A Note on the Fundamental Equation of Self-Thinning in the Logistic Theory of Plant Growth

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Abstract

The fundamental equation of self-thinning, which was proposed in the logistic theory of plant growth for describing the density effect in self-thinning populations, is based on the following two fundamental assumptions: one is that the growth of mean phytomass w follows a general logistic equation; the other is that the final yield $Y(t)$, which is prescribed as the product of the asymptote of mean phytomass $W(t)$ and density ρ, becomes constant irrespective of ρ, i.e. the law of constant final yield is assumed. In the light of the basic principle of self-thinning that the relative growth rate of mean phytomass $(1/w)(dw/dt)$ is given by the sum of the relative growth rate of yield $(1/y)(dy/dt)$ and the relative mortality $(-1/\rho)(d\rho/dt)$, the first assumption brings to the conclusion that the final yield $Y(t)$ is not prescribed by $W(t)\rho$, but is prescribed by $(1-m/\lambda(t))W(t)\rho$ (m, relative mortality; $\lambda(t)$, coefficient of growth), whose value depends on density ρ except for the special case where both $W(t)\rho$ and m are independent of ρ. This inevitable consequence is in conflict with the prescription referring to the final yield $Y(t)$ in the second assumption of the logistic theory of plant growth. As a result, it is suggested that an alternative theory for the density effect in self-thinning populations should be newly constructed to harmonize the assumption referring to the growth of mean phytomass with the assumption referring to the law of constant final yield.

Introduction

The logistic theory of the competition-density (C-D) effect had been first established by Shinozaki and Kira (1956), on the basis of which theory they concluded that the reciprocal equation can describe the density effect inspected at a time constant. They pioneered in the subsequent studies on the density effect of higher plants (e.g. Shidei, 1963; Tadaki, 1969; Yoda 1971; Hozumi, 1973; Harper, 1977; Iwaki, 1979; Ogawa, 1980; Perry, 1985; Watkinson, 1986; Hirano, 1989; Firbank and Watkinson, 1990; Ando, 1992; Silvertown and Doust, 1993).

Since the applicability of the reciprocal equation was theoretically confined to the density effect occurring in nonself-thinning populations, Shinozaki (1961) proposed, in the logistic theory of plant growth, a general solution applicable to the density effect occurring in self-thinning populations. Hozumi (1977, 1980) stressed that the general solution should be considered as the most fundamental equation to show the relationship between mean phytomass w and density ρ in self-thinning populations.

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The relative growth rate of mean phytomass $(1/w)(dw/dt)$ is necessarily given by the sum of the relative growth rate of yield $(1/y)(dy/dt)$ and the relative mortality $(-1/\rho)(d\rho/dt)$ (Hozumi, 1973, 1980), which condition is named the basic principle of self-thinning in this paper. The objective of this study is to examine whether the fundamental equation of self-thinning satisfies the basic principle of self-thinning.

Interrelationship between yield, density and mean phytomass in self-thinning populations

Let us now consider even-aged plant populations starting differently only in initial density. The mean phytomass per plant w is defined with the yield per unit area y and the number of plants per unit area ρ as follows:

$$w \equiv \frac{y}{\rho}. \tag{1}$$

Here, it should be noted that w, y and ρ are regarded as functions of both initial density ρ_i and time t (Hozumi, 1973; Hagihara, 1996a).

Differentiating both sides of Eq. (1) logarithmically with respect to t, we get the following equation (Hozumi, 1973, 1980):

$$\frac{1}{w}\frac{dw}{dt}=\frac{1}{y}\frac{dy}{dt}+m. \tag{2}$$

where m stands for the relative mortality, i.e.

$$m=-\frac{1}{\rho}\frac{d\rho}{dt}. \tag{3}$$

Equation (2) represents a definite interrelationship between yield y, density ρ and mean phytomass w in self-thinning populations. From now on, we designate Eq. (2) as the basic principle of self-thinning. If no self-thinning occurs in populations, i.e. the relative mortality m is zero, then the relative growth rate of mean phytomass $(1/w)(dw/dt)$ is equal to the relative growth rate of yield $(1/y)(dy/dt)$. The logistic theory of the C-D effect (Shinozaki and Kira, 1956) targets just the nonself-thinning populations. It should be kept in mind that the relative growth rate of mean phytomass is never equal to that of yield in nonself-thinning populations.

Fundamental equation of self-thinning in the logistic theory of plant growth

The logistic theory of plant growth (Shinozaki, 1961) is based on the following two fundamental assumptions. One is that the growth of mean phytomass w is assumed to follow a general logistic equation (Shinozaki, 1953):

$$\frac{1}{w}\frac{dw}{dt}=\lambda(t)\left(1-\frac{w}{W(t)}\right), \tag{4}$$

where λ (t), the coefficient of growth, is assumed to be independent of density ρ, but dependent of time t, whereas $W(t)$, the asymptote of w, is a function of both ρ and t. The other is that the final yield $Y(t)$, which is prescribed by

$$Y(t)=W(t)\rho\ , \tag{5}$$

is assumed to become constant irrespective of density ρ (Kira *et al.*, 1953), i.e. the law of constant final yield (Hozumi *et al.*, 1956) is assumed.

Equation (4) can be translated into the integral form (Shinozaki and Kira, 1956; Shinozaki, 1961):

$$\frac{1}{w}=e^{-\tau}\int_0^\tau \frac{e^{\tau}}{W(t)}d\tau+\frac{e^{-\tau}}{w_0}, \tag{6}$$

where τ is called the biological time (Shinozaki, 1961) and is defined as

$$\tau=\int_0^t \lambda(t)dt \qquad \text{or} \qquad d\tau=\lambda(t)dt \tag{7}$$

and w_0, the initial mean phytomass, is assumed to be constant irrespective of density ρ. Inserting Eq. (5) into Eq. (6) yields the form (Shinozaki, 1961):

$$\frac{1}{w}=e^{-\tau}\int_0^\tau \frac{\rho e^{-\tau}}{Y(t)}d\tau+\frac{e^{-\tau}}{w_0}\ . \tag{8}$$

If no self-thinning occurs in populations, i.e. density ρ is constant independent of time t (or $\rho=\rho_c$), then Eq. (8) can be rewritten in the following reciprocal equation of the C-D effect (Shinozaki and Kira, 1956):

$$\frac{1}{w}A\rho_c+B, \tag{9}$$

where

$$A=e^{-\tau}\int_0^\tau \frac{e^{-\tau}}{Y(t)}\,d\tau \tag{10}$$

and

$$B=\frac{e^{-\tau}}{w_0}. \tag{11}$$

The coefficients A and B in Eq. (9) are apparently dependent of t, but independent of ρ_c, so that Eq. (9) can describe the C-D effect at a given growth stage in even-aged nonself-thinning populations.

Since the applicability of the reciprocal equation of C-D effect given by Eq. (9) is confined to the density effect in nonself-thinning populations, Shinozaki (1961) designated Eq. (8), in the case where the density ρ is a function of time t, as a general solution describing the C-D effect in self-thinning populations. Hozumi (1977, 1980) stressed that Eq. (9) containing the variable density ρ should be regarded as the most fundamental equation to describe the w-ρ relationship in self-thinning populations.

Basic principle and fundamental equation of self-thinning

If the growth of mean phytomass w is assumed to follow a general logistic equation given by Eq. (4), then the relative growth rate of yield $(1/y)(dy/dt)$ can be written in consideration of Eq. (1) on the basis of Eq. (2) as

$$\frac{1}{y}\frac{dy}{dt}=\lambda(t)\left(1-\frac{y}{W(t)\rho}\right)-m. \tag{12}$$

Equation (12) is the inevitable conclusion derived from the assumption of the growth of mean phytomass w, i.e. Eq. (4), in the light of the basic principle of self-thinning, i.e. Eq. (2). Equation (12) is synonymous with a model where elements are linearly removed from a logistic growing system, the model which in turn results in a kind of logistic equation (Shinozaki, 1976).

Equation (12) is rewritten in the form:

$$\frac{1}{y}\frac{dy}{dt}=(\lambda(t)-m)\left[1-\frac{y}{(1-m/\lambda(t)W(t)\rho}\right]. \tag{13}$$

It, therefore, follows that the growth of yield y defined as Eq. (13) follows a general logistic equation with the growth coefficient of $\lambda(t)-m$ and the asymptote of $(1-m/\lambda(t))W(t)\rho$. As a result, the final yield $Y(t)$ takes the form:

$$Y(t)=\left(1-\frac{m}{\lambda(t)}\right)W(t)\rho. \tag{14}$$

This result is in conflict with the prescription of the logistic theory of plant growth, where the final yield $Y(t)$ is expressed by Eq. (5), i.e. $W(t)\rho$.

If we assume that the growth of mean phytomass w follows a general logistic equation, i.e. Eq. (4), and the final yield $Y(t)$ is prescribed by Eq. (14), then the solution of Eq. (12) is expressed in the form (see Appendix):

$$\frac{1}{w}=e^{-\tau}\int_0^{\tau}\frac{\rho e^{\tau}}{Y(t)}d\tau+\frac{e^{-\tau}}{w_0}+\int_{\rho_1}^{\rho}\frac{1}{Y(t)}d\rho\ . \tag{15}$$

It is apparent from Eq. (14) that the final yield $Y(t)$ becomes constant irrespective of density ρ in the case where both $W(t)\rho$ and m are independent of ρ. If the final yield $Y(t)$ could be assumed to be constant irrespective of density ρ, i.e. the law of constant final yield (Kira *et al.*, 1953; Hozumi *et al.*, 1956; Shinozaki and Kira, 1956) could be assumed to hold, then Eq. (15) is reduced to the form:

$$\frac{1}{w}=e^{-\tau}\int_{0}^{\tau}\frac{\rho e^{\tau}}{Y(t)}d\tau+\frac{e^{-\tau}}{w_0}-\frac{\rho_i-\rho}{Y(t)}. \tag{16}$$

Equation (16) (or Eq. (15)), which is the conclusion after faithfully following the logistic theory of plant growth (Shinozaki, 1961), is not equated with the fundamental equation of self-thinning given by Eq. (8), except for the case where no self-thinning occurs in populations, i.e. actually realized density ρ is equal to initial density ρ_i.

Conclusion

If the growth of mean phytomass w in self-thinning populations is assumed to follow a general logistic equation (Eq. (4)), it is concluded in the light of the basic principle of self-thinning (Eq. (2)) that the final yield $Y(t)$ is prescribed by $(1 - m/\lambda(t))W(t)\rho$ (Eq. (14)), whose value never become constant irrespective of density ρ except for the special case where both $W(t)\rho$ and m are independent of density ρ. This inevitable consequence is in conflict with the prescription in the logistic theory of plant growth (Shinozaki, 1961), where the final yield $Y(t)$ is prescribed by $W(t)\rho$ (Eq. (5)). As a result, when we apply the fundamental equation of self-thinning (Eq. (8)) for the density effect in self-thinning populations, we are compelled to meet with an intraconflict between the assumption referring to the growth of mean phytomass w (Eq. (4)) and the prescription referring to the final yield $Y(t)$ (Eq. (5)) in the scheme of the logistic theory of plant growth.

Even if the final yield $Y(t)$ could be prescribed by $(1 - m/\lambda(t))W(t)\rho$, but not $W(t)\rho$, it is concluded that the fundamental equation of self-thinning (Eq. (8)) can not be derived on the assumption that the growth of mean phytomass w follows a general logistic equation. In an alternative theory for the density effect in self-thinning populations, it is necessary that the growth of yield y should be assumed to follow a growth equation into which the law of constant final yield (Kira *et al.*, 1953; Hozumi *et al.*, 1956; Shinozaki and Kira, 1956) is successfully incorporated. A detail account of the alternative theory can be seen in the papers by Hagihara (1996a, b).

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Appendix

Setting $1/y=x$, Eq. (12) can be arranged as the linear first-order differential equation:

$$\frac{dx}{dt}+(\lambda(t)-m)x=\frac{\lambda(t)}{W(t)\rho}.$$

The solution of the differential equation is

$$x=\frac{1}{y}=e^{-\int(\lambda(t)-m)dt}\left[\int e^{\int(\lambda(t)-m)dt}\frac{\lambda(t)}{W(t)\rho}dt+K\right],$$

where K is an arbitrary constant. Since m is defined as Eq. (3),

$$e^{\int m dt}=e^{\int -\frac{1}{\rho}\frac{d\rho}{dt}dt}=e^{-\ln\rho}=\frac{1}{\rho}.$$

Considering this result and Eq. (7), the solution is rewritten as

$$\frac{1}{y}=\frac{e^{-\tau}}{\rho}\left[\int\frac{e^{\tau}}{W(t)}d\tau+K\right].$$

Since $y=w^{\rho}$ from Eq. (1), the above equation becomes

$$\frac{1}{w}=e^{-\tau}\left[\int\frac{e^{\tau}}{W(t)}d\tau+K\right].$$

Substituting Eq. (14) for $W(t)$ leads to

$$\frac{1}{w}=e^{-\tau}\left[\int\frac{\rho e^{\tau}}{Y(t)}d\tau-\int\frac{\rho e^{\tau}}{Y(t)}mdt+K\right].$$

Here,

$$\int\frac{\rho e^{\tau}}{Y(t)}mdt=\int\frac{\rho e^{\tau}}{Y(t)}\left(-\frac{1}{\rho}\right)\left(\frac{d\rho}{dt}\right)dt=-\int\frac{e^{\tau}}{Y(t)}d\rho=-e^{\tau}\int\frac{1}{Y(t)}d\rho.$$

Therefore, it follows that

$$\frac{1}{w}=e^{-\tau}\int\frac{\rho e^{\tau}}{Y(t)}d\tau+\int\frac{1}{Y(t)}d\rho+e^{-\tau}K.$$

Considering the initial conditions of $w=w_0$ and $\rho=\rho_i$ at $t=0$ (or $\tau=0$) gives

$$\frac{1}{w_0}=K.$$

As a result, Eq. (15) is derived as

$$\frac{1}{w}=e^{-\tau}\int_{0}^{\tau}\frac{\rho e^{\tau}}{Y(t)}d\tau+\frac{e^{-\tau}}{w_0}+\int_{\rho_1}^{\rho}\frac{1}{Y(t)}d\rho.$$

If the final yield $Y(t)$ can be assumed to be constant irrespective of ρ, the above equation (Eq. (15)) is reduced to Eq. (16):

$$\frac{1}{w}=e^{-\tau}\int_{0}^{\tau}\frac{\rho e^{-\tau}}{Y(t)}d\tau+\frac{e^{-\tau}}{w_0}-\frac{\rho_1-\rho}{Y(t)}.$$

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Errata

A. Hagihara: A note on the fundamental equation of self-thinning in the logistic theory of plant growth. Bull. Coll. Sci., Univ. Ryukyus, No. 64: 69-76, 1997

Page	Position	Wrong	Right
p. 71	Eq. (9)	$\frac{1}{w}A\rho c+B$	$\frac{1}{w}=A\rho_c+B$
p. 72	denominator in Eq. (13)	$(1-m/\lambda(t)W(t)\rho$	$\left(1-m/\lambda(t)\right)W(t)\rho$