Coexistence of Tree Species Based on Structural Diversity

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Introduction

Structural characteristics of woody plants, such as plant height, leaf size, and biomass allocation to the aerial parts, are quite variable even among the species in a single community. Some structural variations that are linked to specific functions can be the basis for functional trade-offs and can therefore provide a chance for stable coexistence of plant species, which share many of the resources they consume (Westoby et al. 2002). Since the late 1980s, much effort has been made to elucidate the contribution of structural diversity to the stable coexistence of tree species. These studies have revealed that structural diversity contributes to stable coexistence in various ways. For example, the difference between structures that minimize biomass loss and structures that offer rapid growth is essential for niche differentiation along a spatial light gradient (Walters et al. 1993; Kitajima 1994). Another structural variation related to crown structure and trunk thickness is important in terms of the different strategies adopted by understory shrubs and canopy trees (Aiba and Kohyama 1997; Kohyama et al. 2003). However, past studies have had several weak points, and some critical questions remain unsolved. First, few of these studies have examined the potential for coexistence based on structural variations among ecologically or taxonomically related species, for which competitive exclusion is likely to operate. Second, differences in strategy at the sapling stage have been undervalued. In addition, phylogenetic constraints have rarely been considered in previous studies, even though these constraints could dramatically influence the results (Felsenstein 1985). Given these problems, we attempted to answer two questions: (i) Does the structural diversity of plant body lead to functional trade-offs and stable coexistence, even in taxonomically related late-successional species? (ii) How do structural variations in saplings, and especially variations in crown architecture (Kohyama 1987), contribute to stable coexistence? To do so, we focused on late-successional species in a Bornean rain forest with reference to their molecular phylogeny.

Materials and Methods

The study was conducted at Lambir Hills National Park, Sarawak, Malaysia (4°2′ N, 113°50′ E; 150 m a.s.l.). In the analysis focused on dipterocarp species, we measured the following structural traits: root mass, trunk mass, support-tissue mass, total leaf area, individual leaf area, crown projection area, plant height, and diameter at ground level. For non-dipterocarp species, we measured the same traits except for root mass. For the dipterocarp species, we also recorded the maximum net photosynthetic rates (A_{max}) of saplings under the closed canopy and the wood density of mature trees. A_{max} was measured in the field in November 2003 and in March 2004 using a portable infrared gas analyzer (LI6400; LI-COR Inc., Lincoln, Nebraska, USA). The wood density of mature trees was obtained from the research literature on tropical timber (PROSEA 1994; Sudou 1970).
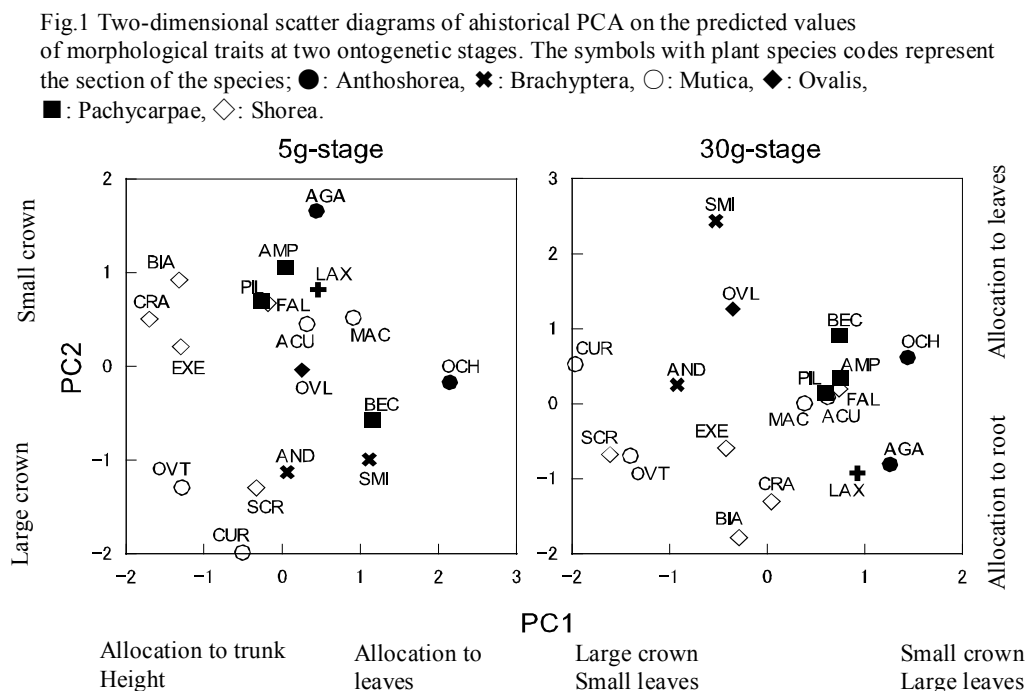
For 11 relatively abundant dipterocarp species, we analyzed their demographics using 5×5 m quadrats (248 in total) distributed in a regular matrix that covered 12 ha throughout two permanent sample plots in the park. In June 2003, all juvenile dipterocarps shorter than 2 m that occurred in the quadrats were numbered, their species was recorded, and their height was measured. In June 2004 (1 year after the first census), the quadrats were re-censused, and the status (i.e., living or dead) of all tagged individuals was verified.

Allometric relationships among the parts of the individual plants were used to describe the structural characteristics of each species at two ontogenetic stages (i.e., with total dry masses of 5 and 30 g). Principal-components analysis (PCA) was performed on the log-transformed estimated values to clarify the constellations of traits by uniting parameters into principal components (PCs). Logistic regression and model selection using the stepwise Akaike information criterion were used to predict the survival rate of juveniles under certain conditions. Using the selected model, survival rates under a canopy openness of 5% at the two ontogenetic stages were estimated. Correlations between structural characteristics and indices of shade tolerance were calculated using the Pearson correlation coefficient for the raw data and, if required, for phylogenetically independent contrasts (Felsenstein 1985).

Results

Sapling structure and regeneration strategy in 18 Shorea species

We tested whether the relationship between juvenile tree structure and function is robust among 18 functionally and taxonomically similar sympatric species of genus Shorea in a tropical rainforest in Borneo. The structural variation in saplings of the genus Shorea was as large as that found in sets of species with much more diverse origins. PCA showed that both crown architecture and the biomass allocation to leaves are major sources of structural variation in the 18 investigated species (Fig. 1). Of these two axes, allocation to leaves was significantly correlated with wood density and showed a limited correlation with

Fig.1 Two-dimensional scatter diagrams of ahistorical PCA on the predicted values of morphological traits at two ontogenetic stages. The symbols with plant species codes represent the section of the species; ●: Anthoshorea, ✖: Brachyptera, ○: Mutica, ◆: Ovalis, ■: Pachycarpae, ◇: Shorea.

photosynthetic rate, whereas crown architecture was significantly correlated with seed size (Fig. 2).

Fig.2 Correlation between PC2 score at the 30g-stage and two indices of shade tolerance
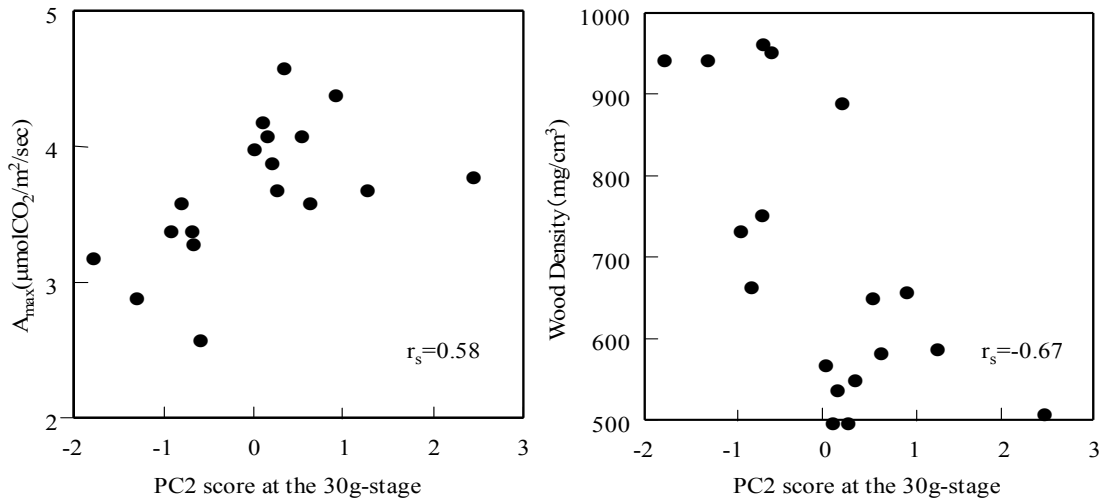
Variation in juvenile survival and related physiological traits among 11 late-successional dipterocarp species

To elucidate the environmental factors and physiological traits that most strongly determine the juvenile survival rate, we focused on 11 late-successional dipterocarp species in 248 quadrats distributed throughout a 12-ha area. We monitored the survival of juvenile (height < 2.0 m) individuals of these species for 1 year. The probability of survival for each species was expressed as a logistic function of plant height and three environmental factors: canopy openness, soil-water potential, and the density of conspecific individuals. Seven species exhibited increased survival under more open canopies, and one species exhibited increased survival and two species exhibited decreased survival at drier sites. Six species showed increased survival as the density of their conspecifics increased, whereas two species showed decreased survival under the same conditions. The magnitudes of the effects of the three environmental factors were similar. However, the interspecific difference in survival was most strongly determined by the dependence of small seedlings on their light environment. Survival under low light was positively correlated with root dry mass and negatively correlated with total leaf area of the juveniles. Species that sustained increased mortality under low light had a set of structural traits (i.e., a high root to leaf area ratio) that would potentially allow rapid growth under bright conditions.

Differences in the dry-mass cost of sapling height growth among 56 woody species co-occurring in a Bornean tropical rainforest.

	R^2	Cross-species analysis			Multiple comparison		
		Adult stature	Crown type	Interaction	Branched	Simple	Compound
M$_W$	0.80	**5.26***	1.12	0.55			
M$_T$	0.80	**8.56****	2.27	0.62			
M$_L$	0.76	0.96	**3.69***	0.94	ab	a	b
M$_S$	0.87	1.67	**10.8*****	0.25	a	b	a
M$_C$	0.74	0.63	1.54	0.71			
A$_L$	0.71	1.74	1.18	0.58			
A$_C$	0.71	0.25	1.08	0.49			
A$_{IL}$	0.94	0.03	**30.3*****	0.70	a	b	b
SLA	0.89	0.08	**5.15****	1.44	ab	a	b
LAI	0.62	1.77	**10.4*****	0.53	a	b	a
D	0.86	**8.59****	**3.63***	0.78	a	b	a
WDI	0.67	0.37	**5.54****	0.33	ab	a	b

Table 2. Summary of two-way ANOVAs with multiple comparisons to test the effect of adult stature and crown type on sapling structural traits. F-values are given for the two main effects and interaction. Degree of freedom of adult stature, crown type and the interaction were 1, 2 and 2. Degree of freedom for residuals were 50 for cross-species analysis. R^2 values were calculated for the model in which the effect of species was nested. Bold values are significant at P < 0.05; *P < 0.05, **P < 0.01, ***P < 0.001. When significant differences were found among crown types, the results of multiple comparisons are also shown. Effects sharing the same letter were not significantly different at P < 0.05.

We analyzed the above-ground structure of saplings from 56 sympatric species in our study forest based on their phylogenetic background to elucidate interspecific variation in the dry-mass cost of height growth and its ecological consequences. The estimated extension cost (i.e., the total above-ground mass) for 1.5-m-tall saplings varied by up to 800% among the 56 species. However, no significant differences in extension cost were observed among saplings with three different crown types (branched, monoaxial simple-leaved, and monoaxial compound-leaved; Table 1), even though the monoaxial crown type has been considered to be an adaptation for achieving rapid height growth. The lack of differences have arisen because the advantages of monoaxial saplings in terms of the structural cost for displaying a given leaf area were unexpectedly small. Understory species had a significantly higher extension cost than canopy species because of their thicker (and consequently, heavier) trunks. For all 56 species combined, the trade-off between height growth efficiency and morphology that enhanced light interception (e.g., larger and more numerous leaves) was prominent. This trade-off, which makes efficient vertical growth incompatible with survival in the understory, potentially enables the stable coexistence of these species in a temporally heterogeneous light environment.

Discussion

Our analyses of the dipterocarp species showed that relatively shade tolerant species are characterized by structural traits that minimize biomass loss, such as a larger allocation to roots and a lower leaf mass per unit area, whereas relatively light-demanding species are characterized by structures that promote rapid growth, such as a large allocation to aerial parts and a high leaf area per mass ratio in both the seedling and the sapling stages. Thus, the light gradient can be partitioned by late-successional dipterocarp species even in the

absence of canopy gaps based partly on the structural trade-offs, which is similar to the partitioning of the light gradient by pioneer species.

In the 18 Shorea species, structural variation in the saplings could be summarized by two independent axes, an axis for biomass allocation and an axis for crown architecture. This represents the first report that the variation in biomass, which has been discussed mainly for first-year seedlings, is independent of the variation in crown architecture at the sapling stage. In our analysis of 56 tree species, including non-dipterocarps, we revealed an eight-fold variation in extension cost along the axis for variation in crown architecture; therefore, this axis could be correlated with height growth rate. Whereas the variation in biomass allocation enables stable coexistence based on spatial heterogeneity in the light environment, the variation in crown architecture enables coexistence based on temporal heterogeneity in the light environment (Kohyama 1987; Kohyama and Hotta 1990).

The partitioning of spatial and temporal variation of light based on structural diversity and environment-dependent survival of ecologically or taxonomically similar tree species suggests that the community structure is rather stable and deterministic, which contrasts with the prediction of the unified neutral theory of biodiversity and biogeography (Hubbell 2001). Though only a few intensive comparisons of related species have previously been reported, a study of pioneer species in genus Macaranga at the same site also concluded that the coexistence of species was stable and deterministic and was based on interspecific variation in physiology and structure (Davies et al. 1998). Based on the results of our study, we believe that greater efforts to elucidate the mechanisms responsible for the coexistence of ecologically and taxonomically related species will be one of the most effective strategies for providing a thorough understanding of tropical forest communities.

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