Relationship between Maximum Stem Volume and Density during a Course of Self-thinning in a *Cryptomeria japonica* Plantation[†]

Ogawa, Kazuharu[1] and Akio Hagihara[2]

[1]*Laboratory of Forest Ecology and Physiology, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan*

[2]*Laboratory of Ecology and Systematics, Faculty of Science, University of the Ryukyus, Okinawa 903-0213, Japan*

ABSTRACT : *Cryptomeria japonica* plantation was monitored every year during 15 years from 1983 to 1997 for stem diameter and volume. The reciprocal equation, $\frac{1}{Y} = A + \frac{B}{N}$, was applied to the relationship between cumulative volume Y and cumulative number N from the largest tree in the stand each year. The parameters A and B, which means respectively the reciprocal of an asymptotic value of total stand stem volume and the reciprocal of the maximum stem volume, are related by a power function. The power functional relationship between A and B derived a linear relationship of B-points (N_B, Y_B; $N_B = \frac{B}{A}$, $Y_B = \frac{1}{2A}$) of each Y-N curve on log-log coordinates. The gradient of B-point line was so steep that the Y-N curve moved parallel upward year by year. The time trajectory of mean stem volume ($\overline{w}$) and density (ρ) provided evidence in favor of the 3/2 power law of self-thinning, because the gradient of $\overline{w} - \rho$ trajectory on log-log coordinates approximated to $-3/2$ at the final stage of stand development. On the basis of the results of Y-N curves and $\overline{w} - \rho$ trajectory, the time trajectory of maximum stem volume $w_{max obs}$ and ρ was derived theoretically. The gradient of $w_{max obs} - \rho$ trajectory on log-log coordinates is calculated to be -0.6105 at the final stage. The gradient of $w_{max obs} - \rho$ trajectory was steeper than that of $\overline{w} - \rho$ trajectory at the early stage, while the former is gentler than the latter at the later stage.

Key words : *Cryptomeria japonica*, Density, Maximum stem volume, Mean stem volume, 3/2 power law of self-thinning, Y-N curve

INTRODUCTION

As trees in a stand grow larger they occupy more and more space, and sooner or later the gaps between trees are filled and they begin to interference with each other's access to resources like light, water and nutrients (Silvertown and Charlesworth 2001). Such interference or competition within the stand induces density-dependent mortality or self-thinning.

Yoda et al. (1963) found that once a stand had reached the maximum or full density, mortality occurred in such a way that

$$\overline{w} = K\rho^{-\alpha} \qquad (1)$$

where $\overline{w}$ is the mean phytomass per plant, ρ is the density, i.e. the number of plants per unit area, K is a constant which varies from species to species, and α has been widely reported to take the value of approximately 3/2 for wide range of species (e.g. White 1980; Westoby 1984; Zeide 1987). Such a stand is said to be following the 3/2 power law of self-thinning (Yoda et al. 1963), or alternatively, the self-thinning rule.

Besides the self-thinning rule given in eqn (1), Hozumi et al. (1968) recognized that maximum stem volume is roughly proportional to $-3/2$nd to -1st power of density in *Cryptomeria japonica* plantations. Assuming the self-thinning rule in eqn (1), Hozumi (1971) theoretically derived a power functional relationship between maximum stem volume and density in *C. japonica* plantations. Yamakura and Shinozaki (1983a, 1983b) also demonstrated that a power functional relationship with an exponent value of $-3/2$ realizes between maximum stem volume and density in *C. japonica* plantations on the assumption of eqn (1). The power functional relationship between maximum stem volume and density can be considered as an additional property attached to the self-thinning rule in eqn (1) (Yamakura 1981).

In the present study, we monitored a sugi(*Cryptomeria japonica*) population every year for 15 years to evaluate the time course of self-thinning. The features of the time-trajectory of mean stem volume and density were translated into a mathematical formula. Furthermore, in order to clarify the dynamics of the stand, *Y-N* curve (Hozumi *et al.* 1968) was applied to the relationship between cumulative volume *Y* and cumulative number *N* from the largest tree in the stand each year. On the basis of the results of the time-trajectory of mean stem volume and density and the *Y-N* curves, the relationship between maximum stem volume and density was derived theoretically, and the stand development was assessed.

MATERIALS AND METHODS

Site description

This study was made on a 21-year-old (as of 1983) sugi *(Cryptomeria japonica* D. Don) stand in the Nagoya University Experimental Forest at Inabu, located about 55 km east of Nagoya, Aichi Prefecture, central Japan. This plantation was situated at an altitude of 960 m on a east-facing 23° slope. A plot of 15 m × 20 m in area was established in 1983. Thinning was not made artificially after planting.

Census and estimation of stem volume

A yearly census was carried out on all the trees in the plot, in which stem girth at the breast height (1.3 m above the ground) was measured in October from 1983 to 1997.

Six to fourteen different-sized sample trees were selected for non-destructively assessing the stem volume every year. Measurements were made of tree height, stem girths at 0.0, 0.3, 1.3 m and at 1.0 m intervals thereafter. From the measurements, stem volume was calculated on the basis of Smalian's formula (e.g. Avery and Burkhart 1994).

The stem volume, V (dm^3), of the trees in the plot was estimated from stem girth at breast height, G (cm), by the yearly allometric formula of $V = gG^h$, where the values of coefficients g and h were respectively in the range of 0.00273 to 0.0390 dm^3 cm^{-h} and 2.131 to 2.789 throughout the experimental period (Ogawa and Hagihara 2003).

Data analysis

Hozumi *et al.* (1968) proposed a method to describe the frequency distribution using cumulative number N and cumulative biomass Y of a partial population consisted of trees whose weight is in the range between maximum weight w_{max} and a given weight w. The cumulative number N and cumulative biomass Y from the largest individual in the partial population are defined as

$$N = \int_w^{w_{max}} \phi(w)\,dw \tag{2}$$

$$Y = \int_w^{w_{max}} w\phi(w)\,dw \tag{3}$$

where $\phi(w)$ is the distribution density function of individual weight w. They analyzed the interrelationship between Y and N, and obtained the following reciprocal equation of *C-D* curve of Type IV (Shinozaki and Kira 1961):

$$\frac{1}{Y} = A + \frac{B}{N} \tag{4}$$

where A and B are constants.

The values of N and Y were calculated on the basis of the following equations (Hozumi *et al.* 1968):

$$N = \sum_w^{w_{max}} f_i \tag{5}$$

$$Y = \sum_w^{w_{max}} f_i w_i \tag{6}$$

where f_i and w_i are tree number and individual stem volume belonged to the size class i, respectively. In other words, N is the sum of the number of trees, which are added in descending order from the largest tree w_{max} to that of a given stem volume w in the stand. Similarly, Y is the cumulative stem volume of trees, which is summed in descending order from the largest w_{max} to that with the volume w. When summed from w_{max} to w_{min} or the smallest tree of the stand, N and Y correspond to stand density and total stem volume in the stand, respectively.

Each value of Y and N was plotted on a double logarithmic scale and eqn (4) was applied to Y and N relations for each year. The two parameters A and B were determined by the least square method of relative error (Hozumi and Shinozaki 1960).

RESULTS

Y-N curve

Examples of *Y-N* curves represented by Eq. 4 for 1983 and 1997 are illustrated in Fig. 1. In each year, the expected curves closely fitted the observed points; in the other 13 years, the fit was similar.

The meanings of parameters A and B in eqn (4) are as follows (Hozumi *et al.* 1968): parameter A is the reciprocal of an asymptotic value y_0 of total stem volume in the stand when N increases toward infinity
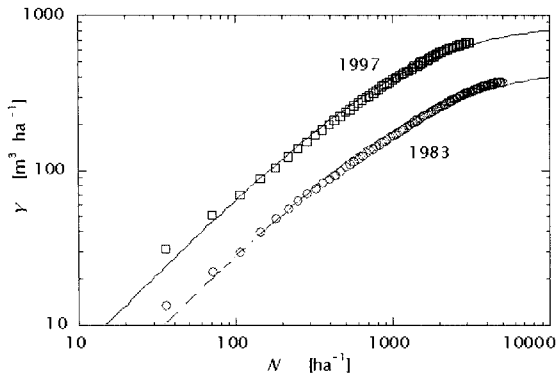
Fig. 1. Relationships between cumulative stem volume Y and cumulative number N in 1983 (○) and 1997 (□). The regression curves are given by eqn (4).

$$A = \frac{1}{y_0} \qquad (7)$$

while parameter B is the reciprocal of the maximum stem volume w_{max} when N decreases toward zero

$$B = \frac{1}{w_{max}} \qquad (8)$$

Generally speaking, y_0 and w_{max} are not identical with the actual stand biomass y and the actual observed stem volume of the biggest tree $w_{max\ obs}$, respectively, because the former group represents the theoretically expected values given by the distribution function (Hozumi et al. 1968). The correlation between w_{max} and $w_{max\ obs}$, as well as y_0 and y, is examined in Fig. 2. Both correlations were approximated by the following power functions:

$$w_{max} = aw_{max\ obs}^{\,b} \qquad (9)$$

$$y_0 = cy^d \qquad (10)$$

where a, b, c and d are constants, and the values of a, b, c and d were calculated to be 0.7699 m^{3-3b}, 1.008, 0.5474 m^{3-3d} ha^{d-1} and 1.155, respectively. Since the exponents b and d in eqns (9) and (10) did not significantly differ from unity at the level of 5%, the theoretical values of w_{max} and y_0 are to be proportional to the observed values of $w_{max\ obs}$ and y, respectively.

Relationship between parameters A and B

Since A and B are reciprocals of y_0 and w_{max} as given in eqns (7) and (8) respectively, the values of A and B tended to decrease monotonously with the stand development (Fig. 3). The correlation
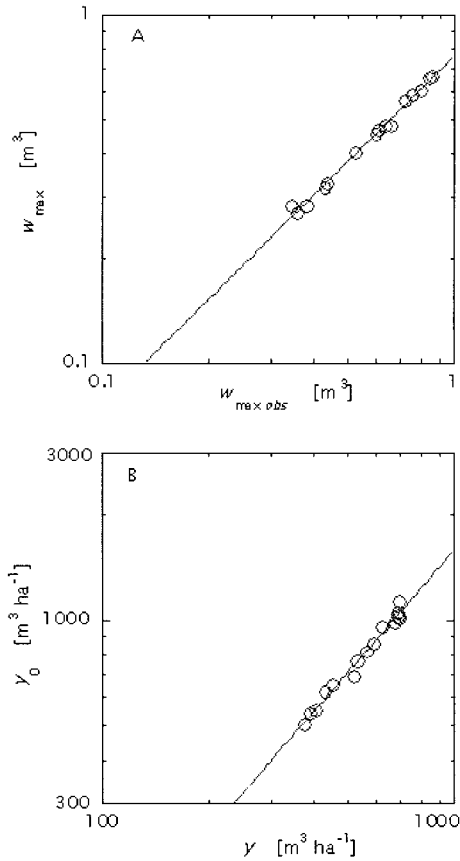

Fig. 2. Correlations between theoretical and observed values. A, Maximum stem volumes of w_{max} and $w_{max\ obs}$. B, Total stand stem volumes of y_0 and y.
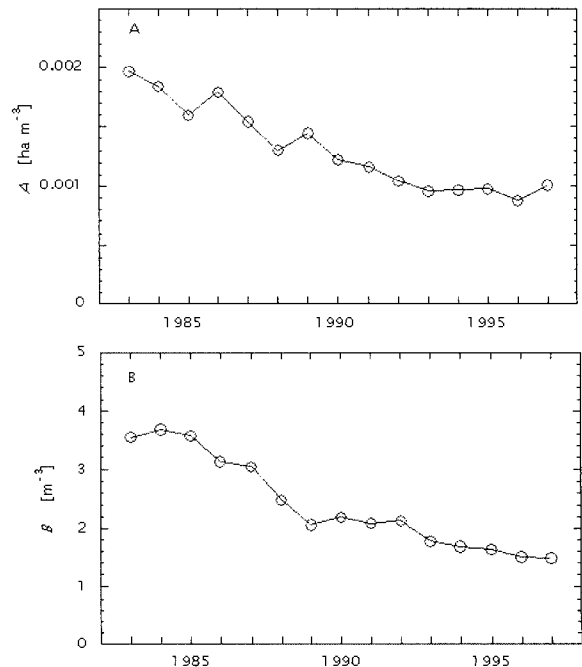

Fig. 3. Time trends of coefficients A and B in eqn (4).

between B and A on log-log coordinates is given in Fig. 4. The relationship was fitted by a power function,

$$B = mA^n \tag{11}$$

where m and n are constants, and the values of m and n were 4126.2 m^{3n-3} ha^{-n} and 1.1242, respectively. Since the value of n was not significantly different from unity at the level of 5%, B is to be proportional to A in the present study. Kikuzawa (1999) reported a power functional relationship between B and A in a *Betula ermanii* stand.

Substituting eqns (7) and (8) into eqn (11) leads to the relationship between the theoretical values of w_{max} and y_0 as follows:

$$w_{max} = \frac{1}{m} y_0^n \tag{12}$$

From eqns (9), (10) and (12), we have the power functional relationship between the observed values of $w_{max\,obs}$ and y,

$$w_{max\,obs} = \left(\frac{c^n}{am} \right)^{\frac{1}{b}} y^{\frac{dn}{b}} \tag{13}$$

Time-trajectory of stem volume and density

The relationship between mean stem volume $\overline{w}$ and density ρ on logarithmic coordinates is shown in Fig. 5. The time-trajectory of $\overline{w}$ and ρ was formulated as

$$\overline{w} = K\rho^{-\alpha} \left(1 - \frac{\rho}{\rho_0} \right)^{\beta} \quad (\alpha - 1 < \beta < \alpha) \tag{14}$$
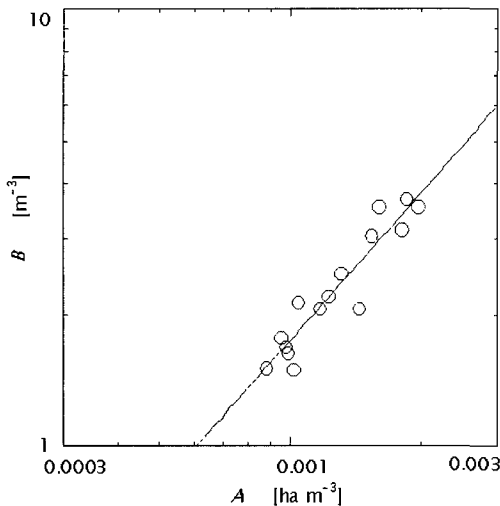

Fig. 4. Correlation between coefficients A and B in eqn (4). The regression line is given by eqn (11) ($R^2 = 0.874$).
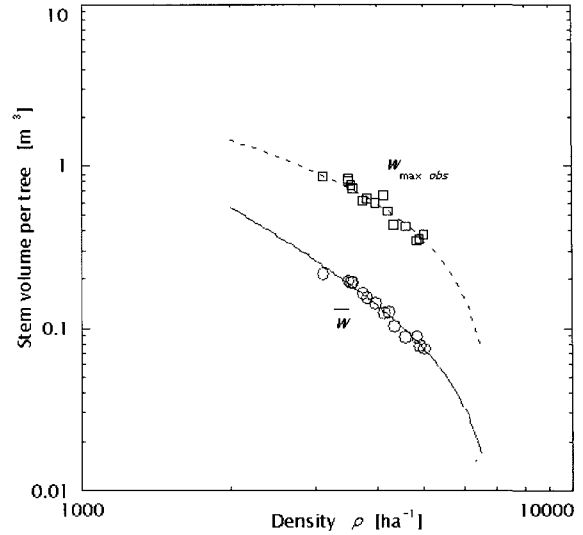

Fig. 5. Time-trajectories of mean ($\overline{w}$, $\bigcirc$) and maximum ($w_{max\,obs}$, $\square$) stem volumes and density. The regression curves are given by eqns (14) and (17). The coefficient of determination in eqn (14) is 0.982.

where K, ρ_0, α and β were coefficients (Hagihara 1996, 2000). The values of K, ρ_0, α and β were calculated as 52693 m^3 $ha^{-\alpha}$, 6923 ha^{-1}, 1.474 and 0.7224, respectively. The $\overline{w}$ – ρ trajectory given by eqn (14) indicates that the $\overline{w}$ – ρ trajectory gradually approaches and eventually moves along the self-thinning line in eqn (1) at the final stage of stand development (Perry 1994). The α value of 1.474, which is close to 3/2, can be regarded as evidence in favor of the 3/2 power law of self-thinning.

In consideration of the following definition, i.e.

$$y \equiv \overline{w}\rho \tag{15}$$

where y is the biomass per unit area, eqn (14) can be written in the form:

$$y = K\rho^{-(\alpha-1)} \left(1 - \frac{\rho}{\rho_0} \right)^{\beta} \tag{16}$$

By combining eqns (13) and (16), the time-trajectory of the observed maximum stem volume $w_{max\,obs}$ and stand density ρ is derived as follows:

$$w_{max\,obs} = \left(\frac{c^n}{am} \right)^{\frac{1}{b}} K^{\frac{dn}{b}} \rho^{\frac{-(\alpha-1)dn}{b}} \left(1 - \frac{\rho}{\rho_0} \right)^{\frac{\beta dn}{b}} \tag{17}$$

As shown in Fig. 5, eqn (17) successfully mimics the time-trajectory of $w_{max\,obs}$ and ρ throughout the stand development.

As the density ρ tends to decrease, eqn (17) can be approached to the linear line of $w_{max\ obs} - \rho$ relation on log-log scale at the final stage of stand development:

$$w_{max\ obs} = \left(\frac{c^n}{am}\right)^{-\frac{1}{b}} K^{\frac{dn}{b}} \rho^{\frac{-(a-1)dn}{b}} \tag{18}$$

where the value of exponent $\dfrac{-(a-1)dn}{b}$ was calculated to be -0.6105.

The gradient of $w_{maxobs} - \rho$ trajectory on log-log coordinates was steeper than that of $\overline{w} - \rho$ trajectory at the early stage, while the former is gentler than the latter at the later stage of stand development. At the final stage of stand development, the gradients were -0.6105 and -1.474 respectively in the $w_{maxobs} - \rho$ and $\overline{w} - \rho$ trajectories.

DISCUSSION

Movement of Y-N curve

Eqn (4) represents an asymptotic curve whose right-hand end represents the total number of trees ρ and stem volume y of the stand. Therefore, the movement of Y-N curve is considered to be closely related to $y - \rho$ (eqn (16)) or $\overline{w} - \rho$ (eqn (14)) trajectory. The position of this curve is determined by its base point or B-point (Shinozaki and Kira 1961), whose coordinates (N_B, Y_B) are expressed as

$$N_B = \frac{B}{A}$$

$$Y_B = \frac{1}{2A} \tag{19}$$

Combining eqns (11) and (19) gives the following power functional relationship between Y_B and N_B or B-point line (Kikuzawa 1993) (Fig. 6):

$$Y_B = \frac{m^{-\frac{1}{n-1}}}{2} N_B^{-\frac{1}{n-1}} \tag{20}$$

The value of exponent $-\dfrac{1}{n-1}$ was calculated as -8.0515, so that the gradient of B-point line was very steep. This shows that Y-N curve approximately moved parallel upward year by year. Such movement of Y-N curve reflects that small-sized individuals
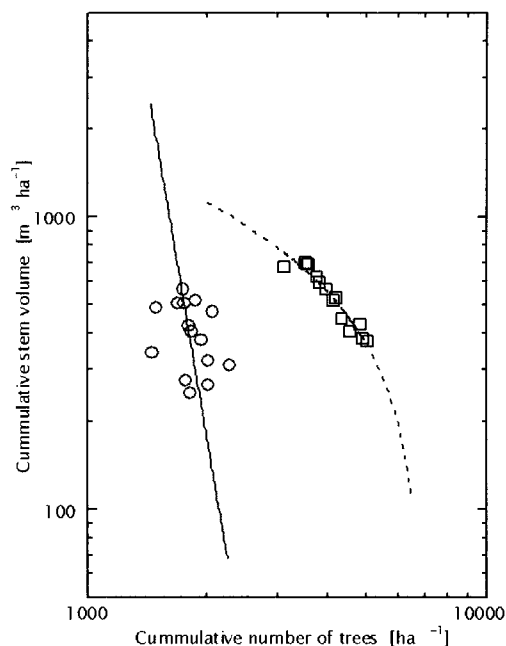
continued to die every year and the order of individual trees from the largest to the smallest did not change in the present stand (Ogawa and Hagihara 2003).

Kikuzawa (1993) observed the linearity of B-point line on log-log scale in a *Betula ermanii* stand with full density. The value of exponent in the B-point line in the *B. ermanii* stand was nearly equal to $-1/2$, which is the same as the value of self-thinning exponent in the power functional relationship between stand stem volume and density. In the present study, when regressing the curve of eqn (16) between stand stem volume y and density ρ on log-log coordinates (Fig. 6), the gradient γ_y of trajectory for y and ρ is mathematically derived as

$$\gamma_y = \frac{d\log y}{d\log \rho} = -(a-1) + \frac{\rho}{\rho - \rho_0} \tag{21}$$

The relationship between γ_y and ρ is illustrated in Fig. 7. The value $(= -8.0515)$ of exponent in B-point line is equal to the value of γ_y at the density of around 6000 ha^{-1} at the early stage of stand development. In the present stand below full density, the value of self-thinning exponent was -0.474 from eqn (16) or (21), which was not equal to the value of exponent of B-point line. It may be specific to the final stage with full density that the selfthinning and B-point lines are parallel to each other.
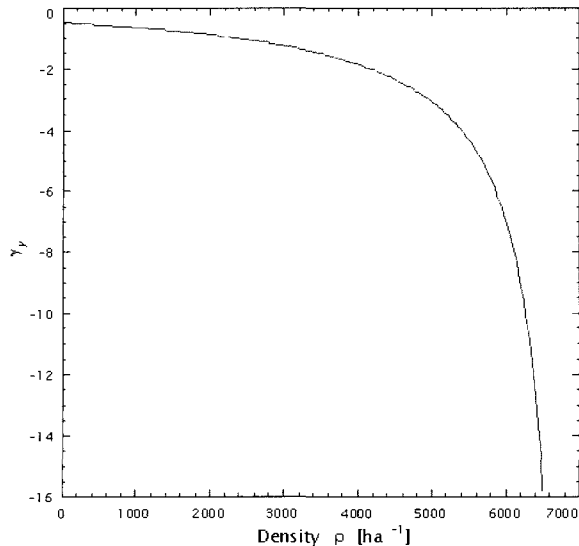
Fig. 7. Relationship of the gradient γ_y of trajectory for stand stem volume y and density ρ in eqn (16) to ρ. The curve stands for eqn (21).

Time-trajectory of maximum stem volume and density

Similar power functional relationships between maximum stem volume and density were observed in a natural forest of *Abies sachalinensis* (Hozumi *et al.* 1968), natural forests of *Betula platyphylla, B. ermanii* and *B. maximowiczii* (Hozumi *et al.* 1968), and plantations of *C. japonica* (Hozumi *et al.* 1968; Hozumi 1971; Yamakura and Shinozaki 1983a, 1983b). In these observations, the values of the exponent were $-3/2$ or $-3/2$ to -1, which was lower than the value ($= -0.6105$) of the exponent in eqn (18) in the present study, which was continued for 15 years in the same plot. This difference may arise from sampling artifact, because all of the data sets utilized to determine the relationship between maximum stem volume and density were not obtained by monitoring permanent plots but derived from a sampling of several plots.

In the present study, the values of the exponents in $\overline{w} - \rho$ and $w_{max\ obs} - \rho$ trajectories were different, which results in that the two trajectories finally coincides with each other at a density point of 611.0 ha^{-1}. Since the two values of $\overline{w}$ and $w_{max\ obs}$ are the same at this point, the stem volumes of individuals becomes the same at the final stage of stand development. The trend of size equalization with the stand development seems reasonable, because density-dependent mortality is usually confined to the smaller individuals, reducing size variation (Ogawa and Hagihara 2003).

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