論文

The Size-Dependence curve as a generalized Competition-Density curve

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HAGIHARA, Akio: **The Size-Dependence curve as a generalized Competition-Density curve.** *Jpn. J. For. Plann.* 24 : 15~23, 1995 The curve given by the generalized power equation, which has been successfully applied to describe relationships between tree functional amounts and tree size, maintained its shape when plotted on logarithmic coordinates for a fixed exponent value regardless of two other coefficient values. It was found that the generalized power equation belonged to a specified tribe of curves, recognized as a generalization of the well-known Competition-Density curve. The generalized Competition-Density curve is newly abbreviated in this paper as the Size-Dependence curve. The Size-Dependence curve includes OGAWA's Relative-Growth curve as a special case. Explicit formulae of the eight different Size-Dependence curve types were systematically represented. The eight different Size-Dependence curve types were united together by appropriately inverting on logarithmic coordinates. A graphic method for obtaining the Size-Dependence curve coefficient values was proposed.

萩原秋男：一般化されたC-D曲線としてのS-D曲線 森林計画誌 24 : 15~23, 1995 樹木個体機能量の樹木サイズへの依存性を定式化するために提案された拡張されたべき関数が示す両対数軸上での曲線は、べき指数の値が一定の場合、他の2つの係数の値に無関係に一定の形状を保った。この曲線はS-D曲線と名付けられた曲線群の一つに属していた。S-D曲線は良く知られたC-D曲線の拡張されたものであり、またR-G曲線をも含む曲線群であった。S-D曲線は8種類の異なるタイプの曲線群から成り、その全てが両対数軸上での平行移動や回転により一つに合体されるという特徴を有していた。S-D曲線を観測値に当てはめる際の係数の求め方が提案された。

I. Introduction

NINOMIYA and HOZUMI (1983 a, 1983 b) proposed a generalized power equation to describe the dependence of the respiration rate of individual trees on characteristics of their size, such as stem diameter at breast height, stem volume, and phytomass. In self-thinning plantations, the generalized power function has been acknowledged as useful in analyzing the tree size dependences of functional amounts such as phytomass increment (NINOMIYA et al., 1983), photosynthesis (MORI and HAGIHARA, 1991; YOKOTA and HAGIHARA, 1993), and respiration (YOKOTA and HAGIHARA, 1993; YOKOTA

et al., 1994).

Alternatively, SHINOZAKI and KIRA (1961) proposed the Competition-Density (C-D) curve, which has seen broad, successful forest ecological applications like analyzing the time trajectory of mean stem volume to tree density in self-thinning plantations (TADAKI, 1963); the allometric relationship between different tree dimensions (OGAWA et al., 1965); the relationship between the respiration rate per unit of phytomass and the diameter of woody organs (YODA et al., 1965; YODA, 1983); the frequency distribution of the phytomass of individual trees in forest stands (HOZUMI et al., 1968; HOZUMI, 1971); the regular changes of

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leaf characteristics such as photosynthetic rate (HOZUMI and KIRITA, 1970), respiratory rate (HOZUMI et al., 1972; HAGIHARA and HOZUMI, 1977), chlorophyll content (KIRITA and HOZUMI, 1973), and specific leaf area (KURACHI et al., 1984) along a radiation gradient through forest canopies; the stratification of forest stands (HOZUMI, 1975); the interrelationship among respiration, biomass, and biomass increment (HAGIHARA and HOZUMI, 1983; NINOMIYA and HOZUMI, 1983b); the chemical reaction of anthracene-ethyl alcohol solution (MORI et al., 1983), and the vertical distribution of foliage area (HAGIHARA and HOZUMI, 1986). This paper reports aspects of a fourfold investigation, dealing first with peculiar properties of the generalized power function proposed by NINOMIYA and HOZUMI (1983 a, 1983 b). Second, the generalized power equation is shown to belong to a specified tribe of curves (subsequently called "curve tribe" or "tribe"), recognized as a generalization of the C-D curve proposed by SHINOZAKI and KIRA (1961). The tribe is newly named here as the Size-Dependence (S-D) curve of tree functions. Third, eight different types of the S-D curve are represented and discussed. Finally, a method for obtaining S-D curve coefficient values is discussed.

II. Generalized Power Equation

NINOMIYA and HOZUMI (1983 a, 1983 b) proposed a generalized power equation to describe the dependence of the respiration rate y on the body size characteristic x , such as stem diameter at breast height, stem volume or phytomass of individual trees:

$$y = g(x - x_{\min})^h, \quad (1)$$

where g , h , and $x_{\min}$ are coefficients. Figure 1 illustrates an example depicting the relationship between the aerial respiration y of individual trees and their foliage mass x in a young hinoki (*Chamaecyparis obtusa* (SIEB. et ZUCC.) ENDL.) stand

Fig. 1. The Size-Dependence curve* used to describe the tree size dependence of a whole-tree function.

*Based on equation (1), where y and x , respectively, represent the annual aerial respiration and the foliage mass of individual trees in a *Chamaecyparis obtusa* plantation (YOKOTA et al., 1994).

(YOKOTA et al., 1994).

Biologically, equation (1) means that as the body size x approaches its critical size $x_{\min}$, below which trees cannot survive in the forest stand, the respiration rate y drops abruptly. However, the relationship satisfies the following equation in the range where the body size x is sufficiently larger than $x_{\min}$:

$$y = g x^h. \quad (2)$$

It is well-known that the relationship between an animal's characteristic y and its body size x usually takes the form of equation (2), called a power formula because the dependent variable y changes as some power h of the independent variable x (PETERS, 1983). Likewise, HOZUMI and SHINOZAKI (1974) designated any functional amount per individual tree y satisfying equation (2) as one belonging to the allometric tribe with respect to the body size x .

Hereafter, as proposed in this paper, the $\ln y$ - $\ln x$ curve, such as Figure 1, given by the generalized power function (equation 1), is called the S-D curve of tree functions.

III. Competition-Density Curve

SHINOZAKI and KIRA (1956) proposed the logistic theory describing the effect of plant density on average phytomass in higher plants, i.e., the Competition-Density effect. The theory expresses the average phytomass y as a function of the plant density x as follows:

$$\frac{1}{y} = Ax + B, \quad (3)$$

where A and B are determined at each growth stage and, thus, functions of time. The y to x curve given by equation (3) when plotted on logarithmic coordinates inherently keeps its shape despite changes in the A - and B -value. Furthermore, SHINOZAKI and KIRA (1961) concluded that even when x (or y) is replaced by $1/x$ (or $1/y$) in equation (3), no modifications are necessary in mathematical formulations. Therefore, the y to x relation can represent four different curve types. Yet another four types of y to x relationships develop by exchanging x and y for each other in each of the previous four y to x relationships. The resulting curve tribe, including the eight types of y to x relationships on logarithmic coordinates, was called the C-D curve by SHINOZAKI and KIRA (1961).

IV. Properties of the Size-Dependence Curve

Following SHINOZAKI and KIRA's (1961) mathematical manipulation for the C-D curve, the specific properties of the S-D curve, given by equation (1) when plotted on logarithmic coordinates, are examined below. A simple case is introduced where both values of g and $x_{\min}$ (equation 1) equal one, and generate a normalized form of equation (1), i.e.,

$$y = (x-1)^h. \quad (4)$$

In the $\ln y$ - $\ln x$ curve given by equation (4), if we set

$$y = \exp \eta \quad (\text{or } \ln y = \eta) \quad \text{and} \quad (5)$$

$$x = \exp \xi \quad (\text{or } \ln x = \xi),$$

then equation (4) reduces to

$$\exp \eta = (\exp \xi - 1)^h, \quad (6)$$

depicting the equation (4) S-D curve when plotted on logarithmic coordinates.

Next, considering equation (5) with

$$g = \exp \alpha \quad (\text{or } \ln g = \alpha) \quad \text{and} \quad (7)$$

$$x_{\min} = \exp \beta \quad (\text{or } \ln x_{\min} = \beta),$$

then equation (1) reduces to

$$\exp (\eta - \alpha - h \beta) = (\exp (\xi - \beta) - 1)^h, \quad (8)$$

depicting the equation (1) S-D curve when plotted on logarithmic coordinates. Now, setting

$$\eta' = \eta - (\alpha + h \beta) \quad \text{and} \quad (9)$$

$$\xi' = \xi - \beta$$

transforms equation (8) into

$$\exp \eta' = (\exp \xi' - 1)^h. \quad (10)$$

Equation (10) is obviously the same mathematical form as equation (6). Substituting (η, ξ) for (η', ξ') in equation (10) merely causes parallel displacement of the coordinate axes (see Figure 2). Therefore, changes of the g - and $x_{\min}$ -value will never alter the S-D curve's shape. Any two S-D curves whose g - and $x_{\min}$ -values are different, can always be united by appropriate parallel shifting of the coordinate axes.

The S-D curve shape is characterized by the following properties. When

$$x = x_{\min} \quad (11)$$

in equation (1), y tends to zero. Drawing from equations (5) and (7) allows equation (11) to become

$$\xi = \beta, \quad (12)$$

which depicts a vertical line on logarithmic coordinates. However, when x is large, compared to $x_{\min}$ in equation (1), equation (1) exactly duplicates equation (2) which becomes

Fig. 2. The Size-Dependence curve on the η - ξ or the η' - ξ' coordinates.*

*The S-D curve on the η - ξ coordinates is given by equation (1), while the S-D curve on the η' - ξ' coordinates is given by equation (4).

$$\eta = \alpha + h\xi, \quad (13)$$

also depicting a straight line with slope h on logarithmic coordinates. Figure 3 shows that the two straight lines given by equations (12) and (13) represent asymptotes of the S-D curve.

Equation (13) tells that the S-D curve rises at the right tail as the h -value increases. Figure 4 shows the change in shape of the S-D curve given by the normalized equation (4) with changing values of h .

V. Estimating Coefficient Values of the Size-Dependence Curve

The asymptotes intersection point, P in Figure 3, as specified by equations (12) and (13), is given by

$$x_P = x_{\min} \quad \text{and} \quad (14)$$

Fig. 3. Fundamental elements of the Size-Dependence curve.*

*Two asymptotes ($\eta = \beta$ and $\eta = \alpha + h\xi$), B-line ($\eta = \alpha + h\beta$), and S-line ($\xi = \ln 11 + \beta$), and P, B, and S points of the S-D curve.

$$y_P = g x_{\min}^h.$$

Point B, another important fixed point, exists at the intersection between the S-D curve and the line ($\eta = \alpha + h\beta$ in Figure 3 or the B-line in Figure 4) passing through point P. Point B's coordinates are

$$x_B = 2 x_{\min} \quad \text{and} \quad (15)$$

$$y_B (= y_P) = g x_{\min}^h.$$

Note that the distance between the two points P and B is always $\ln 2$ regardless of the h -value. Furthermore, another fixed point S is defined as the intersection of the S-D curve and the line ($\xi = \ln 11 + \beta$ in Figure 3 or the S-line in Figure 4)

Fig. 4. Changes* in the shape of the Size-Dependence curve.

*Given by equation (4) with the value of h .

perpendicular to the B-line. The coordinates of point S are

$$x_S = 11 x_{\min} \quad \text{and} \quad (16)$$

$$y_S = 10^h y_B.$$

Knowing the coordinates of points B and S allows tentative evaluation of the values of $x_{\min}$, h , and g (equations 15 and 16) which are given by

$$x_{\min} = \frac{x_B}{2}, \quad (17)$$

$$h = \log\left(\frac{y_S}{y_B}\right),$$

and

$$g = \frac{y_B}{x_{\min}^h}.$$

VI. The Size-Dependence Curve Tribe

Even when x (or y) is replaced with $1/x$ (or $1/y$) in equation (1), no modifications are necessary, just as with the C-D curve derivation (SHINOZAKI and KIRA, 1961). Similarly, the S-D curve tribe can be represented by the following four types of y to x relationships:

$$\text{I) } y = g(x - x_{\min})^h,$$

$$\text{II) } y = g\left(\frac{1}{x} - \frac{1}{x_{\max}}\right)^h,$$

(18)

Fig. 5. Types I to IV (equation 18) of the Size-Dependence curve.*

*This group is characterized by the horizontal position of the B-line.

$$\text{III) } \frac{1}{y} = g(x - x_{\min})^h,$$

and

$$\text{IV) } \frac{1}{y} = g\left(\frac{1}{x} - \frac{1}{x_{\max}}\right)^h,$$

where $x_{\min}$ and $x_{\max}$ represent the minimum and the maximum x -value, respectively. The four S-D curve types are united by an appropriate inversion with respect to an abscissa or an ordinate axis on logarithmic coordinates. As shown in Figure 5, this group is characterized by the horizontal position of the B-line. When h in equation (18) is equal to one, equation (18) becomes identical with the second group of the C-D curve tribe proposed by SHINOZAKI and KIRA (1961).

Four additional S-D curve types are introduced as follows:

$$\text{V) } y = g x^h + y_{\min},$$

$$\text{VI) } y = \frac{1}{g x^h} + y_{\min},$$

$$\text{VII) } \frac{1}{y} = g x^h + \frac{1}{y_{\max}}, \quad \text{and}$$

$$\text{VIII) } \frac{1}{y} = \frac{1}{g x^h} + \frac{1}{y_{\max}},$$

(19)

where $y_{\min}$ and $y_{\max}$ represent the minimum and the maximum y -value, respectively. Type V can be obtained by exchanging x and y for each other in Type I. Similar correspondence exists between Types II and VI, Types III and VII, and Types IV and VIII. The four S-D curve types in equation (19) are united by being correctly rotated on logarithmic coordinates. Types V to VIII form a group whose B-line is vertical (Figure 6). When h in equation (19) is equal to one, equation (19) becomes identical with the first C-D curve group proposed by SHINOZAKI and KIRA (1961). Figure 7 describes the interrelationships between S-D curve types.

OGAWA et al. (1965) found that the allometric relationship between different tree dimensions could be fairly well described by a generalized allometric function given by equation Type VIII. OGAWA (1980) further proposed the Relative-Growth (R-G) curve tribe given by equation Types V to VIII, which includes the generalized allometric function (Type VIII) as a special case. As a result, the generalized allometric function is included in the R-G curve tribe (equation 19),

Fig. 6. Types V to VIII (equation 19) of the Size-Dependence curve.*

* This group is characterized by the vertical position of the B-line.

Fig. 7. Interrelationships between types of the Size-Dependence curve.*

*The types connected with the horizontal, the vertical, and the diagonal lines are symmetrical with respect to an abscissa axis, an ordinate axis, and a straight line with an inclination of 45° (or -45°) on logarithmic coordinates, respectively.

which in turn can be included in the S-D curve tribe (equations 18 and 19).

Table 1 summarizes cardinal values of the S-D curve tribe. The tentatively estimated values of the coefficients $x_{\min}$ ($x_{\max}$, $y_{\min}$ or $y_{\max}$), h , and g may serve as initial values for the least squares method of nonlinear regression. Biological data tend to show the relative rather than the absolute error. The relative error of the variable y is shown by a zone of constant width on the ordinate axis along the S-D curve on logarithmic coordinates. This is of great advantage for graphically assessing coefficient values on logarithmic coordinates.

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Table 1. Cardinal values of the S-D curve.

Type	$y - x$	$x_{\min}, x_{\max}$ $y_{\min}, y_{\max}$	h	g
I	$y = g(x - x_{\min})^h$	$x_B/2$	$\log(y_S/y_B)$	$y_B/x_{\min}^h$
II	$y = g(1/x - 1/x_{\max})^h$	$2x_B$	$\log(y_S/y_B)$	$y_B x_{\max}^h$
III	$1/y = g(x - x_{\min})^h$	$x_B/2$	$\log(y_B/y_S)$	$1/(y_B x_{\min}^h)$
IV	$1/y = g(1/x - 1/x_{\max})^h$	$2x_B$	$\log(y_B/y_S)$	$x_{\max}^h/y_B$
V	$y = gx^h + y_{\min}$	$y_B/2$	$\log(x_B/x_S)$	$y_{\min}/x_B^h$
VI	$y = 1/(gx^h) + y_{\min}$	$y_B/2$	$\log(x_S/x_B)$	$1/(y_{\min} x_B^h)$
VII	$1/y = gx^h + 1/y_{\max}$	$2y_B$	$\log(x_B/x_S)$	$1/(y_{\max} x_B^h)$
VIII	$1/y = 1/(gx^h) + 1/y_{\max}$	$2y_B$	$\log(x_S/x_B)$	$y_{\max}/x_B^h$

(x_B, y_B) , coordinate of B-point; (x_S, y_S) , coordinate of the S-point. Concerning the B- and S-point, see Figure 3.

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