canopy trees, a forest can suffer decline with time. However, the relative

abundance of small-sized trees can also be explained by a low ratio of mortality to growth at a demographic equilibrium (Condit et al. 1998; Zavala et al. 2007). To examine the dynamic status of forest structure, we can compare the observed tree size distribution with the projected size distribution from mortality and growth rate under the assumption of stable or equilibrium populations (Kohyama et al. 2003; Muller-Randau et al. 2006).

This chapter examines the demographic properties across three forest types of tropical lowland rain forests reflecting nutritional and hydrological conditions, and compares observed tree size distributions and projected distributions based on demographic rates. The question why there is a dense layer of small-sized trees in heath forest compared with other forest types in lowland Kalimantan is addressed, and possible reasons for canopy architecture differences among forest types in relation to ecosystem-level properties are discussed.

Materials and methods

Study sites

For this chapter, data were analyzed from Lahei site, at which two 1-ha plots representing heath forest and one 1-ha plot representing peat swamp forest, and Serimbu site with two 1-ha plots representing mixed dipterocarp forest. The site descriptions are given in Chapter II. To summarize, repeated censuses for all trees ≥ 15 cm in girth at breast height were carried out in these permanent plots. Stem dbh

was obtained by dividing the girth at breast height divided by π . Census years were 1997 and 1999 for the Lahei plots, and 1992 and 1995 for the Serimbu plots. These forests based on plot data have been described by Miyamoto et al. (2003) for heath forest at Lahei, by Nishimua et al. (2007) for peat swamp forest at Lahei, and by Kohyama et al. (2003) for mixed dipterocarp forest at Serimbu.

Plot data analysis

The procedure of plot data analysis of tree size distribution and demographic rates (size growth rate, mortality, and recruitment rate) were the same as employed for Chapter IV, and the details are shown in the Methods of Chapter IV.

Results

The number of trees varied among forest types (Table 5.1). Heath forest showed the highest tree density and the lowest total basal area compared with peat swamp and mixed dipterocarp forests. This suggested that small-sized trees were the most abundant in heath forest.

In all forest plots, relative growth rate and mortality varied with tree size. Relative growth rate in dbh decreased with increasing dbh. Mortality decreased with tree size (Figure 5.1). The parameters of growth and mortality rates varied among forest types (Table 5.2).

There was good agreement between observed tree size distribution and the

projected equilibrium size distribution in all plots across the three forest types (Figure 5.3). This implied that demographic properties sufficiently explain the pattern of forest structure.

Heath forests were represented by abundant small-sized trees compared with other forest types. They showed high growth rate and low mortality up to 10 cm in diameter (Figure 5.1a, b) and high recruitment rate at the boundary diameter of 6 cm. These findings suggested that dense understory trees of heath forests were not caused by slow growth (resulting in stacking in the understory) but by high recruitment (associated with fast turnover). By contrast, canopy mortality was highest in heath forests, which may be due to nutrient-deficient conditions. In the two heath forest plots, heath forest 1 showed less dense understory in the projected equilibrium distribution than heath forest 2 (Figure 5.3). This difference could be attributed to the fact that heath forest 1 was recovering after selective logging of the commercial timber tree *Agathis borneensis*.

Discussion

In this chapter, the findings showed that heath forest is maintained with a high turnover rate. i.e. high mortality for canopy trees and high recruitment rate, as well as high growth rate, particularly for small-sized trees in the understory. In contrast, mixed dipterocarp forest maintained its tree population with low canopy mortality, low relative growth rate and low rate of recruitment.

The present results support the general properties of heath forest structure, with high abundance of understory trees compared with mixed dipterocarp forest (Mackinnon et al. 1996; Richards 1996). It can be assumed that low soil nutrient conditions in heath forest contribute to the slow rate of diameter increment, and which leads to the dense stagnant layer of understory trees. Actually, the present results implied a contrasting explanation that the understory subpopulation of heath forest is maintained by high recruitment rate, regardless of high growth rate and low mortality. In contrast, canopy trees in heath forest suffer high mortality. Smaller maximum tree size in heath and peat swamp forests, reflecting the nutrient-poor environment, was caused by high canopy mortality, rather than slow growth of canopy trees.

The present results pose a new interesting question of why heath forest plots exhibit high growth rate, low mortality, and high recruitment rate under nutrient-limiting conditions. Several factors could contribute to the high vital rate in heath forest, such as human impact; past logging activities generating canopy gaps, in which trees have the chance to grow rapidly. Another possibility is that the relatively sparse canopy reflects high mortality of canopy trees, with short height compared with mixed dipterocarp forest (Miyamoto et al. 2007), bringing about a less shaded understory. Small total basal area in heath forest implied a less shaded understory. Forest-level leaf mass was smaller in heath forest than mixed dipterocarp forest, and the shading by leaf mass was further reduced by low SLA in heath forest (Rahajoe and Kohyama 2003). A hypothesis is proposed here that the primary

limiting factor for growth and survival of small-sized trees in the understory of lowland rain forest is light rather than nutrient availability, even in nutrient-limited heath and peat swamp forests, because of their nutrient requirement being related to tree size. Because canopy trees with large size suffer high mortality due to nutrient limitations, small understory trees enjoy favorable conditions for fast growth, low mortality, and high recruitment rate. Therefore, the dense understory tree layer in heath forest is formed and maintained with high turnover rate.

Peat swamp forest is characterized by intermediate demographic properties between heath and mixed dipterocarp forests. This situation was completely different compared with conditions after a severe drought in 1997, resulting in higher mortality in peat swamp forest than heath forest, whereas growth rate was higher in heath forest than in peat swamp forest (Nishimua et al. 2007).

The present study showed that differences in demographic rates can explain differences in tree size structure among lowland forest types. This is a new finding that heath and peat swamp forests are maintained dynamically.

Table 5.1 Total basal area and tree density of examined forest plots.

Plots	Total basal area (m ² ha ⁻¹)	Tree density (ha ⁻¹)
Heath forest 1	25.4	1489
Heath forest 2	30.3	1617
Peat swamp forest	44.9	1211
Mixed dipterocarp forest 1	41.8	1000
Mixed dipterocarp forest 2	44.1	1087

Table 5.2 Parameters of growth rate and mortality models (eqns 4-1 and 4-2).

Location	Growth rate parameters		Mortality rate parameters	
	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>
Heath forest 1	0.023	0.034	0.019	0.280
Heath forest2	0.045	0.049	0.020	0.547
Peat swamp forest	0.023	0.028	0.073	-0.188
Mixed dipterocarp forest1	0.016	0.021	0.073	-0.500
Mixed dipterocarp forest2	0.013	0.022	0.019	-0.089

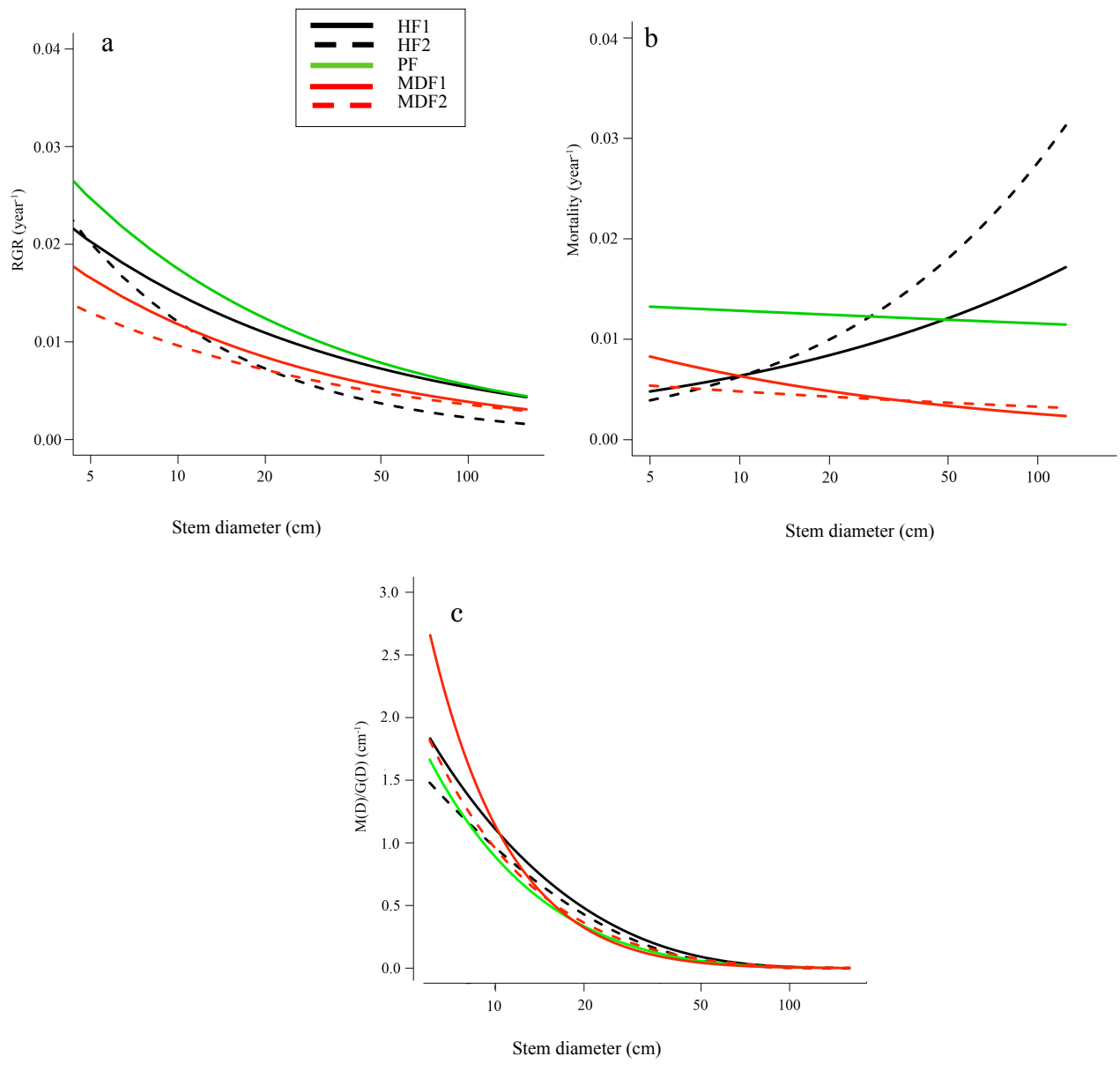


Figure 5.1 Estimated size-dependence of mean relative growth rate (a), mortality (b) and ratio of mortality to growth rate (c) in stem diameter.

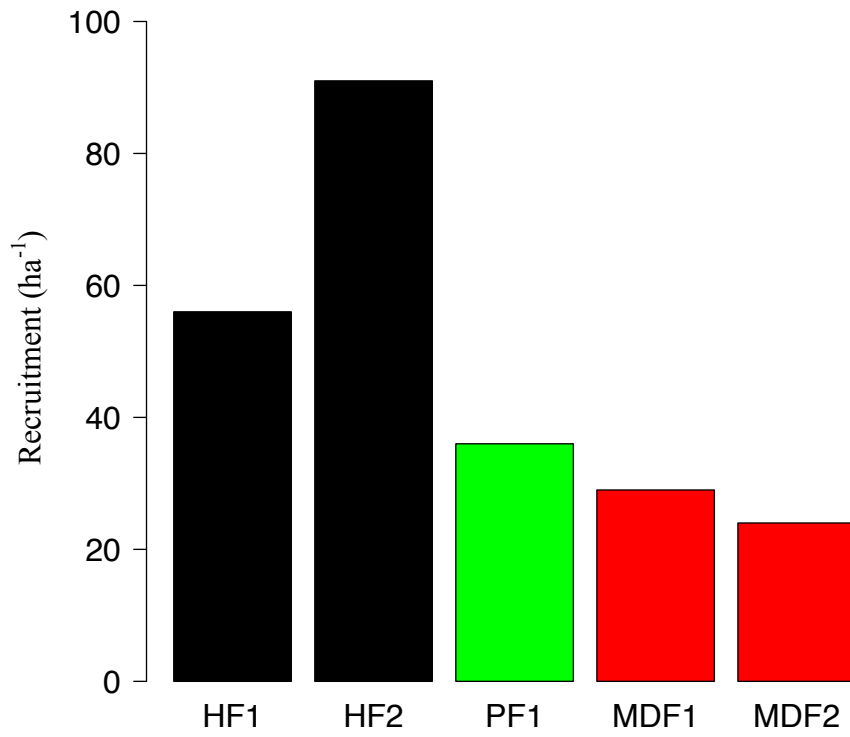


Figure 5.2 Recruitment rates of trees at the boundary size of 6 cm stem diameter.

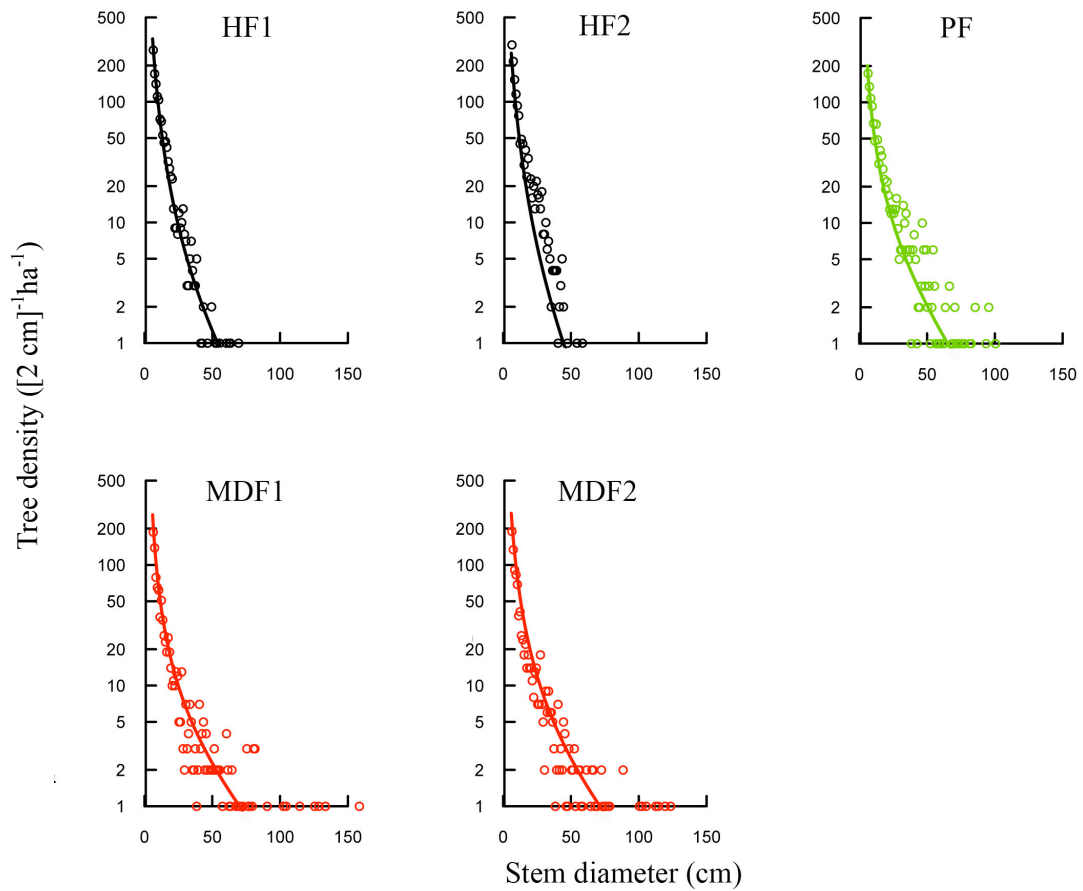


Figure 5.3 Projected size distribution of five plots; two plots of heath forest (HF), one plot of peat swamp forest (PF), and two plots of mixed dipterocarp forest (MDF).

Chapter VI

General discussion

This dissertation examines sapling and tree performance in relation to forest types in lowland forests of Kalimantan, Indonesian Borneo. Each of three forest types, i.e. heath, peat swamp and mixed dipterocarp forests, has unique properties, as described in Chapter I. The morphological properties of tropical tree saplings were examined in these forest types (Chapter III). At the level of forest plots, tree demography and tree size structure were compared across forest types (Chapter V). The long-term demographic properties and tree size distribution were analyzed in peat swamp forest of the Sebangau basin in Central Kalimantan, based on permanent plot censuses over 12 years (Chapter IV). Based on these results, seeks to answer the following questions posed in Chapter I: (1) how does the performance of saplings in terms of architecture and functional traits change in response to forest type, (2) how do demographic properties vary across the three forest types, and (3) how do demographic properties vary among forest stands and species in peat swamp forest of the Sebangau peat dome. Here, I summarize the findings described in previous chapters and discuss how trees maintain their populations in different forest conditions.

This study showed that there was inter-forest type differentiation in architecture and functional traits of saplings (Chapter III) and in plot-level demographic properties (Chapter V), although demographic properties were similar

across plots in Sebangau peat swamp forest with various peat depths and distances from the Sebangau river (Chapter IV). Demographic properties provide good prediction of tree size distribution in old-growth forest plots (Chapter V), suggesting that these plots are close to a demographic equilibrium state. In contrast, plots examined in the peat dome of Sebangau suggested that these plots were still undergoing recovery since selective logging disturbance a decade ago (Chapter IV).

The properties of saplings were in accordance with those reported for small trees (ca. 5-10 cm in stem diameter) in the understory (Miyamoto et al. 2007) and forest floor seedlings (Nishimura and Suzuki 2001). Differences in sapling morphology within species that have a wide distribution range across forest types were also detected. Intra-specific changes in morphology occurred in such a manner to adjust to the community-wide properties of each forest type. Trees of heath and peat swamp forests showed lower SLA and N content of leaves and higher stem wood density than those in mixed dipterocarp forest. One can assume that these traits reflect adaptation to the nutrient-poor conditions in heath and peat swamp forests in frequently waterlogged flat land.

Stems of saplings were slenderest in heath forest, followed by peat swamp forest, and the least slender were in mixed dipterocarp forest (Chapter III). This tendency was also true for larger-sized understory trees between heath and mixed dipterocarp forests, whereas the reverse was the case for large canopy trees (Miyamoto et al. 2007). Interestingly, growth rate in stem diameter was faster in heath and peat swamp forests than in mixed dipterocarp forest (Chapter V) in spite of

nutrient limitations in heath and peat swamp forests. When taking into account the fact that stems were more slender but with denser stem wood in heath and peat swamp forests than in mixed dipterocarp forest, understory trees in heath forest showed much higher growth rate in terms of biomass gain than in mixed dipterocarp forest. Therefore, it is evident that the relatively high densities of understory trees in heath forest are due to high rate of recruitment and low mortality rate, not by high growth rate (Chapter V).

In contrast to understory trees, canopy trees showed slower growth rate and higher mortality in heath and peat swamp forests than in mixed dipterocarp forest (Chapter V). Lower net primary productivity in heath and peat swamp forest than in mixed dipterocarp forest (Rahajoe and Kohyama 2003, Miyamoto et al. 2007) was, therefore, attributed to the low assimilation capacity of large-sized canopy trees. This fact further suggests the possibility that the understory in heath and peat swamp forest is less shaded than in mixed dipterocarp forest, because of a lower density of canopy trees, which possess foliage leaves of low SLA. Canopy foliage with low SLA, even at the same mass of foliage leaves, cast less shade underneath.

Taking into account this possibility that the understory of heath and peat swamp forests is less shaded than that of mixed dipterocarp forest, high tree growth rate and per-capita recruitment rate in heath and peat swamp forest was possibly due to relatively good light conditions. Low SLA and slender stem shape at sampling stage in heath and peat swamp forests (Chapter III) could be partly due to the brighter understory. To separate the effect of edaphic/hydrological conditions and

light conditions, there is a need to explicitly measure these conditions in target forests, and to observe plastic changes in leaf and crown properties along light gradients observed from forest edges or tree-fall gaps to shaded forest floors.

The demographic properties of peat swamp forest were intermediate between those in heath and mixed dipterocarp forests, but it appeared to be a sensitive ecosystem, as demonstrated by the severe drought recorded in 1997 (Nishimura et al. 2007). On the other hand, trees of large-statured species in peat swamp forest of Sebangau tended to grow slower and survive better, and those of small-statured species maintained their populations in the understory with high per-capita recruitment rate. At stand and species levels, the Sebangau peat swamp forest tree population was still in the process of recovery after selective logging, although some stands had already attained a stable state judging from demographic projections of equilibrium size distribution (Chapter IV). In contrast, peat swamp forest at Lahei had reached a demographic equilibrium stage (Chapter V). Comparing demographic properties between the two peat swamp forests, trees at Lahei tended to grow faster with higher mortality than trees at Sebangau peat swamp forest. Therefore, the stable Lahei forest did not imply slow turnover compared with Sebangau stands undergoing recovery.

In this study, I demonstrated sapling morphology and tree demography in response to forest conditions. Different strategies that result in differing demographic properties were found in response to forest conditions, and which contribute to facilitate the maintenance of natural forest ecosystems with high productivity. The

present findings provide essential information for the sustainable management of the remaining lowland forests from disturbance, by paying attention to the unique properties for each forest type.

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Acknowledgements

I would never have been able to finish my study without a lot of help from many people. First of all, I would like to express my sincere gratitude to my supervisor, Professor Takashi S. Kohyama, for his valuable advice, guidance, patience, understanding, and for providing a good atmosphere during my studies at the plant ecology laboratory.

I would like to thank the director of the Indonesian Institute of Science (LIPI), Botany division, Dr. Eko Baroto Walujo, who gave me the permission to continue my studies, Dr. Herwint Simbolon who gave me the opportunity to join this program, and Dr Joeni S. Rahajoe for valuable advice and discussions. My thanks also go to all the staff and technicians at LIPI.

My thanks also go to all my lab colleagues in plant ecology, Drs. Yosiko Iida, Augustin Orou Matilo, Rie Miyata, Satomi Shiodera, Luis Chaves, Chika Egawa and Yuri Hoyo for their helpful suggestions, Jun-ichi Fujinuma, Sunmonuo Azizat Idowu, Doddy J. Irawan, Nanae Nomura, Harisoa Rakotonoely for helping with data analysis and discussions, and for all the fun we have had.

I wish to thank Dr. Suwido H. Limin for management and full support in conducting field research. I thank the local people and my best fieldwork friend, Ismail Apandi. My fieldwork would not have been possible without their help.

This study was supported by the SATREPS project “Wild Fire and Carbon Management in Peat Forest in Indonesia” jointly sponsored by the Japan Science and

Technology Agency and Japan International Cooperation Agency, and the Global Center for Excellence Program of Hokkaido University “Establishment of Center for Integrated Field Environmental Science” sponsored by the Japan Society for the Promotion of Science

Finally, I thank my family, for always supporting me with their best wishes, which kept me in a positive frame of mind.

Appendix 1.

Species sampled in three forest types for sapling architecture and functional traits (cf. Chapter III).

No	Site	Code	H-D (cm, cm)	H-Cw (cm, cm)	H-Cd (cm, cm)	SLA (cm ² g ⁻¹)	N (mg g ⁻¹)	Wd (g cm ⁻³)	Wc (g g ⁻¹)	WI (g g ⁻¹)
1	MDF	Af	-2.39	-0.74	-4.32	142.2	19.48	0.66	0.55	0.65
2	MDF	Ap	-2.47	-0.86	-4.23	173.6	20.10	0.62	0.43	0.60
3	MDF	Cl	-2.42	-0.96	-4.49	179.9	21.78	0.61	0.38	0.60
4	MDF	Cc	-2.48	-0.92	-4.40	130.6	16.20	0.66	0.41	0.55
5	MDF	Dc	-2.40	-0.93	-4.44	143.6	15.35	0.66	0.34	0.48
6	MDF	Dt	-2.35	-0.88	-4.35	141.3	16.58	0.60	0.42	0.55
7	MDF	Db	-2.42	-0.82	-4.32	189.6	15.75	0.56	0.47	0.59
8	MDF	Et	-2.49	-0.83	-4.16	188.2	19.03	0.53	0.43	0.58
9	MDF	Ez	-2.40	-0.77	-4.26	160.6	19.23	0.84	0.36	0.68
10	MDF	FsS	-2.42	-0.99	-4.33	205.8	31.93	0.64	0.44	0.57
11	MDF	Hd	-2.63	-0.85	-4.30	170.8	15.98	0.71	0.37	0.57
12	MDF	Ksl	-2.37	-0.91	-4.32	151.0	19.25	0.50	0.35	0.58
13	MDF	Mb	-2.48	-0.95	-4.39	192.0	19.08	0.60	0.41	0.61

Appendix 1. (Continued)

No	Site	Code	H-D (cm, cm)	H-Cw (cm, cm)	H-Cd (cm, cm)	SLA (cm ² g ⁻¹)	N (mg g ⁻¹)	Wd (g cm ⁻³)	Wc (g g ⁻¹)	Wl (g g ⁻¹)
14	MDF	Mp	-2.45	-0.92	-4.15	164.2	20.90	0.54	0.37	0.56
15	MDF	Nk	-2.45	-0.87	-4.23	124.9	15.50	0.64	0.40	0.58
16	MDF	Po	-2.46	-0.89	-4.24	138.8	14.35	0.68	0.37	0.65
17	MDF	Pg	-2.52	-1.01	-4.43	208.1	22.38	0.58	0.43	0.67
18	MDF	Sme	-2.37	-0.98	-4.42	142.3	15.10	0.45	0.46	0.57
19	MDF	Smu	-2.49	-0.88	-4.34	156.4	17.98	0.50	0.35	0.57
20	MDF	Sp	-2.42	-0.76	-4.37	190.2	19.38	0.21	0.29	0.63
21	MDF	Spr	-2.45	-0.89	-4.39	188.7	20.25	0.40	0.38	0.59
22	MDF	Spa	-2.42	-0.73	-4.33	154.9	17.18	0.58	0.37	0.58
23	MDF	Sq	-2.50	-0.81	-4.59	148.0	17.08	0.41	0.26	0.53
24	MDF	Sm	-2.39	-0.92	-4.49	126.4	17.53	0.54	0.42	0.53
25	MDF	Sc	-2.37	-0.89	-4.45	112.9	17.58	0.73	0.43	0.61
26	HF	Cch	-2.63	-1.15	-4.21	87.6	7.73	0.78	0.39	0.51

Appendix 1. (Continued)

No	Site	Code	H-D (cm, cm)	H-Cw (cm, cm)	H-Cd (cm, cm)	SLA (cm ² g ⁻¹)	N (mg g ⁻¹)	Wd (g cm ⁻³)	Wc (g g ⁻¹)	Wl (g g ⁻¹)
27	HF	Ms	-2.43	-1.12	-4.56	91.5	12.38	0.66	0.43	0.40
28	HF	Hf	-2.71	-0.96	-4.33	156.3	13.57	0.79	0.37	0.46
29	HF	Nkh	-2.52	-1.09	-4.48	69.4	13.46	0.69	0.37	0.55
30	HF	Sa	-2.65	-1.13	-4.35	125.9	8.66	0.79	0.40	0.53
31	HF	Sr	-2.58	-1.02	-4.37	147.1	11.8	0.58	0.53	0.52
32	HF	Sth	-2.68	-1.07	-4.43	138.5	10.93	0.51	0.65	0.55
33	HF	Ss	-2.56	-1.24	-4.51	84.7	9.40	0.66	0.69	0.68
34	HF	Ta	-2.53	-1.10	-4.40	71.6	13.01	0.75	0.51	0.60
35	HF	Tm	-2.65	-1.10	-3.97	50.3	7.59	0.81	0.46	0.36
36	PF	Ccp	-2.63	-1.15	-4.17	81.5	12.73	0.52	0.73	0.56
37	PF	Ds	-2.49	-1.16	-4.26	112.4	11.01	0.34	0.46	0.75
38	PF	Gv	-2.56	-1.06	-4.38	118.9	13.08	0.81	0.39	0.69
39	PF	Hc	-2.45	-0.98	-4.74	172.8	10.46	0.50	0.69	0.71

Appendix 1. (Continued)

No	Site	Code	H-D (cm, cm)	H-Cw (cm, cm)	H-Cd (cm, cm)	SLA (cm ² g ⁻¹)	N (mg g ⁻¹)	Wd (g cm ⁻³)	Wc (g g ⁻¹)	Wl (g g ⁻¹)
40	PF	Nkp	-2.49	-1.12	-4.38	95.5	13.67	0.66	0.43	0.64
41	PF	Pl	-2.57	-1.00	-4.55	142.2	12.68	0.73	0.49	0.71
42	PF	Pr	-2.44	-1.27	-4.59	166.0	10.87	0.87	0.38	0.65
43	PF	Stp	-2.55	-0.94	-4.23	166.0	16.22	0.54	0.69	0.66
44	PF	Sca	-2.56	-1.14	-4.28	146.8	16.06	0.91	0.36	0.62
45	PF	Xe	-2.63	-0.99	-4.26	191.4	14.23	0.80	0.37	0.57

HF, heath forest; PSF, peat swamp forest; MDF, mixed dipterocarp forest; Code, species code as in Table 3.1; H-D, intercept of H vs. D allometry; H-Cw, intercept of H vs. Cw allometry; H-Cd, intercept of H vs Cd allometry; SLA, N, Wd, Wc, Wl functional trait measures shown in Table 3.2.

Appendix 2.

Demographic rates and structural measures of species examined in Sebangau forest (cf. Chapter IV).

Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)	Upper diameter (cm)	Relative growth rate (year ⁻¹)	Mortality (year ⁻¹)	Recruitment rate (year ⁻¹ per-capita)
acrpor	49	0.241	11.1	0.0272	0.0316	0.0816
bluela	62	0.617	22.2	0.0127	0.0142	0.0323
calbif	55	1.016	28.5	0.0267	0.0331	0.0364
calino	62	0.674	18.2	0.0175	0.0352	0.0323
caltey	73	1.087	25.1	0.0218	0.0267	0.0274
camcor	44	0.880	29.8	0.0303	0.0246	0.0455
cragla	37	0.329	17.1	0.0466	0.0523	0.0541
diodaj	42	0.514	22.6	0.0106	0.0127	0.0238
dieexi	25	0.503	27.3	0.0119	0.0171	0.0160
gartet	23	0.242	17.4	0.0096	0.0184	0.0435
gonban	28	1.038	40.3	0.0101	0.0252	0.0357
gymeug	33	0.324	18.7	0.0123	0.0278	0.0303
horcra	55	0.683	20.8	0.0116	0.0151	0.0182

Appendix 2. (Continued)

Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)	Upper diameter (cm)	Relative growth rate (year ⁻¹)	Mortality (year ⁻¹)	Recruitment rate (year ⁻¹ per-capita)
litele	31	0.228	14.0	0.0264	0.0413	0.0323
litlep	27	0.246	19.1	0.0297	0.0179	0.0370
litres	29	0.244	17.3	0.0223	0.0392	0.0345
litruf	30	0.235	14.0	0.0372	0.0228	0.0667
madser	25	0.370	26.8	0.0188	0.0441	0.0000
neophi	87	0.917	18.5	0.0097	0.0232	0.0115
palcoc	36	0.593	27.4	0.0213	0.0187	0.0278
pallei	254	3.507	25.7	0.0207	0.0163	0.0472
sanema	42	0.446	20.9	0.0317	0.0240	0.0238
shopar	39	0.212	13.0	0.0373	0.0373	0.0769
shogui	61	0.811	20.3	0.0304	0.0115	0.0328
stesco	33	0.353	19.6	0.0148	0.0145	0.0303
syzcas	88	1.288	27.4	0.0192	0.0292	0.0455
syzcla	41	0.431	21.5	0.0251	0.0376	0.0488

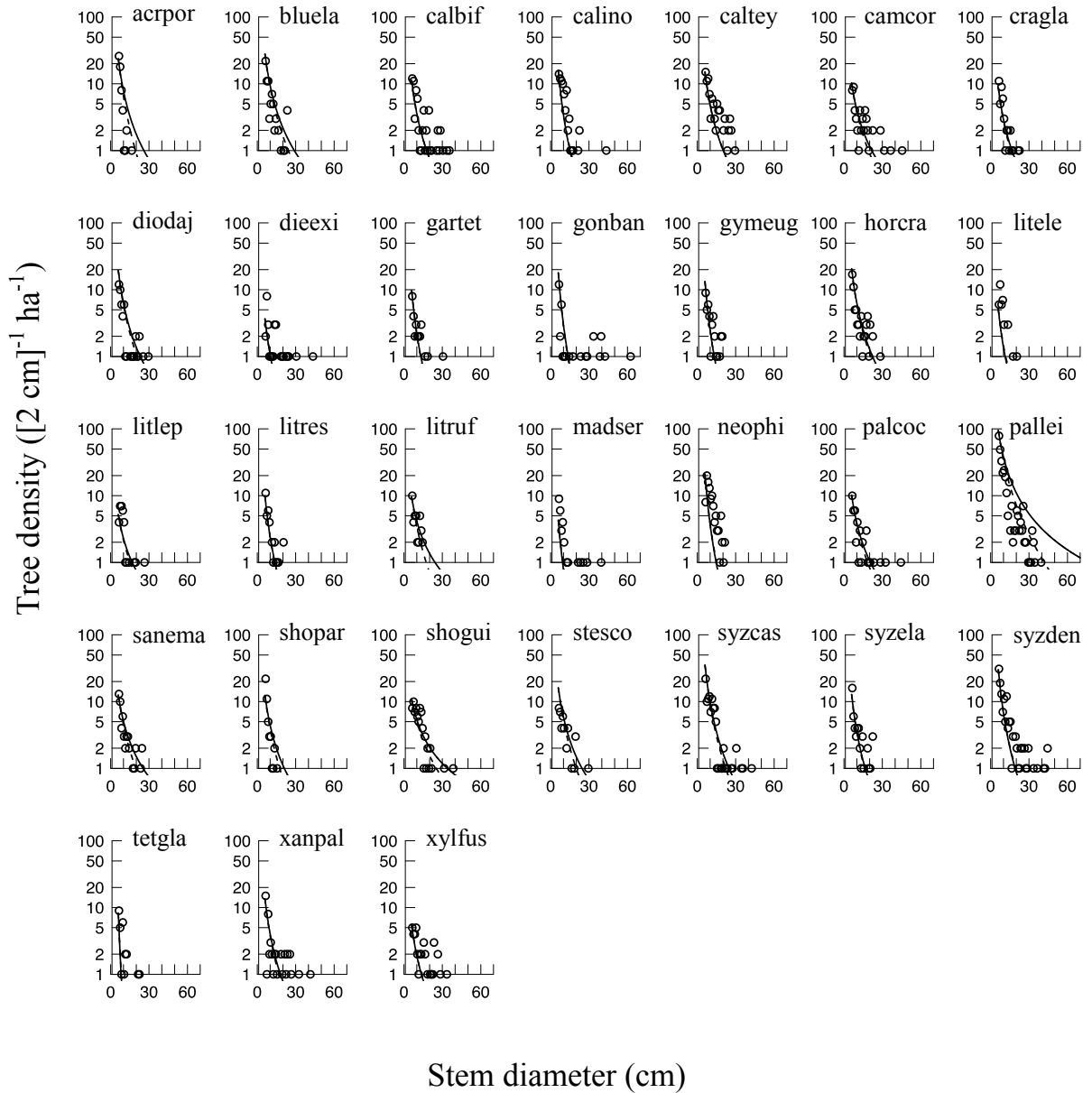
Appendix 2. (Continued)

Code	Tree density (ha ⁻¹)	Basal area (cm ² m ⁻²)	Upper diameter (cm)	Relative growth rate (year ⁻¹)	Mortality (year ⁻¹)	Recruitment rate (year ⁻¹ per-capita)
syzden	111	1.993	29.8	0.0161	0.0312	0.0270
tetgla	22	0.180	18.3	0.0071	0.0416	0.0000
xanpal	40	0.733	26.3	0.0234	0.0319	0.0500
xylfus	33	0.637	26.5	0.0359	0.0385	0.0303

Species codes as shown in Table 4.1.

Appendix 3.

Observed size distribution (circles) and projected equilibrium size distribution (solid lines) of 31 abundant species in Sebangau peat swamp forest (Chapter IV).



Species codes as shown in Table 4.1.