# **Tree Size Structure of Stands and Each Species in Primary Warm-Temperate Rain Forests of Southern Japan**

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The frequency distribution of trunk diameter was analyzed for forest stands of various developmental stages and for each tree species population in primary warmtemperate evergreen rain forests, dominated by *Distylium facemosum,* on Yakushima Island of southern Kyushu, Japan. Trunk diameter distribution in stands showed the inverse J shape. A regression model,  $\ln f(x) = b + b_1x + b_2 \ln x$ , expressed the distribution well, where x is diameter and  $f(x)$  trunk density at x. Three coefficients of the model, calculated from the data in 20 stands, clearly showed tinear relations to each other and they had high correlations with the basal area per stands. The result suggests that b and  $b_1$  increase and  $b_2$  decreases with stand age. Fourteen populations of abundant tree species also showed inverse J-shaped diameter distribution, which can be well expressed by the above model. In both open sites (gaps) and closed stands, these species were abundant and their characteristics in diameter distribution were persistent.

Key words : Regression model -- Stand development -- Trunk diameter distribu $tion - Yakushima$  Island - Warm-temperate rain forest.

Natural vegetation of the warm-temperate region of Japan is a rain forest consisting of evergreen broad-leaved trees. Although most of present warm-temperate forests in Japan are secondary ones resulting from human activity, there remain relatively undisturbed forests in mountain regions of southern Japan. Especially, Yakushima Island, 60 km south of Kyushu, preserves this type of primary forests over a large area, and offers good study sites.

In this paper, I analyze the tree size structure of well-preserved warm-temperate rain forests in Yakushima Island. This type of forest is composed of many tree species with similar life forms. Comparing the population structure of these species with each other is the other purpose of this paper. I introduce a simple regression model representing the trunk diameter distribution of populations in stable forest systems. Through fitting the model, it becomes possible to find some regular trends of diameter distribution in stands and species populations.

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#### **Study Sites and Methods**

The main study site is located on the south-facing slope on the north-bank of the River Segire in Yakushima Island  $(30^{\circ}25^{\prime}\text{N} 131^{\circ}25^{\prime}\text{E})$ . Altitude ranges 490-570 m above sea level. This area of the Segire basin has been kept undisturbed by human activity, and is covered by warm-temperate forests dominated by *Distylium racemosum.* The altitudinal range of 400-800 m above sea level of the island, occupied mainly by *Distylium-dominated* forests, is generally steep, but this study site is on an exceptionally gentle slope. The study site was on even topography on a river terrace of about 15 ha. The parent rock of the mountain area of the island is Miocene granite (Sato and Nagahama, 1979). Extremely wet climate is a feature of the area. At Kosugidani of the Arakawa basin (alt. 640 m), 17 km east from the Segire forest, precipitation reaches 680 cm per annum exceeding 20 em for every month; annual mean temperature is 13.4 C with a range between 2.1 C in January and 23.8 C in July (Sako and Minami, 1968).

A continuous canopy layer at about 20 m in height covers the study area of the Segire basin, while canopy openings or gaps are found in places in the area. A gap means, in this paper, a part of forest which is not covered by foliage of the canopy layer, and its projection area is not less than  $10 \text{ m}^2$ . The discriminating size between canopy trees of a closed canopy and trees of top layer in a gap is defined to be 10 m in tree height. In 30 m × 900 m belt transect, 26 gaps appeared and they were 4.7% of the total area sampled.

In 1980 and 1981, I established 20 plots of  $20 \text{ m} \times 20 \text{ m}$  area on canopy-closed stands, total area 8,000 m<sup>2</sup>. Slope direction was S60°W-S60°E; slope inclination, 20 $\pm$ 8" (mean, standard deviation). Species names and diameters at breast height (dbh) of all trunks above 2 cm in dbh were recorded. Heights of all saplings (above 50 cm tall and below 2 cm in dbh) were recorded with their species names within  $5 \text{ m} \times 5 \text{ m}$ subplot in each of four 10  $m \times 10$  m grids of the plot. Saplings surveyed in this study were only of species which appeared able to grow up to more than 2 em in dbh. Beside these plots in the closed stands, 22 gaps were surveyed in 198i. A gap plot is regarded as an oval-shaped part, as represented by two vertically crossing axes in the canopy foliage opening of the gap. Gap area is calculated as an ellipse from these two axes. Total area of 22 gaps was  $1,834$  m<sup>2</sup>; mean area and standard deviation of gaps were  $83 \pm 55$  m<sup>2</sup>. For each gap, I took a census of all trees above 2 cm in dbh, and set one or two  $5 \text{ m} \times 5 \text{ m}$  subplot(s) at the center of each gap for sapling census.

The composition of the tree species in the studied plots is presented in the Appendix. The study forest was identified as a *Distylium-Cyclobalanopsis* association by phytosociologieal studies (Miyawaki, 1980). It is a unique characteristic of this study site that evergreen oak species such as *Quercus salicina* and *Q. acuta* (both belonging to subgenus *Cyclobalanopsis),* which are common in other forests of the same community type in steeper sites of the island, are rare in the Segire basin and did not appear in my plots. It may come from that the Segire forest is formed on the most stable substrate. Another characteristic is abundant growth of *Podocarpus naqi*, a

coniferous species with 'broad leaves'.

This paper also analyzes the data of the 1983 survey of the primary warmtemperate rain forest dominated by *Distylium racernosum* in the basin of the River Koyohji. The basic results of this survey were already published (Kohyama *et al.,*  1984). The Koyohji forest is  $4.5 \text{ km}$  southwest from the Segire forest. Two plots  $(0.2$  ha in alt. 700 m and  $(0.25)$  ha in alt. 520 m; both on the west-facing slope) were established. The census methods carried out were the same as in the Segire forest. The Koyohji forest is on steeper topography  $(27 \text{ and } 24 \text{° for each plot, placed on the})$ most gentle sites), and the species composition was very similar to that of the Segire forest.

As this paper deals only with distribution of dbh above 2 cm, mean dbh is influenced by this minimum limit size of 2 cm. Therefore, the coefficient of variation *(CV)* in dbh distribution for a given population is defined as  $SD/(\bar{x}-2)$ , where  $\bar{x}$  is mean dbh (cm) and SD is standard deviation of dbh.

### **Results**

## *Tree size distribution fof each stand*

Both in closed stands and in gaps, the frequency distribution of dbh was extremely inverse J-shaped, and gave a downward-convex pattern even when plotted on a logarithmic scale (Fig. 1). Here, I propose an empirical equation to fit such an extremely positive-skewed distribution. It is expressed by the product of a power function and an exponential function :

$$
f(x) = ax^{b_2} \exp(b_1 x), \tag{1}
$$



Fig. 1. Frequency distribution of trunk diameter (above 2 cm) in warm-temperate forests of Yakushima Island. Left : Closed stands in the Segire forest (circles and full line), broken line is the result of the Koyohji forest (including both close stands and gaps) adjusted to the same area. Right: Gaps in the Segire forest (circles and full line), broken line shows the closed stand line, the same as in the left figure, adjusted to the same area. Fitted lines, by Eq. (2). Data of 2 cm-interval dbh classes ; averaged classes are linked by left-tailed bar.

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where x is tree size (in the present case, dbh in cm),  $f(x)$  is frequency of trees at x, and a,  $b_1$  and  $b_2$  are coefficients. Rewriting Eq. (1),

$$
\ln f(x) = b + b_1 x + b_2 \ln x, \tag{2}
$$

where  $b=\ln a$ . By using Eq. (2), we can easily estimate coefficients: the ordinary multiple regression method gives the estimates of coefficients by minimizing the sum of squares of residuals in terms of  $\ln f(x)$ . Here, I present the frequency distribution of tree size on semi-log scale in Fig. 1 and in the later figures. As Eq.  $(1)$  has the same form as the probability density function of the gamma distribution, I call the multiple regression by Eq. (2) the gamma-type regression model.

This paper uses dbh distribution with classes of 2 em-interval for regression, and employs the midpoint size  $(2d+1 \text{ cm for class } 2d \text{ to } 2d+2 \text{ cm}, d \text{ is integer})$  as x. When assorting the observed dbh into size classes, empty classes pose a practical problem in that the data of these classes cannot be used for regression. In such ease, it is convenient to adopt an expedient of averaging data: if there are  $k$  continuous empty classes and n trees exist in the next larger class, all of these  $k+1$  classes are assumed to have  $n/(k+1)$  trees.

Each of three regression coefficients has characteristic meaning in the model Eq. (2). When  $b_2=0$ , the model shows an exponential distribution and  $b_1$  gives the slope of the regression line in the x-ln  $f(x)$  diagram. When  $b<sub>2</sub> < 0$ , the distribution exhibits more positive-skewed form than exponential distribution (as the case in Fig. 1), and when  $b_2 > 0$ , less positive-skewed form. The coefficient b determines the height of the regression curve in the  $x$ -ln  $f(x)$  diagram. In the corresponding statistical model of the gamma distribution, coefficients are defined in the range  $b_1 < 0$  and  $b_2 > -1$  (by using symbols of Eq. (2)), but the regression model does not necessarily confirm these boundary conditions.

Fig. I shows that regression lines both in closed stands and gaps fit the observed



Fig. 2. Frequency distribution of trunk diameter (above 2 cm) in five closed stand plots of 20  $m \times 20$  m, in the Segire forest. Fitted line, by Eq. (2). Plots are placed in sequence of  $b_2$ of Eq.  $(2)$ , which is a supposed sequence of stand aging (left to right). Data of 2 cminterval dbh classes ; averaged classes are linked by left-tailed bar. Circles are sequentially filled only for discrimination among plots.

data well. The dbh distribution in the Koyohji forest is also expressed well by the gamma-type regression model, and the shape is very similar to that of the Segire forest (Fig. 1).

The gamma-type regression model also applies well to each of the  $400 \text{ m}^2$  plots in closed stands (Fig. 2). Furthermore, there are regular relationships among the three regression coefficients (Table 1). The relations among coefficients were linear, and through the following equation we can express stand structure by means of only one variable  $b_2$ :

$$
\begin{array}{l} b\!=\! 3.18\!-\! 1.75 b_2,\\ b_1\!=\! -0.0980\!-\! 0.0439 b_2. \end{array}
$$

Each of the maximum dbh, basal area and *CV* of dbh distribution showed high correlation with each of the coefficients of the model, and mean dbh showed no correlations (Table 1). As both maximum dbh and basal area are related to the developmental state of stands, one can hypothesize that the form of dbh distribution changes in a regular manner such that b and  $b_1$  increase and  $b_2$  decreases with stand age (cf. Table 1). In the gamma distribution as a statistical model, there exist relations that mean  $(\bar{x})$  is equal to  $-(b_2+1)/b_1$  and variance is equal to  $(b_2+1)/b_1^2$ . However, these relations cannot be detected in 20 plot data, which arises from the difference in the basic idea for estimating coefficients between the statistical model and the regression model.

The five plots presented in Fig. 2 are arranged in the order of hypothetical stand age. Fig. 2 and the above relationships among the three coefficients show that the positive skewness, and the tree density of both small (less than abdut 6 cm in dbh) and large size-classes (over about 30 cm in dbh) increase with stand age, while the density of medium-sized trees (6-30 cm in dbh) does not clearly change with stand age. The trend of  $b_{2}$  decrease with time is also observed in the change of stand structure from gap plots to closed stand plots (Fig. i).

# *Tree size distribution for each species*

Each tree species population composing the Segire forest shows a definite pattern in dbh distribution. Here, I analyze the major 14 tree species with high tree density (see Appendix). They comprised  $98\%$  of the number of trees above 2 cm in dbh,  $97\%$ of the number of saplings (above 50 cm tall and below 2 cm in dbh), and occupied  $93\%$ of total basal area in 0.8 ha closed canopy plots. All of the 14 species are abundant both in closed stands and in gaps. Tree and sapling densities of these 14 species in gaps have a close correlation with those in closed stands (r is 0.879 and 0.861, respectively). They are also main components of the Koyohji forest  $(93\%$  in tree density,  $95\%$  in sapling density and  $83\%$  of total basal area for 0.45 ha census; Kohyama *et al.,* 1984). Among them, *Myrsine seguinii, Eurya japonica, Symplocos glauca, Symplocos tanakae* and *Rhododendron tashiroi* are subcanopy species which seldom grow up to the top canopy of closed stands, and the other nine can grow up to form the main canopy.



\* Significant value:  $\pm 0.532$  in  $P = 0.05$ ,  $\pm 0.661$  in  $P = 0.01$ ,  $\pm 0.780$  in  $P = 0.001$ .<br>\*\* Regression coefficients of the gamma-type model fitting (Eq. (2)).

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Fig. 3. Comparison of dbh distribution of 14 abundant tree species between closed stands and gaps in the Segire forest. Left, mean trunk diameter ; right, *CV* of trunk diameter. Full species names of trees are listed in Appendix.

Mean and *CV* of dbh of each species population, both of which characterize the dbh distribution pattern of species as shown later, were fairly stable irrespective of developmental stage of stands (Fig. 3). All 14 species showed the stable distribution pattern that smaller dbh class shows higher frequency (Fig. 4). The form of dbh distribution in  $x$ -ln  $f(x)$  diagram for almost all species in the Koyohji forest is very similar to that in the Segire forest, though there are differences in density (Fig. 4). Several populations show, however, different dbh distribution patterns between these two forests. *Litsea acuminata* (La), *Podocarpus nagi* (Pn) and *Symplocos glauca* (Sg) had lower relative frequency of trees in larger-classes in the Koyohji forest, while *Myrsine sequinii* (Ms) gave the reverse trend.

The gamma-type regression model of Eq. (2) is also applicable to the dbh distribution of each species population (Fig. 4). Three estimated regression coefficients show correlation with each other among 14 species (Table 2). The range of fluctuation of each coefficient is larger for 14 species than that for 20 plots of closed stands (Tables 1 and 2), which reflects the among species variation in dbh distribution pattern.

Comparing Table 2 with Table 1, one can find a remarkable difference: the coefficients of the gamma-type regression model applied for 14 species populations are not correlated with the maximum dbh and the basal area, but b and  $b_2$  correlated with mean dbh. The *CV* of dbh has a close relation with the three coefficients in 14 populations, as well as in 20 plots of closed stands. As there is no significant correlation between mean dbh and *CV* of dbh (Table 2), the three coefficients are well expressed by both mean dbh  $(\bar{x})$  and  $CV$  of dbh:



The relations between statistical measures of the distribution (mean, variance) and model coefficients  $(b_1, b_2)$ , expected from the gamma distribution as a statistical model,



Diameter at breast height (cm)

Fig. 4. Frequency distribution of trunk diameter (above 2 cm) for 14 abundant tree species in closed stand plots of the Segire forest (open circle and full line), and in the Koyohji forest plots (dots). Data of 2 cm-interval dbh classes; averaged classes are linked by left-tailed bar. Regression line is from Eq. (2), except Cj and Cs in which from Eq. (4). Full species names of trees are listed in Appendix.

cannot be observed in 14 species case, which is similar to the above result in the 20 stands case.

When the gamma-type regression is applied for less positive-skewed dbh distribution than the negative exponential model (semi-log straight line), such as for *Camellia japonica* (Cj) and *Camellia sasanqua* (Cs) in Fig. 4, a peak on the regression curve may appear in smaller size-classes though such a peak cannot be detected directly from observed data. It arises from an essential feature of the gamma-type model  $(f(0)=0)$ when  $b_2 > 0$ ). One possible technique for avoiding the false peak for populations with less positive-skewed distribution is to introduce one more coefficient  $i$ , and to change x to  $x + i$  in Eq. (2), but the coefficient estimation becomes less simple in such a four coefficient model. Here I use another regression model in which coefficients are estimated by the same procedure as for the gamma-type model :

$$
f(x) = a' \exp(b'_1 x + b'_2 x^2) \qquad \text{or} \tag{3}
$$

$$
\ln f(x) = b' + b'_1 x + b'_2 x^2, \tag{4}
$$

where  $b'=\ln a'$ . I call this the normal-type regression model because Eq. (3) has the same structure as the probability density function of the normal distribution. It is notable that three regression coefficients  $b'$ ,  $b'_1$  and  $b'_2$  correspond respectively in their appearances to coefficients b,  $b_1$  and  $b_2$  of the gamma-type regression model. This model expressed better the less positive-skewed populations  $(C<sub>j</sub>$  and  $C<sub>s</sub>$  of Fig. 4); however, in other cases, the gamma-type model was much better for expressing the distribution.

As is clear from the relations among the three coefficients of the gamma-type regression models (Table 2), there are regular trends in dbh distribution among 14 species populations presented in Fig. 4. We obtain easily the decreasing ratio of  $f(x)$ to x,  $\left[ \frac{df(x)}{dx} \right]$  (x), which is the slope of x-ln  $f(x)$  curve of Fig. 4, for each of the two regression models:  $b_1 + b_2/x$  for gamma-type model, and  $b'_1 + 2b'_2x$  for the normaltype model. By analyzing the relation between  $\ln f(x)$  calculated from models and its slope of decline with respect to  $x$ , we see that the positive correlation exists for  $2-$ 4 and 4-6 em dbh classes, no correlation for 6-8 em class, and the negative correlation for 8-10 cm and larger classes  $(P=0.05)$ . The trees less than 6 cm in dbh are all the members of understory layer and those above 8 em compose mainly the subcanopy to canopy layer, in closed stands (cf. Kohyama *et al.,* ]984).

I think the above positive correlation for small-sized trees less than 6 em in dbh, or the tendency that species with high small tree density has a steep decline of slope of density with tree size, reflects the among-species differences in pattern of recruiting and maintaining successors under the canopy. The species with both high density and steeply decreasing slope in small size classes must choose a strategy for high fecundity, and those with the inverse tendency for low mortality. The negative correlation between frequency and its decline ratio with dbh for large size classes apparently reflects the species-specific potential maximum size, and, perhaps, reflects the speciesspecific potential duration in surviving at canopy layer. This hypothetic explanation should be ensured by observing size-specific growth rate of each species, which can introduce the time axis in the pattern of fairly stable size distribution of each species.

#### **Discussion**

The inverse J-shaped dbh distribution of stable uneven-aged forests in cooltemperate zone has been frequently expressed by an exponential distribution (Meyer, 1952; Leak, 1965). However, more positively skewed distribution is common in warm-temperate rain forests (Kitazawa *et al.,* 1959 ; Tagawa, 1977), in tropical forests (Hartshorn, 1978), and also in cool-temperate deciduous forests when a large area is involved (West *et al.,* 1981). The gamma-type model applied in this paper is useful for such distribution in natural forests not only in its goodness of fit to data but also

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in its simplicity. This model cannot be applied to the semi-log 'rotated sigmoid curve' with a point of inflection in cool-temperate forests (Goff and West, 1975 ; West *et al.,*  1981). This curve can also be observed in a secondary warm-temperate forest (Nagano, 1978). The model expressing this curve should have at least one more coefficient.

Statistical distribution models, such as the exponential distribution (Leak, 1965), the gamma distribution (Nelson, 1964), the Weibull distribution (Bailey and Dell, 1973) and so on, have been applied to express the dbh distribution. In any of these statistical models, coefficients can be easily estimated from the statistical values in dbh distribution. However, we must take note that fitting these statistical models to dbh distribution is erroneous when the frequency distribution data are truncated in a given size. The measurement of tree size is generally made above a given size in unevenaged forests, because seedling census consumes a long time and because dbh cannot be defined for trees smaller than breast height. In such eases, the regression method that is used in this study is suitable for estimating coefficients of dbh distribution models.

Two unique techniques using regression methods are published for estimating size-distribution functions. One of them is Hozumi's MNY-method (Hozumi *et al.,*  1968; Hozumi and Shinozaki, 1970; Hozumi, 1971). The resultant models of this method contain an exponential function and one sort of power function, which are included by the gamma-type model. The other is Yamakura's finite difference method (Yamakura and Shinozaki, 1980). These methods are distinguished for introducing biologically meaningful procedures to derive distribution functions, while the estimation of coefficients is not straightfoward. The gamma-type regression is advantageous by its simplicity and straightfoward estimation of coefficients, at least when inverse J-shaped distribution is concerned. Applying the least square method to logarithmictransformed data is surely reasonable for extremely positive-skewed data.

The change of the dbh distribution pattern with stand age after gap formation in primary warm-temperate forests is quite different from that after artificial dear-felling of trees in secondary warm-temperate forests. In an early secondary succession after felling, the frequency of small size trees declines with stand development (Satake, 1970 ; Nagano, 1978), which is the contrary of my result from primary forest. Mature stands in primary forests may distinguished from old growth stands of secondary forests by the ability of recruiting small trees, or the advance regeneration waiting for natural gap formation.

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Appendix. Species composition of the tree community of the Segire for-

\* Trees are above 2 cm in dbh, saplings are above 50 em tall and below 2 em in dbh ;

**\*\*** Deciduous trees ; the others, evergreen.

Closed stands			Gaps	
No. of saplings* in $2,000 \text{ m}^2$	<b>Basal</b> area $(cm2m-2)$	No. of trees* in 1,834 m <sup>2</sup>	No. of saplings* in 650 m <sup>2</sup>	Basal area $\rm (cm^2 m^{-2})$
116( 9)	0.82	97(1)	63 (12)	0.95
89 ( $\left( 0\right)$	25.02	43(1)	32(3)	7.40
302( 9)	7.07	55 (0)	190(8)	0.93
154( 41)	3.64	78 (2)	160 (42)	2.57
229 ( 3)	0.41	68 (0)	68 (3)	0.46
141 ( 34)	5.94	49 (1)	79 (10)	3.98
145 ( $\left( 0\right)$	4.38	43 (0)	89 (0)	3.99
77 ( 4)	$3.24\,$	22(0)	6) 55 - 1	0.63
240 ( 5)	0.76	36(0)	141( 4)	0.73
116 ( 7)	0.45	28(2)	68 ( 2)	0.42
19( 3)	1.99	22(0)	7( 1)	1.43
36( $\left( 0\right)$	3.08	24(0)	2) 36 $\left($	2.83
12( 5)	1.26	16(2)	17 $\left( 0 \right)$ - (	0.78
7 ( $\left( 0\right)$	0.34	5(0)	25 $\left( 0\right)$ $\left($	0.36
6 ( $\left( 0\right)$	0.19	3(0)	2) 7 €.	$\rm 0.23$
14 ( $ 0\rangle$	0.05	2(0)	8 $\left( 0\right)$ $\left($	0.05
$\boldsymbol{0}$	0.48	$\theta$	$\mathbf{0}$	
$\overline{0}$	0.26	(0) 1	1 $\left( 0 \right)$ $\left($	0.002
1( $\left( 0\right)$	0.07	2(0)	$\mathbf{0}$	0.01
$\bf{0}$	1.72	$\boldsymbol{0}$	$\bf{0}$	
3( 2)	0.01	$\mathbf 0$	$\mathbf{1}$ $\left($ $\left( 0\right)$	
$\left( 0\right)$ 1 $\overline{ }$	0.06	$\mathbf{1}$ (0)	$\boldsymbol{0}$	0.02
$\mathbf{0}$	1.10	$\boldsymbol{0}$	7 $\left( 0 \right)$ $\left($	
$\mathbf 0$	0.06	$\mathbf 0$	19 (0)	
$\mathbf 0$	0.01	1(0)	$\bf{0}$	0.03
$\theta$	0.50	$\mathbf 0$	$\overline{0}$	
$\theta$	$\rm 0.05$	1(0)	1 $\left( 0\right)$ €	0.65
$20\,$ 1) $\left($	0.004	1(0)	$\boldsymbol{3}$ $\left( 0\right)$ $\left($	1.41
$\mathbf 0$	0.004	$\mathbf{0}$	$\boldsymbol{0}$	
$\boldsymbol{0}$		1(0)	$\boldsymbol{0}$	0.01
1728 (123)	62.97	599 (9)	1077 (95)	29.89

est (alt. ca. 500 m); nomenclature after Mitsuta and Nagamasu (1984)

number in parentheses, individuals of vegetative origin from larger ones.