

# Forest Architecture of Lambir Rain Forest Revealed by a Large-Scale Research Plot

## II. Physiognomic Dimensions

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### ABSTRACT

The stand structure of a mixed dipterocarp forest at Lambir was analyzed by using the data, which were obtained from a fifty-two hectare research plot established within the Lambir National Park, Miri, Sarawak, East Malaysia, though a range of data analyses was inevitably confined to the topics of physiognomic dimensions owing to floating species identification data. The forest height evaluated by a height curve model was the tallest in Lambir among three research sites, BCI, Pasoh, and Lambir. By dividing 52 ha plot into 1300, 20 m x 20 m stands, the physiognomic dimensions, such as the biomass, tree density, maximum dbh, and basal area per stand, were calculated and their dependency on topography was statistically tested. The results of statistical tests suggested the significant difference of physiognomic dimensions between stands marked by different topographic conditions in terms of slope altitudes, angles, directions, and convexity degrees. The correlated changes in physiognomic dimensions and local topographies implied the dependency of the occurrence of three growth phases (gap, building, and mature phases) in the forest growth cycle upon topography. The size structure of the stands was analyzed by using dbh data and by assuming the exponential distribution of dbh. The stands were characterized by stratified subpopulations, whose total number per stand was in a range between two and seven. The variation in the number of sub-populations per stand corresponded well to the altitude difference between stands, suggesting correlated changes among the forest stratification, forest growth cycle, and topographies. All these results suggested the predictable change of the huge and complex architecture of the Lambir rain forest with respect to topography or environmental conditions such as soil water. Furthermore, the results seemed to be favored by the equilibrium hypothesis rather than non-equilibrium hypothesis as a working mechanism of tropical biodiversity, though floristic composition can be independent from physiognomic dimensions.

## INTRODUCTION

A long-term and large-scale research of a tropical rain forest was recently initiated on a hilly slope at the Lambir National Park, Sarawak, East Malaysia. The research involved at establishment of a 52 ha research plot for the multi-purpose use in researches, forest conservation, park management, etc. In a preceding study (Yamakura et al., 1995), we described an outline of the research program and study site. Furthermore, we analyzed the detailed structure of the topography or physiography of our plot built under a deep canopy of mixed dipterocarp forest with various dipterocarp dominants. The altitude difference between the highest and lowest points in the plot was ca. 150 m, showing steep topography at Lambir. Hypsodiagrams in quantitative geography suggested the more hilly and complex topographies of our plot at Lambir compared with other similar research plots at Pasoh in Peninsula Malaysia (Manokaran et al., 1990) and BCI in Panama (Hubbell & Foster, 1983). The detailed statistics of four topographic variables, such as altitudes, angles, directions, convexity indices of slopes, were calculated for respective 1,300 quadrats 20 m x 20 m in area within the plot. These statistics also clarified the steep and complex topographies of the plot. Using these results, the present study analyzes the forest structural patterns of physiognomic dimensions, such as tree height, stem diameter, stand biomass, etc. The first forest inventory record from a large-scale research plot should offer an unprecedented opportunity for understanding the structural aspects of species or floras. However, the topics of species are ignored here, since our species data are floating at present in 1994, as already described in the preceding study (Yamakura et al., 1995).

## METHODS

Our research was carried out on steep slopes in the Lambir National Park with an approximate latitude of 4°E and longitude of 114°E, respectively, in Sarawak, Malaysia. The most of the park area is covered by an undisturbed original vegetation, the mixed dipterocarp forest common in lowlands in Borneo. Our study site was chosen so as to represent the mixed dipterocarp forest. The general descriptions of the study site with respect to the park history, climate, physiography, geology, soil, and vegetation are abbreviated here, since they were given in the preceding study (Yamakura et al., 1995).

The land survey for plot demarcation was initiated in November 1990 and finished in March 1992, spending about 1.5 years (cf. Chai et al., 1995; Yamakura et al., 1995). It was followed by the assessment of trees or forest inventory, which was initiated in August 1991 and finished in September 1993. A total of 358,905 trees 1.0 cm and greater in stem diameter at breast height (dbh) were individually labeled, mapped, identified to species, and measured by dbh. In labeling trees, we divided the 52 ha plot into 1,300 quadrats 20 m x 20 m in area and prepared different series of labels specific to each quadrat. Further details of the inventory work are also abbreviated here, since they were described in a separate paper (Chai et al., 1995). The data entry of forest inventory records into computers was initiated in September 1993 and continued till April 1994 (Chai et al., 1995). Therefore, about four years were spent for all the necessary field and laboratory works in plot establishment. Besides

these forest inventory works, 112 trees were sampled within the 52 ha plot and their tree height was measured by one of us (T.Y.), for a determination of a tree height curve indispensable for stand biomass estimation.

## RESULTS

### Tall Forest Stature

The relation between dbh and tree height was approximated by a height curve model consisted of a hyperbolic equation of height to dbh (Ogawa et al., 1965), i.e.

$$1/H = 1/(AD) + H^* , \quad (1)$$

where H is tree height in m, D is dbh in cm, and A and H\* are coefficients specific to a forest. The coefficient A was highly correlative with the biomass density or forest biomass divided by H\*. The other coefficient H\* stands for the possible maximum tree height specific to the forest (Ogawa et al, 1965; Ogawa, 1969; Kira & Ogawa, 1971). The coefficients, A and H\*, estimated from the 112 sample trees by the least squares method were 2.162 m/cm and 63.0 m, respectively (Fig. 1). The maximum tree height of 1.0 m was recorded from a tree of *Shorea inappendiculata* 116.5 cm in dbh, which was used in coefficient estimation. Trees over 70 m in height might be sparsely distributed in the plot, though their height measurements were impossible owing to the dense canopy at the lower forest stratum. The estimates of A and H\* at Lambir were greater than those at BCI (A = 1.64 m/cm, H\* = 42.8 m; this study) and Pasoh (A = 2.0 m/cm, H\* = 61.0 m; Kato, Tadaki, & Ogawa, 1978), suggesting the more dense biomass packing and taller forest architecture of the Lambir rain forest. Although the statistical test for discerning coefficient differences between Pasoh and Lambir was impossible owing to the lack of original data at Pasoh, the differences of the coefficients between two sites might be smaller because the dispersion of observed data at Lambir in the dbh vs. tree height diagram was large (Fig. 1). According to Ogawa's experience in some Southeast Asian forests (Ogawa, 1969), the coefficient A tends to decrease as the other coefficient H\* increases, since biomass density correlative with A decreases with an increase of forest height correlative with H\*. Therefore, the positive correlation between A and H\* at three sites was an unusual example in coefficient changes so far known through several preceding studies in tropical Asia. However, if biomass density and forest height increase along environmental gradients, the positive relation between A and H\* is possible.

The differences of tree height curves among three sites seemed to coincide well with the mean duration of dry months in a year. The seasonal rhythm of rainfall at BCI is characterized by long and clear dry spells, which start in late December or early January, continue ca. 18 weeks, and end around April (Windsor, 1990). The rainfall pattern in the tropics coincides well with the shifts of ITCZ driven by the effects of the changing zenithal position of the sun, in general. At Pasoh, the seasonal rainfall rhythm has two rainfall peaks around April and November, respectively, and two short dry periods intermitting the everwet climate around February and July, respectively. About one month dry spell in June with little rainfall less than 100 mm/month is clearly recognizable in the Walter's climate diagram in Fig. 2. The rainfall at Lambir exceeds

100 mm in all the months of a year without showing clear dry seasons (Fig. 2). Thus, the climate at Lambir is the wettest among three sites.

The soil nutrient is an important factor for the height growth of forest trees in some Southeast Asian forests without severe droughts (Yamakura et al., 1989). The soil chemical properties at BCI seemed to be the richest in nutrients among three sites, since the soil at BCI is derived from basalt. The nutrient contents of Lambir soils (Katagiri, 1990) were similar to or less than those at Pasoh (Yoda & Kira, 1982). Therefore, the soil nutrient might be less important in comparing forest height among three sites. The effect of dry spells on height growth is severer than that of soil nutrients, following the Liebig's law of minimum as a general principle in plant ecology (Numata, 1974).

### Huge Stand Biomass and Its Big Local Variations

By dividing the 52 ha plots into 1,300 quadrats 20 m x 20 m in area, the several physiognomic dimensions were calculated for respective quadrats, which are tentatively designated the forest stands in the present study. The calculated dimensions were the tree density, maximum dbh, basal area, and aboveground biomass. A summary of the statistics of these dimensions is given in Table 1. The similar results were also given in a separate paper by one of us (Chai et al., 1995). Stand biomass in Table 1 represents aboveground biomass excluding roots and were estimated by the allometry method (Research Group on Forest Productivity, 1960; Ogawa & Kira, 1977). The allometric relations were obtained by harvesting sample trees in the mixed dipterocarp forest with *Shorea laevis* Ridl. dominant at Sebulu, Kutai District, East Kalimantan in Indonesian Borneo (Yamakura et al., 1986). These allometry equations are reproduced here by the following empirical equations,

$$WS = 2.903 \times 10^{-2} (D^2 H)^{0.9813}, \quad (2)$$

$$WB = 0.1192 WS^{1.059}, \quad (3)$$

$$WL = 0.9146 \times 10^{-2} \{WS + WB\}^{0.7266}, \quad (4)$$

where D is dbh in cm, H is tree height in m, WS is stem dry weight in kg, WB is branch dry weight in kg, and WS+WB in kg stands for the sum of WS and WB of an individual tree. Tree height H was tentatively estimated from dbh or D by using Eq. (1) with coefficients, A = 2.162 m/cm and H\* = 63 m, as already described. Therefore, all the dimensions in biomass computation were estimated by dbh without measuring the other dimensions.

The variance statistics of different physiognomic dimensions in Table 1 clearly suggests the big local variations of forest architecture within the plot, as shown by an example of the spatial distribution of biomass per quadrat or stand in the plot (Fig. 3). The spatial pattern in biomass seemed to be parallel to those of the other dimensions listed in Table 1, since the dimensions in Table 1 were significantly correlative between each other and since biomass was calculated by incorporating dbh, tree height, and tree density (cf. Eqs (1)-(4)). Therefore, the spatial pattern of stand biomass was

thought to be a representative of those of the other physiognomic dimensions and was investigated in its details.

A diameter of respective circles in Fig. 3 is proportional to stand biomass, of which frequency distribution is shown in Fig. 4. The largest and smallest biomass values were 1,826 ton/ha and 9 ton/ha, respectively. The mean biomass was 520 ton/ha (Fig. 4). According to the experience by one of us in East Kalimantan in Indonesian Borneo (Yamakura et al., 1986), the biomass differences between different forest stands resulted from the difference of growth stages in terms of the forest growth cycle (Whitmore, 1984). Hence, small circles in Fig. 3 and smaller biomass classes in Fig. 4 correspond to the gap phase in the forest growth cycle, while large circles represent the mature phase. The mean stand biomass, 520 ton/ha, in Lambir was little greater than that of 509 ton/ha in the aforementioned forest in East Kalimantan, where the gap, building, and mature areas within a 1.0 ha study plot were in the ratios 0.10:0.15:0.75 (Yamakura et al., 1986). Although the ratios of areas was unknown in Lambir, the area ratios in Lambir might be comparable to those in East Kalimantan.

In general, the stand biomass tends to be proportional to forest height. If we tentatively measure forest height by the possible maximum height  $H^*$  in Eq. (1), it was 63 m in Lambir and 88.4 m in the aforementioned forest in East Kalimantan. Forest height measured by the observed maximum tree height was 61 m in Lambir and 70.7 m in East Kalimantan. However, the mean biomass in Lambir was little greater than that in East Kalimantan, suggesting a difference in biomass density between two sites. The aboveground biomass divided by forest height is designated the biomass density or plant mass packing per unit forest space, which is defined by a product of unit land area and forest height. Biomass divided by forest height is more or less constant and its average is similar to or less than the physical density of the air mass ( $1.3 \text{ kg/m}^3$ ) (Hozumi, 1964). Biomass density tends to be levelled off by an increase of forest height because the natural forest disturbances due to the tree falls or senescence of big trees are generally severe in tall forests than in lower forests. Following this tendency in biomass density, mean stand biomass in our Lambir plot was thought to result from an optimum condition, which reconciles a contradiction between forest height growth and biomass density accumulation to keep stand biomass at its climax. Thus, biomass in our Lambir rain forest is huge.

### **Correlated Changes in Stand Biomass and Topography**

We thought that the big local variations of the physiognomic variables, such as biomass, in the 52 ha plot were highly correlative with the phases in the forest growth cycle, as already described. However, biomass may change with respect to other factors, such as topographic conditions, if the frequencies of respective growth phases of the forest growth cycles are highly correlative with the concerned factors. To confirm a possibility of the dependency of biomass on topographies, the 1,300, 20 m x 20 m stands were classified into several groups following the stand topographic conditions analyzed in the preceding study (Yamakura et al., 1995). We had already examined topographic variables; altitudes, angles, directions, and convexity indices of slopes. Furthermore, we categorized the variables into several classes by their respective values. For example, the index of the convexity of slopes, ICS, was classified into three groups representing convex, monotonous (or flat), and concave

slopes, respectively. Following the ICS classes in the preceding study, the respective 1,300 biomass estimates were lumped into three classes by ICS of the stands. The occurrences of biomass estimates in respective classes of convex, flat, and concave slope categories are shown in Fig. 5. Mean biomass values were 422, 508, and 640 ton/ha for concave, flat, and convex slopes, respectively. The t-test suggested the significant difference ( $P < 0.001$ ) between these three mean biomass values. Thus, the biomass was correlative with ICS as one of topographic variables. Besides the t-test, the ANOVA-test was also applied to confirm the dependency of biomass on ICS. The result of the test supported that of the t-test. This dependency of biomass on topography was true for the other variables, the tree density, maximum dbh, and basal area (Table 3). Therefore, physiognomic dimensions clearly depended upon the topographic variables, suggesting the topographic influence on the occurrence of the three growth phases, gap, building, and mature phases, in the forest growth cycle.

### Size Structured Forest Stands

The 1,300, 20 m x 20 m quadrats are also tentatively designated stands, here. Any one of stands thus defined was consisted of big and small trees, and was highly size structured. The size structure of a forest stand had been represented by the frequency distribution of individual tree size, such as dbh, in forest researches (Hozumi, Shinozaki, & Tadaki, 1968; Yamakura & Shinozaki, 1980). Following the conventional aspects in preceding researches, the frequency distribution of dbhs of individual trees is analyzed in this section.

A model of a probability density function of random variables, Weibull distribution, was first adopted to describe the frequency distribution of dbh in a stand, since it has a wide applicability to observed data (Japanese Standards Association, 1972). It is well known as one of non-normal continuous distributions, favored by recent forest researches (Stauffer, 1979; Cao & Burkhardt, 1984; Jayaraman & Rugmini, 1988), and written in the form,

$$f(x) = (m/\alpha)(x - \xi)^{m-1} \exp[-(x - \xi)^m/\alpha], \quad (5)$$

$$F(x) = 1 - \exp[-(x - \xi)^m/\alpha], \quad (6)$$

where  $x$  is dbh in cm,  $f(x)$  is the probability density function of  $x$ ,  $F(x)$  is the distribution function of  $x$ , and the other symbols,  $m$ ,  $\alpha$ , and  $\xi$ , are coefficients specific to a stand. The coefficient  $m$  gives determinative effects on the shape of  $f(x)$  in the  $x$  vs.  $f(x)$  diagram. The coefficient  $\alpha$  is concerned with the scaling of  $x$ . The other coefficient  $\xi$  is available for truncating  $x$ . In applying  $f(x)$  of Eq. (5) to observed data, the coefficient  $\xi$  was assumed to be 1.0 cm because the minimum dbh was 1.0 cm in our forest inventory.

The estimation of the coefficient  $m$  of Eqs. (5) and (6) was done by using the popular statistical method based on the following definitional equation of the coefficient of variation of  $x$  (Japanese Standards Association, 1972), i.e.

$$CV[x] = \frac{D[x]}{E[x]} = \frac{\sqrt{\Gamma\left(\frac{2}{m}+1\right) - \Gamma^2\left(\frac{1}{m}+1\right)}}{\Gamma\left(\frac{1}{m}+1\right)} \quad (7)$$

where,  $CV[x]$  is the coefficient of variation,  $D[x]$  is the standard deviation of  $x$ ,  $E[x]$  is the mean of  $x$ , and the symbol  $\Gamma$  denotes the gamma function. After estimating the coefficient  $m$ , the other coefficient  $a$ , was estimated by the equation (Japanese Standards Association, 1972),

$$\alpha = \sum x^m / N^* \quad (8)$$

where  $N^*$  stands for the number of samples per stand. An example of the fit of the Weibull distribution is shown in Fig. 6, by using the estimated coefficients. The chi-square test supported the applicability of the distribution function to the observed data in all the stands, when a dbh class interval of 5.0 cm was used in the test. The frequency distribution of the estimated coefficients is given in Fig. 7. The coefficient  $a$  increased with an increase of the coefficient  $m$ . Here, it is noteworthy that the most of estimated  $m$  values are less than 1.0, excluding four estimates. The four estimates of  $m$  are greater than 1.0 but never exceed 1.2. When  $m = 1.0$ , the Weibull distribution gives the exponential distribution. When  $m < 1.0$ , the Weibull distribution can express a highly skewed L-shaped frequency distribution of samples. This type of frequency distributions is monotonous in shape without having any modal sample value.

Although the chi-square test suggested the fit of the Weibull distribution to the observed dbh data, a more sensitive test was tried by using a probability paper. In the case of the Weibull distribution, a numerical transformation of  $x$  and  $F(x)$ ,  $\log \log [1 / \{1 - F(x)\}]$  and  $\log x$ , gives a probability paper (cf. Eq.(6)). If a set of data of samples follows the Weibull distribution, a trajectory of  $\log \log [1 / \{1 - F(x)\}]$  is linear with respect to  $\log x$  in the probability paper. However, the relationship between  $\log \log [1 / \{1 - P(x)\}]$  and  $\log x$  was not linear in the probability paper and approximated by several segmental linear lines (Fig. 8), which suggested the complex size structure with discrete subpopulations. The occurrence of the subpopulations might reflect a mosaic of subpopulations with different birth histories.

### Stratification of Individuals

If the discrete subpopulations are included in the whole sample population, the further understanding of the sample population is given by discerning respective subpopulations consisting the whole sample population. It follows that the stratification of individual trees in a stand into subpopulations is helpful for the better recognition of our study forest. Following this idea, the stratification of individual trees was carried out as described below.

For stratifying the individuals, we adopted the probability paper of the exponential distribution of dbh, since most of the estimates of the coefficient  $m$  of Weibull distribution (Eq. (5)) were smaller than 1.0 and suggested a monotonous



frequency curves with respect to dbh, and since the exponential distribution is easy to handle. We write the exponential distribution of dbh in the form,

$$f(x) = \exp[-x / \mu] / \mu, \quad (9)$$

$$F(x) = 1 - \exp[-x / \mu], \quad (10)$$

where the symbols,  $x$ ,  $f(x)$ , and  $F(x)$ , are the same with those in Eqs. (5) and (6). The symbol  $\sim$  denotes the coefficient specific to a stand and coincides with the mean of  $x$ . Here, we introduce the ordered ranking of individual trees arranged in a descending order of their dbh and tentatively denote it by  $N(x)$ . The  $N(x)$  is expressed by the equation (Hozumi & Shinozaki, 1970; Hozumi, 1975),

$$N(x) = N^* \int_x^{\infty} f(x) dx = N^* \exp[-x / \mu] \quad (11)$$

$$x = \mu \log N^* - \mu \log N(x)$$

where  $N^*$  is the total number of individuals of the stand. Eq. (11) offers a basis of the probability paper of the exponential distribution. It follows that the  $\log x$  vs.  $\log N(x)$  relation is one of expressions of the probability paper for the exponential distribution (Fig. 9).

The  $\log x$  vs.  $\log N(x)$  relation was graphically drawn for respective 1,300 stands, as shown in Fig. 9. The several segmental linear lines were necessary to approximate the observed  $\log x$  vs.  $\log N(x)$  relation. Each segmental line was thought to express a subpopulation. The number of stratified subpopulations per stand counted for 1,300 stands was in a range between two and seven. Its mean was 4.3 per stand with a standard deviation of 0.82, implying the multi-layer system of the tropical rain forest explained by Richards (1952, 1983). The variation of this quantity among stands might reflect the phases of the forest growth cycle. Furthermore, the number of subpopulations per stand tended to increase with a decrease in altitude (Fig. 10). This tendency in the number of subpopulations was consistent and confirmed by the ANOVA-test. However, its correspondence to slope angles, directions, and ICS values was denied by the ANOVA-test.

Using the results of the stratification of individuals, the mean dbh per stand was calculated for each of 5,576 subpopulations discerned by stratification. The mean values thus obtained decreased with an increase of tree density per subpopulation (Fig. 11 & 12). The trajectory of mean dbh to tree density per subpopulation in Fig. 11 might be written in the form,

$$1/D_i = \rho_i/K + 1/L, \quad (12)$$

where the symbol  $i$  is an identification number of subpopulations,  $D_i$  is mean dbh per subpopulation,  $\rho_i$  is tree density per subpopulation, and  $K$  and  $L$  are coefficients specific to the data. However, when we calculated the average of  $D_i$  and  $\rho_i$  by classifying the data into six groups (Fig. 12), a linear line for two variables became clear, i.e.

$$\log D_i = 2.170 - 0.7882 \log p_i \quad (13)$$

The absolute value of the line gradient, 0.7882, is rather greater than 0.5 expected by the physical dimensions of two variables, implying the severe suppression of smaller trees by the larger trees.

The density dependency of plant growth is well known in forestry and plant ecology and was reported by several studies of single-story forests composed of single species (Reineke, 1933; Yoda et al., 1963; Hozumi & Shinozaki, 1970; Harper, 1977; White, 1981) and natural forest communities with superimposed multi-stories consisting of various species (Yamakura, 1989). Although the subpopulations in the present study might not strictly correspond to the stories or layers in terms of forest stratification conceptualized by Richards (1952), the dependency of mean dbh upon tree density in subpopulations supported the facts so far found in the preceding studies.

## DISCUSSION

The forest stature of our Lambir rain forest was the highest among the three forests at BCI in Panama, Pasoh in West Malaysia, and Lambir in Sarawak, though the its difference between Pasoh and Lambir might be insignificant owing to the large dispersion of observed data in the dbh vs. tree height relation. The forest at BCI was the lowest among three sites and highly affected by the long dry spells. The largest forest stature in Lambir suggested that the favorable ever-wet climatic conditions, such as in Lambir, without severe dry spells throughout a year is indispensable for tree height growth in tropical rain forest in the world. Hence, a biological principle, no life without water, could clearly explain the differences in forest height among three sites. It follows that the forest at BCI might experienced a severe climatic sieve in terms of forest architecture. If the climatic moisture condition, especially rainfall, is favorable enough to allow the moist forest in all the localities inside Sarawak, the forest height differences between rain forests in Sarawak should be explained by factors other than rainfall, i.e topographic and edaphic conditions (Richards, 1952; Ashton & Hall, 1992).

Mean stand biomass calculated for respective 1300, 20 m x 20 m quadrats seemed to arrive at the climax in its development, which is attained by reconciling the antagonistic requirements from forest height growth and biomass density growth. The mean aboveground biomass values calculated by Brown et al. (1989) for undisturbed tropical rain forests in three continents were 170 ton/ha in America, 260 ton/ha in Africa, and 214 ton/ha in Asia. These values were far smaller than biomass at Lambir, 520 ton/ha, since the biomass values estimated by Brown et al. included the estimates from the forests in dryer climatic conditions. An implication from the differences between the estimates is that the vanishment of Sarawak rain forest contributes to the large loss of tropical forest biomass. The Biomass differences among BCI, Pasoh, and Lambir were obscure, since biomass have never been calculated at BCI and Pasoh.

In addition to biomass, other physiognomic dimensions were also handled in the present study. All the dimensions including biomass represented large local variability within the plot. The variation of these dimensions was highly predictable with respect to topography. The determinant effect of topography on the forest

structure was not consistently investigated in preceding studies so far carried out in tropical rain forests, since the topographic conditions were rather difficult in their quantification and evaluation and since the large research plot is necessary for getting meaningful topography data. The effects of topography might be substituted by some other factors, such as soils, in the preceding studies (eg. Ashton, 1964; Ashton & Hall, 1992) because the topography is inevitably combined with other factors (solar radiation, soil water, wind, rainfall, disturbance, etc.) and represents a mixed factor consisting of the different but mutually related aspects, altitude etc. (Yamakura et al., 1994). The predictable changes of the physiognomic dimensions with respect to topographies suggests the forest architecture adapted to environmental conditions, denies the random or chance occurrence of the architecture in a given land space, and will be favored by the niche theory (Hutchinson, 1957) or equilibrium hypothesis rather than the non-equilibrium hypothesis (Hubbell & Foster, 1986), though floristic composition can be independent from forest architecture.

All the individual trees in respective 20 m x 20 m stands were stratified into several subpopulations by a probability paper of the exponential distribution of dbh. The stratification of individuals with respect to tree height is one of phenomena included in the concept of forest stratification emphasized by Richards (1952) and was numerically analyzed by several studies (Hozumi, 1975; Yamakura, 1987). Dbh handled in the study was approximately linear with respect to tree height, if dbh was in an narrower range (cf. Fig. 1). According to the former experience by one of us (Yamakura, 1989), the results of the stratification of individuals by dbh corresponded well to those of stratification by tree height. Hence, the stratification of individuals by dbh in the present study seemed to be comparable to that by tree height. However, the difference between stratification by dbh and stratification by tree height should also be examined in studies at Lambir, in the future.

Although it remained obscure that whether the subpopulations corresponded to the layers in terms of Richards, the number of subpopulations varied between stands. This variation in classified subpopulations might suggest the dependency of forest stratification on the topography and phase of the forest growth cycle (Oldeman, 1978). To confirm the occurrence of subpopulations in the present study, demographic data of the birth, growth, and death of trees are necessary (Yamakura, 1987). For example, the exponential distribution of dbh can be easily transformed into a corresponding distribution function of any one of parameters of tree growth, such as relative growth rates of dbh or  $d(\text{dbh})/dt/\text{dbh}$  in Malthusian dbh growth, when a growth function of dbh is explicitly given. All the parameters of individual tree growth should satisfy the conditions limited by the exponential distribution or distribution function. Therefore, the derived distribution function of relative growth rates of dbh will offer a standard scale for evaluating the possibility of forest stratification by using observed dbh growth data.

The mean dbh per subpopulation followed the power law system studied by Yoda et al. (1963). The system is well known and recognized as a phenomenon, which represents an adjustment of plants to the overcrowding or competition for living space between individuals. Therefore, the density dependency in sub-population dbh growth harmonizes with the equilibrium hypothesis, as well as the stratification of individuals.

The non-equilibrium hypothesis proposed by Hubbell and Foster (1986) is one of the most stimulus theories for the explanation of working mechanisms of tropical biodiversity. To test the applicability of the theory to Lambir rain forest, the finalization of our species data are necessary in the earliest opportunity. Concerning this, some forest architectural aspects of species will be discussed by using a part of species data so far compiled, though the conclusion of the discussion will be inevitably tentative and hypothetical.

### CONCLUSION

The forest height differences between three research sites, BCI, Pasoh, and Lambir, corresponded well to the dry spells in rainfall rhythms at three sites. This implied a severe climatic sieve at BCI. The physiognomic dimensions such as biomass were significantly correlative with complex Lambir topographies, suggesting topographic influence on the occurrence of respective growth phases in the forest growth cycle in Lambir. Furthermore, the forest was highly size structured and was recognized as a mosaic of 1,300, 20 m x 20 m stands with different stratified subpopulations, which were constrained by the density dependency of mean dbh growth per subpopulation. These results clarified the huge and complex architecture of the Lambir rain forest and seemed to support the equilibrium hypothesis rather than non-equilibrium hypothesis as the working mechanisms of the biodiversity in tropical rain forest, though floristic composition can be conceptually free from any constraints of physiognomic dimensions.

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## Discussion for Yamakura *et al.*'s papers

**Ashton** I am very interested to see the early graphs in our paper in which you show the Lambir has the tallest forests, the distribution of which is different from Pasoh and certainly from BCI. I wonder if there is any method whereby you can test the statistical significance of the difference or whether that you think this will be very meaningful. Did you test whether there are statistical differences between them?

**Yamakura** I didn't measure any physical differences. I simply applied conventional method. The statistical differences would have been easy to test if I had measured tree heights.

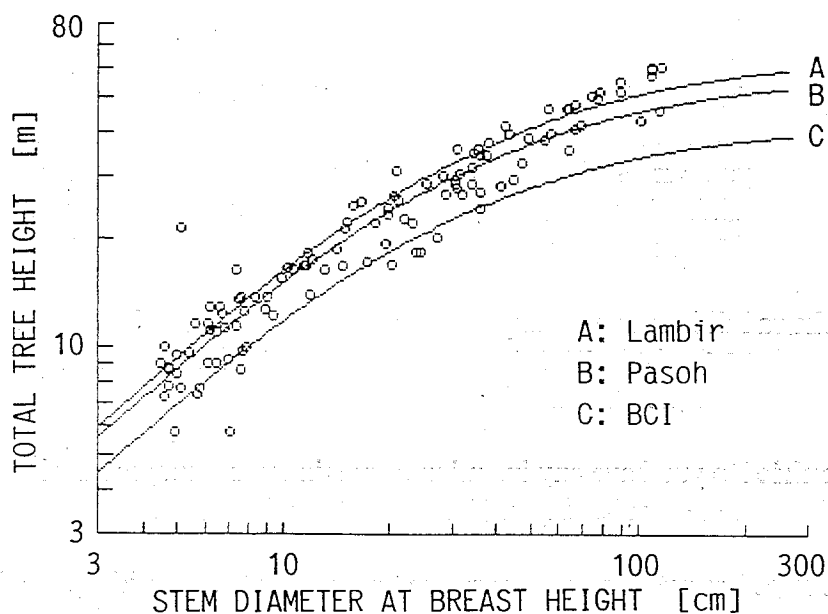
**LaFrankie** Do you have any intention of making your topographical measurements more precise, say at 10 m or 5 m grid intervals?

**Yamakura** Yes we do want to map the topography to 5 m grid to get a better understanding of the relationship between species distribution and topography. Maybe we can combine soil measurement with this, but it is a major exercise.

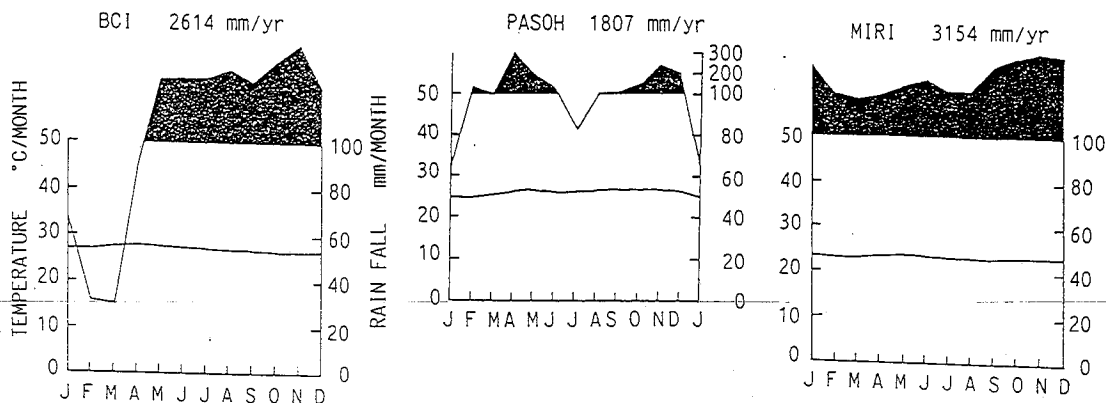
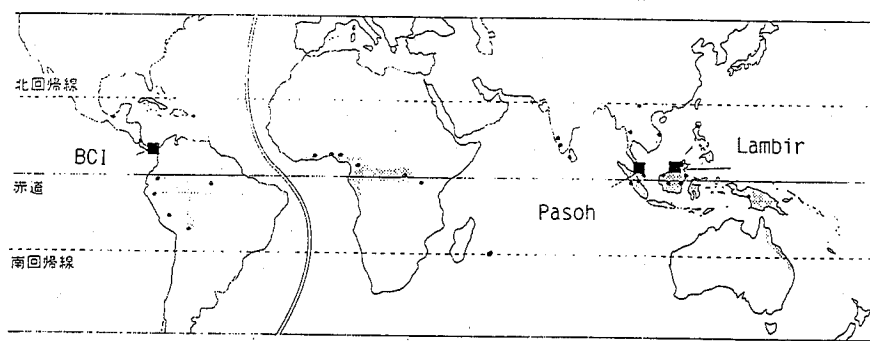
**LaFrankie** Is it possible after slopes have been corrected that the plot will be smaller than 50 ha or 52 ha? This might have a bearing on the densities of trees.

**Yamakura** This has still to be worked out.





**Fig. 1.** Tree height curves at three research sites, BCI, Pasoh, and Lambir. Height curves consisting of a hyperbolic equation of tree height ( $H$ , m) to stem diameter at breast height ( $dbh = D$ , cm) are written in the form,  $1/H = 1/(AD) + 1/H^*$ , with coefficients  $A$  and  $H^*$  specific to the forest. Clear circles represent observed values at Lambir. Symbols, A, B, and C, stand for the sites, Lambir, Pasoh, and Barro Colorado Island (BCI), respectively.



**Fig. 2.** Walter's climatic diagrams at three research sites. The climatic diagram at BCI depends on the records by Windsor (1990). The diagram of Pasoh is reproduced with amendments from the graphs drawn by Kira (1978). Data compiled by Kurashima et al. (1964) and by Department of Civil Aviation and Meteorological Services, British Borneo Territories (1961) are used for the diagram at Lambir.

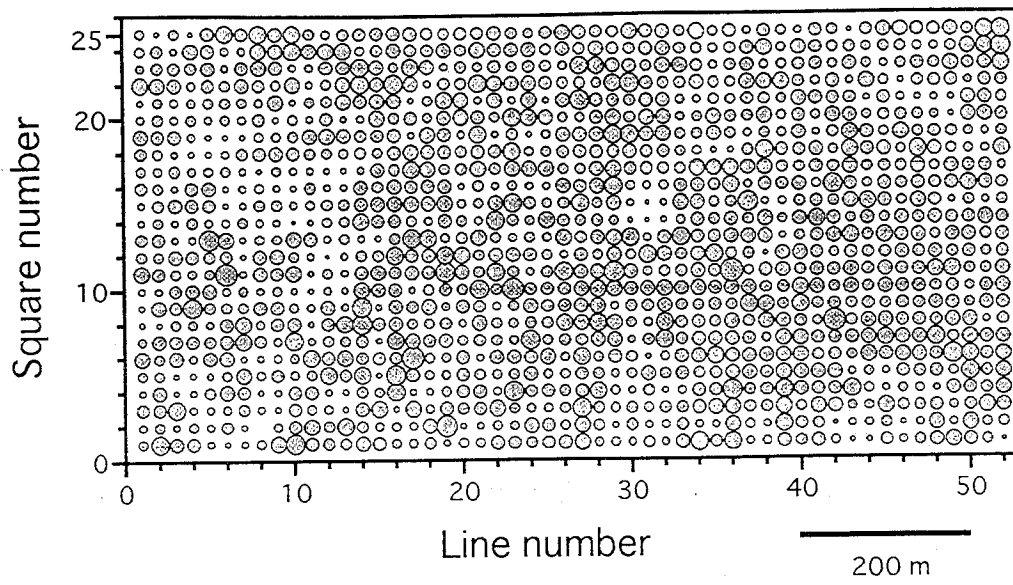


Fig. 3. Spatial pattern of aboveground biomass in the 52 ha plot. The diameter of a circles is proportional to stand biomass estimated by a 20 m x 20 m quadrat.

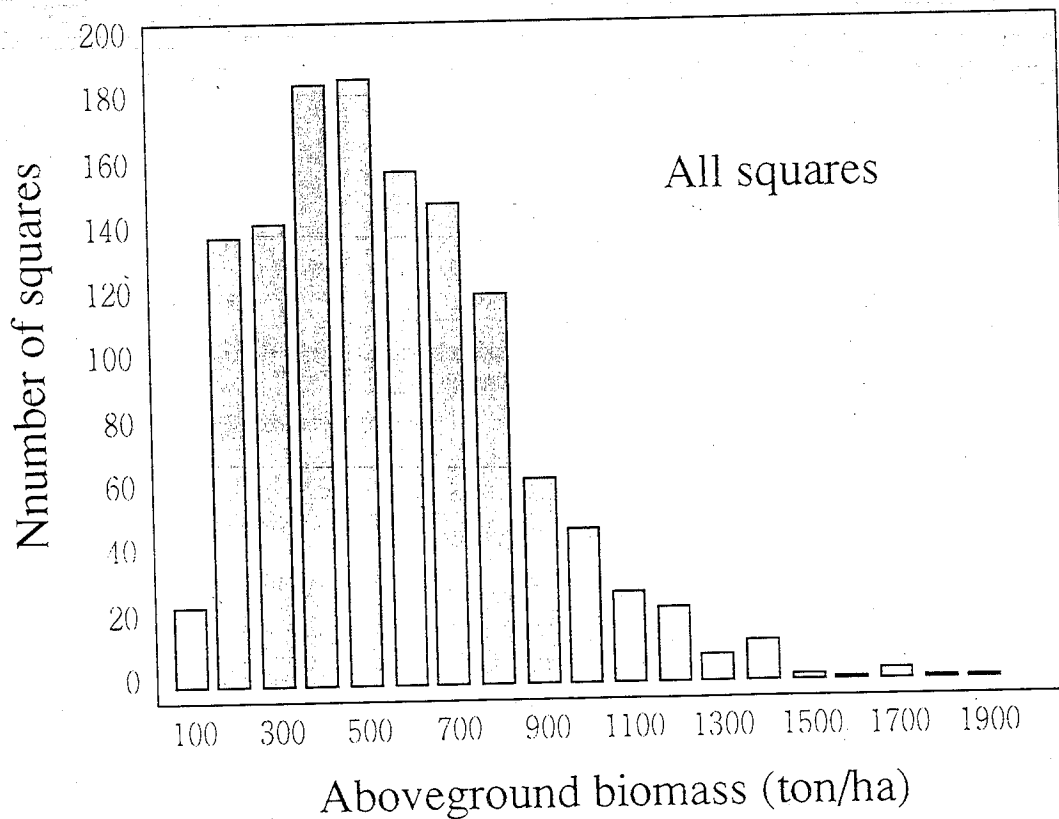


Fig. 4. Frequency distribtuion of aboveground biomass estimated for respective 1,300, 20 m x 20 m stands or squares.

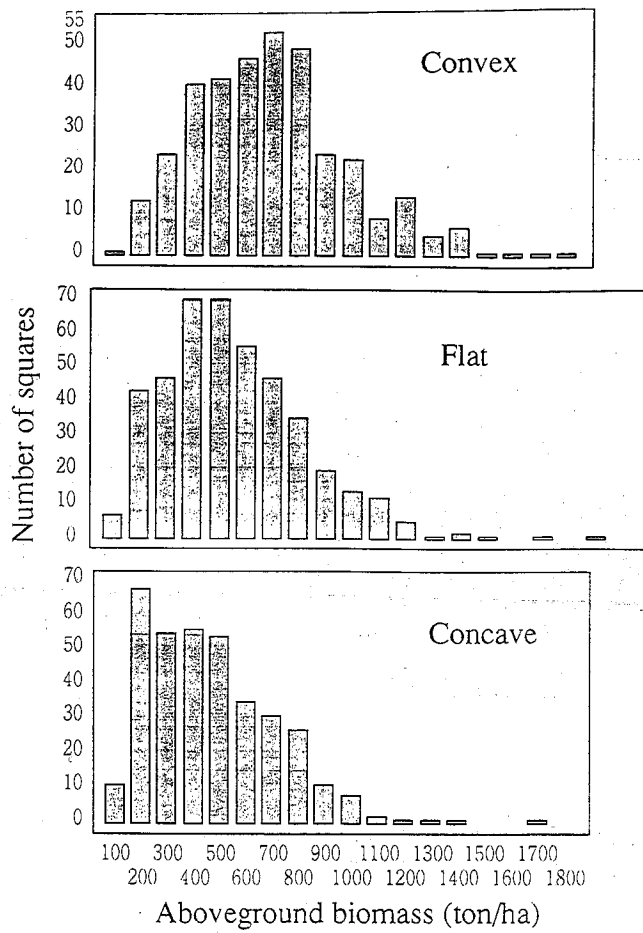


Fig. 5. Changes in aboveground biomass with respect to the convexity or concavity of slopes. The categorization of slopes into convex, flat, and concave slopes depended on the ICS index introduced in the preceding study (Yamakura et al., 1995), which is expected to be referred for details.

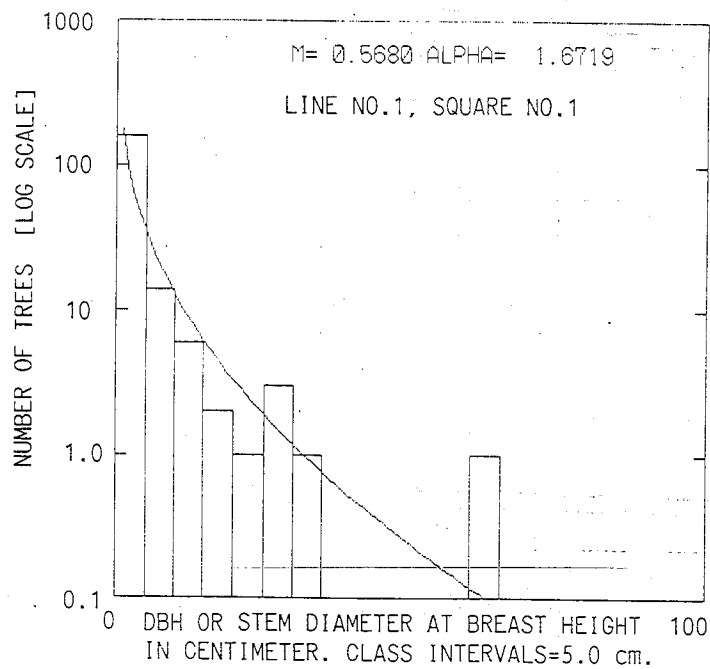


Fig. 6. Example of a frequency distribution of dbh in a sample stand 20 m x 20 m in area. Bars represent observed frequencies, while a smooth curve stands for frequencies expected from the Weibull distribution.

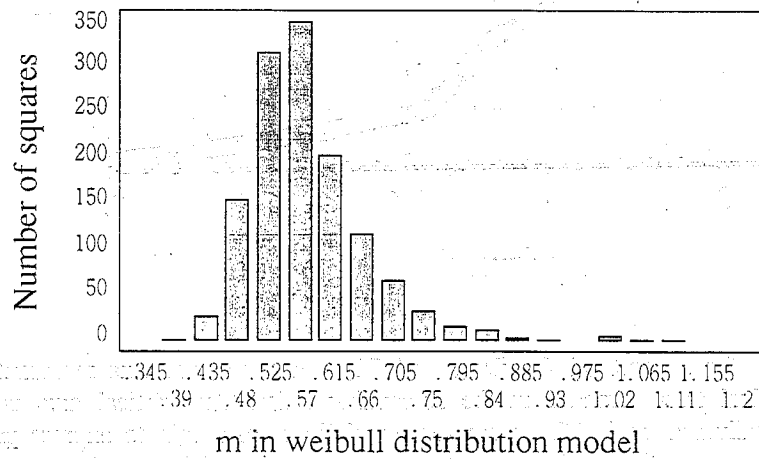
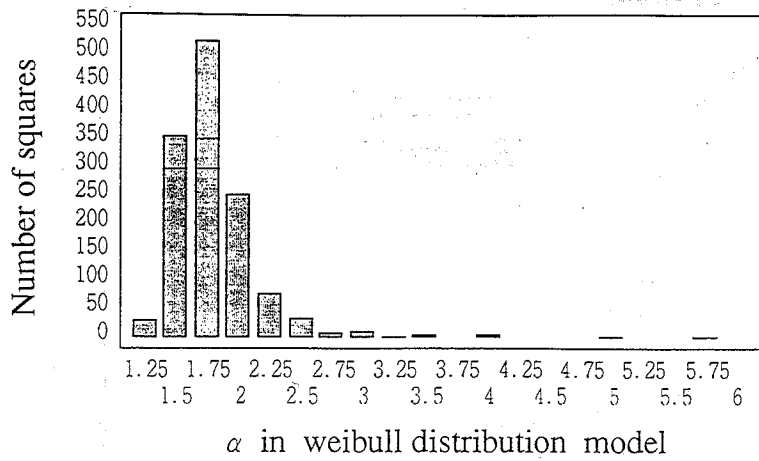


Fig. 7. Frequency distribution of coefficients,  $\alpha$  and  $m$ , of Weibull distribution.

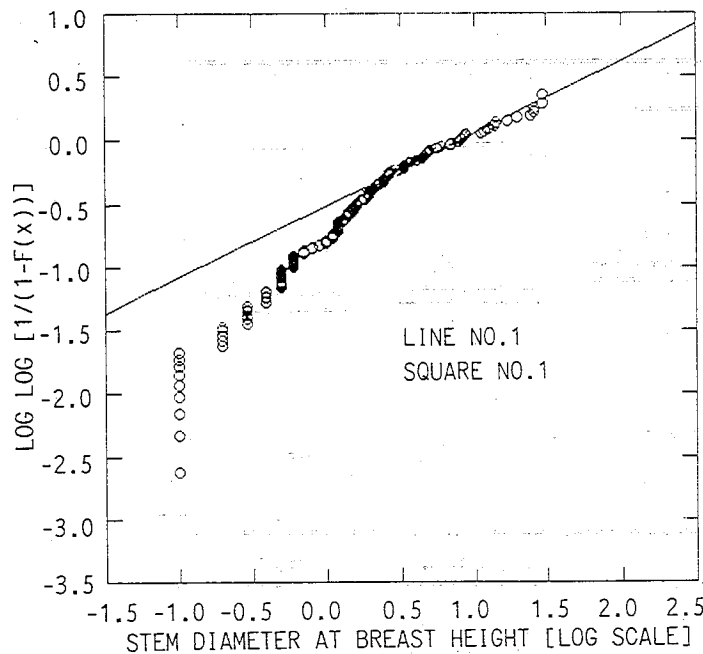


Fig. 8. Probability paper of Weibull distribution. A straight line stands for an expected trajectory calculated by the Weibull distribution whose two coefficients are estimated by the conventional statistical methods. Circles show observed values. Several segmental linear lines are necessary to cover

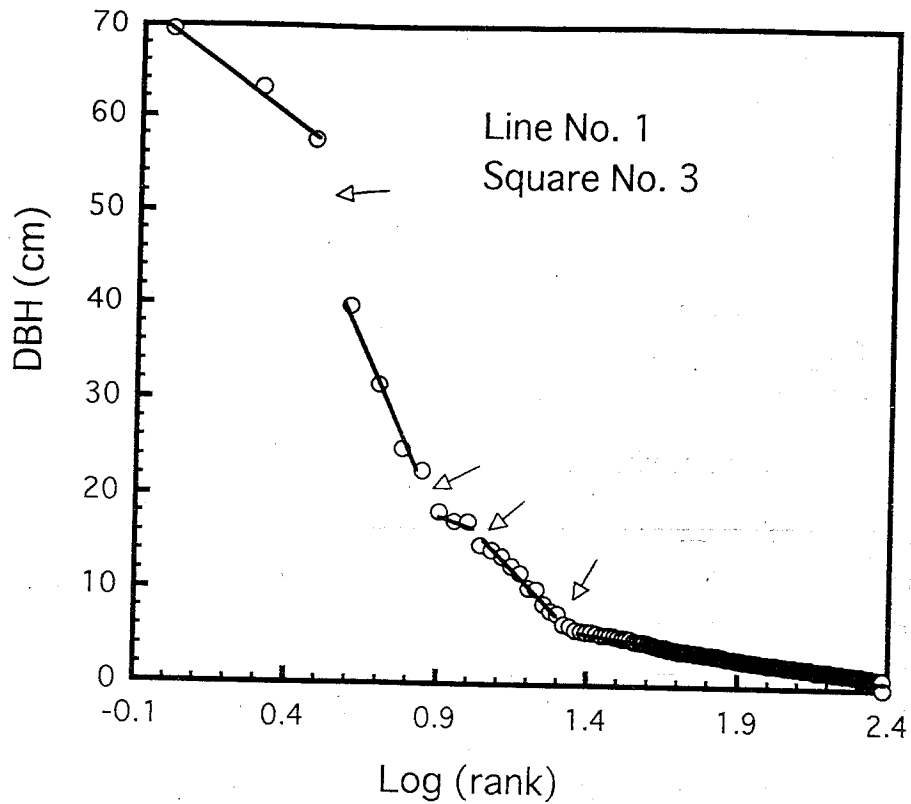


Fig. 9. Probability paper of the exponential distribution of dbh. The horizontal axis represents an ordered ranking of individual trees arranged in the descending order. The vertical axis is dbh corresponding to a given individual rank. The linear segmental lines are thought to express partial populations or subpopulations consisting a whole sample population per stand 20 m x 20 m in area. The arrows show boundaries between subpopulations. Five subpopulations are recognizable. For details, see the text.

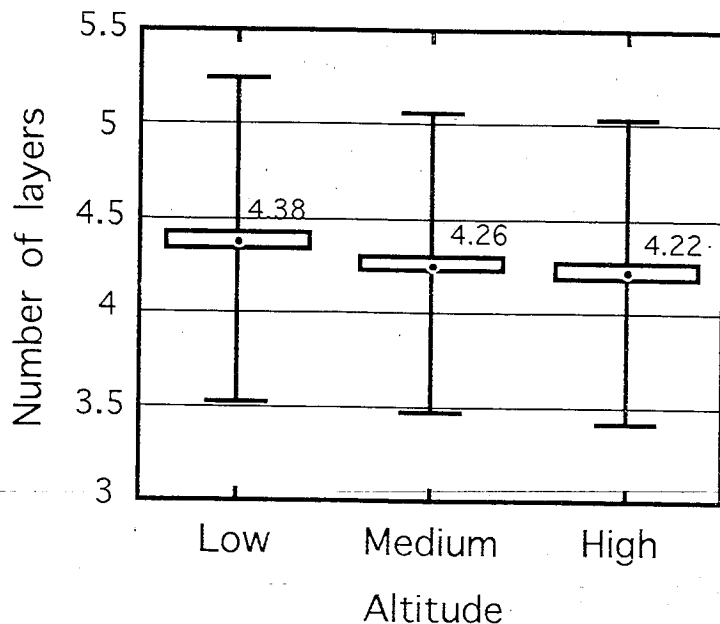


Fig. 10. ANOVA test for Changes of the number of subpopulations per stand with respect to stand altitudes. The differences between three altitude classes are significant ( $P < 0.01$ ).

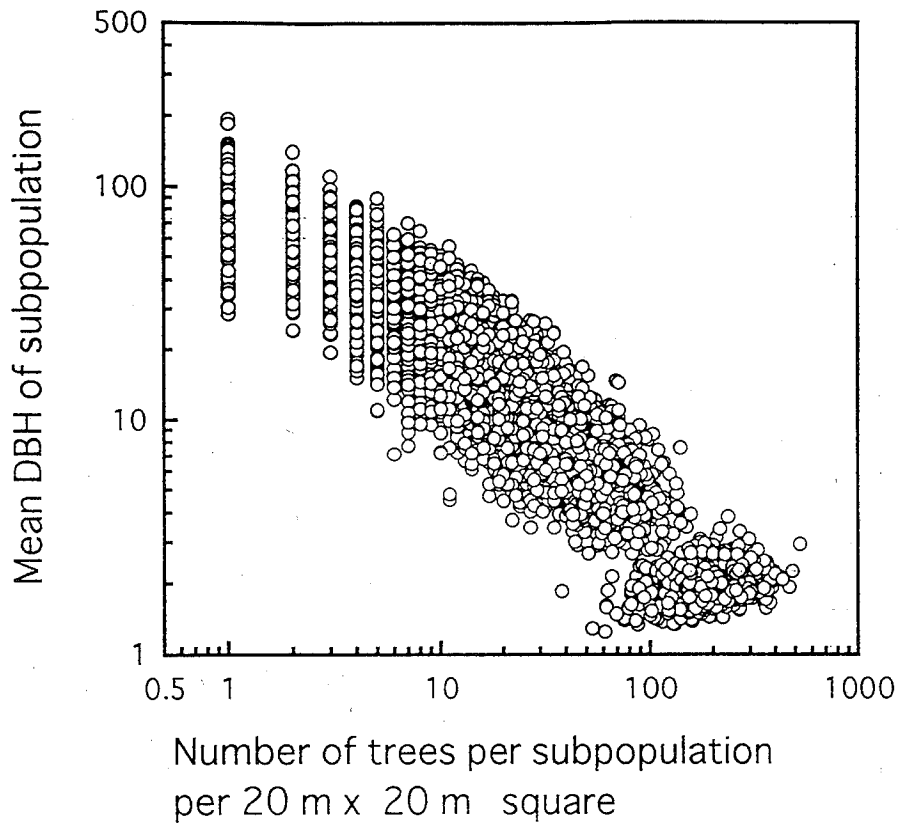


Fig. 11. Density dependency of mean dbh growth upon tree density per subpopulation in stratified forest stands.

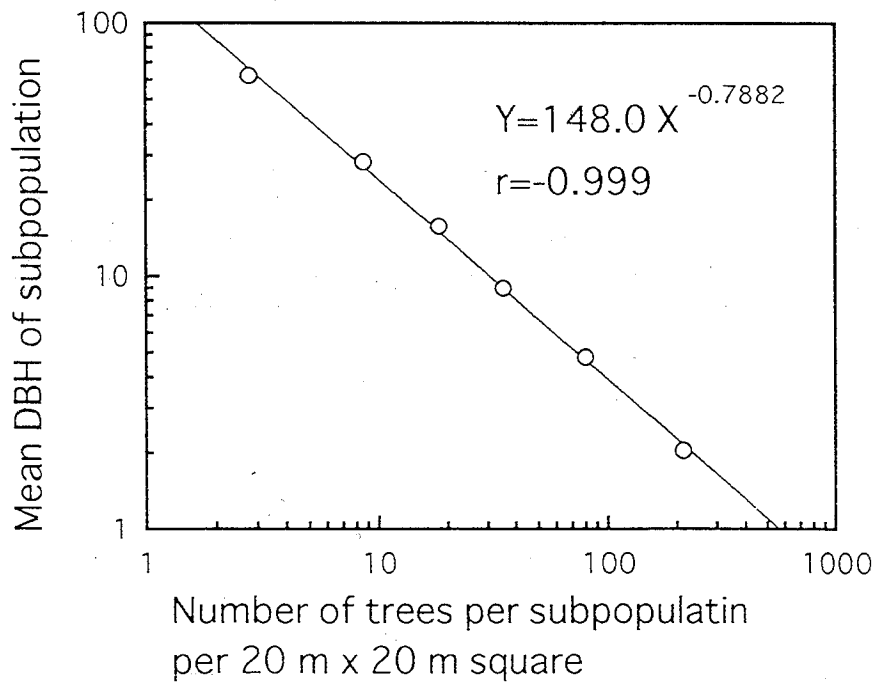


Fig. 12. Linear trajectory between logarithmic values of two variables, mean dbh and tree density, in a subpopulation. All the observed values in Fig. 11 were lumped into six groups by tree density intervals, 1-5, 6-12, 13-25, 26-47, 48-144, and 145-524, which were chosen so as to evenly distribute samples among the groups. The number of samples in the aforementioned density groups are 1031, 850, 928, 795, 897, and 1075, respectively. A open circle stands for the observed mean value of samples in each of the six data groups.