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	作成者: Hagihara, Akio, 萩原, 秋男
	メールアドレス:
	所属:
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Mathematical and Biological Considerations on Yield- and Competition-Density Effects in Self-thinning Plant Populations

Akio HAGIHARA*

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

Abstract

A mathematical model for describing the density effect occurring in self-thinning populations is developed on the basis of the following three basic assumptions: (1) the growth of yield follows the general logistic equation; (2) final yield becomes constant irrespective of initial density; and (3) there exists a functional relationship between actual and initial densities. The resultant equation takes the same reciprocal form as the reciprocal equation derived from Shinozaki-Kira's theory, i.e., the logistic theory of the C-D effect, which deals with the density effect occurring in nonself-thinning populations. It is, however, recognized that one of the two coefficients is quite different in mathematical interpretation between the two reciprocal equations based on the present theory and the logistic theory of the C-D effect, respectively. The present conclusion is consistent with the empirical facts that the reciprocal relationship between yield (or mean phytomass) and density is discernible in not only nonself-thinning populations, but also self-thinning populations. The present model is expected to systematically interpret underlying mechanisms between the density effect, which is observed at a time constant among populations varying in initial density, and self-thinning, which is observed along a time continuum in any given population.

Introduction

The density effect refers to the relationship at a particular moment in time between yield per unit area (or mean phytomass per plant) and plant density in populations grown at different levels of density holding growth factors, other than space, the same. On the other hand, self-thinning refers to the time-trajectory of yield (or mean phytomass) and density, i.e., how yield (or mean phytomass) increases as density decreases in a population over time. It is well-known that overcrowded populations are governed by the 3/2 power law of self-thinning, which had been first formulated by Yoda et al. (1963). Figure 1 diagrams the relationship between the competition-density (C-D) effect and self-thinning, whereas Fig. 2 diagrams the relationship between the yield-density (Y-D) effect and self-thinning.

The reciprocal equations for describing the density effect (Bleasdale and Nelder, 1960; Nelder 1962; Shinozaki and Kira, 1961; Bleasdale 1967, Farazdaghi and Harris, 1968; Watkinson, 1980; Vandermeer, 1984) originate in the logistic theory of the C-D effect, which had been first established by Shinozaki and Kira (1956). Since the logistic theory is con-



Fig. 1. Diagram showing the relationship between the C-D effect and selfthinning on logarithmic coordinates. The dotted curves and the solid curves stand for the C-D effect and self-thinning, respectively. The solid line represents the 3/2power law of self-thinning. The arrows show the progress of time. The w_0 stands for initial mean phytomass.



Fig. 2. Diagram showing the relationship between the Y-D effect and selfthinning on logarithmic coordinates. The dotted curves and the solid curves stands for the Y-D effect and self-thinning, respectively. The solid line represents the 3/2power law of self-thinning. The arrows show the progress of time. The y₀ stands for initial yield.

cerned with nonself-thinning populations, there exist difficulties to reasonably relate the density effect with self-thinning within the scheme of the logistic theory of the C-D effect. This problem has been so far left unsolved (Hozumi, 1977, 1980, 1983; Minowa, 1982; Naito, 1992). In this paper, a theory applicable to the density effect occurring in self-thinning populations is constructed in line with the logistic theory of the C-D effect. The model derived from the present theory is expected to reasonably link the density effect to self-thinning.

Interrelationships among yield, mean phytomass and density in selfthinning populations

Let us now consider a series of populations grown over a wide range of densities holding growth factors, other than space, the same. Successive decreases in density, i.e., selfthinning, occur owing to competitive interactions among individual plants in populations over time. At any given time, mean phytomass per plant w is related to yield per unit area y and the number of plants per unit area ρ , i.e., actual density:

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

Differentiating both sides of Eq. (1) logarithmically with respect to time t gives the following equation (Hozumi 1980):

$$\frac{1}{w} \frac{dw}{dt} = \frac{1}{y} \frac{dy}{dt} - \left(-\frac{1}{\rho} \frac{d\rho}{dt}\right) \quad . \tag{2}$$

Equation (2) implies that the relative growth rate of yield (1/y)(dy/dt) is never equal to the relative growth rate of mean phytomass (1/w)(dw/dt) in self-thinning populations. If the relative mortality rate $(-1/\rho)(d\rho/dt)$ is zero, i.e., no self-thinning occurs in populations, the relative growth rate of yield is equal to the relative growth rate of mean phytomass.

The logistic theory of the C-D effect (Shinozaki and Kira, 1956) is based on the following two basic assumptions: (1) the growth of mean phytomass follows the general logistic equation (Shinozaki, 1953); and (2) the law of constant final yield (Kira et al., 1953; Hozumi et al., 1956) holds. In light of Eq. (2), the former assumption for the growth of mean phytomass, prior to the growth of yield, causes a conflict to the latter assumption, as far as self-thinning populations are concerned (Hagihara, 1997). Therefore, we can not apply the logistic theory of the C-D effect to the density effect occurring in self-thinning populations.

Conspecific individual plants are integrated into a higher level of biotic components, i.e., plant populations, which grow in a similar manner to a whole plant. Realization of the constant final yield regardless of density in a population after a sufficient lapse of time (Donald, 1951; Kira et al., 1953) characterizes the growing behavior of plant populations. In this context, it is reasonable to assume that the growth of yield y follows the general logistic equation:

$$\frac{1}{y}\frac{dy}{dt} = \lambda(t)\left(1-\frac{y}{Y(t)}\right) . \tag{3}$$

where Y(t) is the asymptote of y and $\lambda(t)$ is the growth coefficient. Although the general logistic equation never gives a specifically determined curve, we can assume that it offers the most promise for describing population growth. Any change in actual population growth could be reasonably traced with the general logistic equation, where the two arbitrary parameters Y(t) and $\lambda(t)$ are allowed to be functions of time t (Shinozaki, 1953). Figure 3 diagrams the growth of yield y according to the general logistic equation.

Density-dependent mortality

In the time frame of self-thinning, plant populations can not be denser than an asymptote of density, whose level becomes lower over time (Yoda et al., 1963; Ando, 1968; Watkinson, 1980, 1986; Firbank and Watkinson, 1990). Figure 4 depicts the relationships between actual density ρ and initial density ρ_i at any given time t in *Pinus densiflora* stands. The relationship can be described with the following equation proposed by Shinozaki and Kira (1956):

$$\frac{1}{\rho} = \frac{1}{\rho_{\rm i}} + \varepsilon \left(t \right) \,. \tag{4}$$



Fig. 3. Diagram showing the growth of yield y according to the general logistic equation, i.e., Eq. (3), where the growth coefficient λ and the asymptote Y are respectively changeable step by step from λ_1 and Y_1 to λ_4 and Y_4 as time t progresses. The solid line stands for the actual growth of y.



Fig. 4. Relationships between actual density ρ and initial density ρ_i in *Pinus densiflora* stands (data from Tadaki et al. (1979)). The curves are given by Eq. (4).

where $\varepsilon(t)$ is the reciprocal of the asymptote of ρ at t as ρ_i tends to infinity, and is apparently independent of both ρ and ρ_i , but is a function of t alone.

Mathematical formulation of the density effect in self-thinning populations

A theory applicable to the density effect occurring in self-thinning populations is constructed in line with the logistic theory of the C-D effect. In the present theory, Eqs. (3) and (4) are adopted in the following assumptions:

(i) The growth of yield y follows the general logistic equation given by Eq. (3).

$$\frac{1}{y}\frac{dy}{dt}=\lambda(t)\left(1-\frac{y}{Y(t)}\right).$$

(ii) The growth coefficient $\lambda(t)$ is independent of initial density ρ_i .

$$\frac{\partial \lambda(t)}{\partial \rho_{i}} = 0 .$$
 (5)

Under the assumption of logistic growth, growth is largely free from the inhibitory influence of ρ_i in the early period of growth.

(iii) The law of constant final yield (Kira et al., 1953; Hozumi et al., 1956) holds.

$$\frac{\partial Y(t)}{\partial \rho_{i}} = 0 \quad . \tag{6}$$

(iv) Initial mean phytomass w_0 , defined as initial yield y_0 divided by initial density ρ_i , is constant regardless of ρ_1 .

$$w_0 = \frac{y_0}{\rho_1} \,. \tag{7}$$

$$\frac{\partial u_0}{\partial \rho_i} = 0 . ag{8}$$

This assumption is supported with the fact that seeds are sown simultaneously at t = 0 irrespective of ρ_i .

(v) The relationship between actual density ρ and initial density ρ_i at any given time t is described with Eq. (4).

$$\frac{1}{\rho} = \frac{1}{\rho_1} + \varepsilon(t) .$$

$$\frac{\partial \varepsilon(t)}{\partial \rho_i} = 0 \left(= \frac{\partial \varepsilon(t)}{\partial \rho} \right).$$
(9)

In the logistic theory of the C-D effect (Shinozaki and Kira, 1956), mean phytomass w, instead of yield y, was assumed to follow the general logistic equation:

$$\frac{1}{w}\frac{dw}{dt} = \lambda(t)\left(1 - \frac{w}{W(t)}\right),\tag{10}$$

where W(t) is the asymptote of w. As far as nonself-thinning populations are concerned, Eq. (3) is equivalent to Eq. (10), as might be expected from Eq. (2). Assumptions (ii) to (iv) are essentially the same as the assumptions adopted in the logistic theory of the C-D effect. In the logistic theory of the C-D effect, the final yield Y(t) was defined as:

$$Y(t) = W(t)\rho . \tag{11}$$

However, Eq. (11) does not hold in self-thinning populations (Hagihara, 1997), so that Eq. (11) is necessarily excluded from the present theory. Assumption (v) is newly incorporated into the present theory.

Using Eq. (7), the solution of Eq. (3) is written in the form:

$$\frac{1}{y} = e^{-\tau} \int_0^{\tau} \frac{e^{\tau}}{Y(t)} d\tau + \frac{e^{-\tau}}{w_0} \frac{1}{\rho_i} .$$
 (12)

Here, τ is called biological time (Shinozaki 1961) and is defined as (Shinozaki and Kira, 1956):

$$\tau = \int_{0}^{t} \lambda(t) dt .$$
⁽¹³⁾

With abbreviations of

$$A = e^{-\tau} \int_0^{\tau} \frac{e^{\tau}}{Y(t)} d\tau \tag{14}$$

and

$$B = \frac{e^{-\tau}}{w_0} , \qquad (15)$$

Eq. (12) can be rewritten in the form:

$$\frac{1}{y} = A + \frac{B}{\rho_i} . \tag{16}$$

Both the coefficients A and B in Eq. (16) are apparently independent of initial density ρ_i from Eqs. (5), (6) and (8), but are functions of time t alone. Equation (16) describes the Y-D effect realized between yield y and initial density ρ_i at any given time in populations. It should be noted that Eq. (16) is essentially synonymous with the reciprocal equation of the Y-D effect based on the logistic theory of the C-D effect, as pointed out by Hagihara (1996). Conclusively speaking, Eq. (16) holds in not only self-thinning populations, but also nonselfthinning populations.

Substituting Eq. (4) into Eq. (16), we have

$$\frac{1}{y} = A_1 + \frac{B}{\rho} , \qquad (17)$$

where

$$A_{t}\left(=A-B\varepsilon(t)\right)=e^{-\tau}\int_{0}^{\tau}\frac{e^{\tau}}{Y(t)}d\tau-\frac{e^{-\tau}}{w_{0}}\varepsilon(t) . \qquad (18)$$

The coefficients A_1 and B in Eq. (17) are of course independent of actual density ρ (see Appendix), but are functions of time t alone. Equation (17) describes the Y-D effect realized between yield y and actual density ρ at any given time in populations. It should be noted that the coefficient A_1 in Eq. (17) is quite different in mathematical interpretation from the coefficient A in Eq. (16). If no self-thinning occurs in populations (i.e., since $\rho = \rho_1$, $\varepsilon(t) = 0$ from Eq. (4), so that $A_1 = A$ from Eq. (18)), Eq. (17) is identical to Eq. (16). Equation (17) can, therefore, describe the Y-D effect at any given time in not only selfthinning populations, but also nonself-thinning populations.

Considering Eq. (1), Eq. (17) is transformed to the following equation:

$$\frac{1}{w} = A_t \rho + B . \tag{19}$$

Equation (19) describes the C-D effect realized between mean phytomass w and actual density ρ at any given time in populations. If no self-thinning occurs in populations, Eq. (19) is identical to the reciprocal equation of the C-D effect based on the logistic theory of the C-D effect. It, therefore, follows that Eq. (19) is also applicable to the C-D effect in not only self-thinning populations, but also nonself-thinning populations.

Conclusion

The density effect in self-thinning populations can be described with the same formed reciprocal equation as the reciprocal equation derived from the logistic theory of the C-D effect established by Shinozaki and Kira (1956), the theory which is confined to nonself-thinning populations. However, it should be noted that the coefficient A in Eq. (16), which is essentially the same as the reciprocal equation of the Y-D effect derived from the logistic theory of the C-D effect, is quite different in mathematical interpretation from the coefficient A_t in Eq. (17) (see Eq. (18)). The present conclusion is consistent with the empirical facts (e.g., Yoda et al., 1963; Ando, 1968, 1992; Drew and Flewelling, 1977; Tadaki et al., 1979; Thoranisorn et al., 1990; Shibuya, 1994; Tadaki, 1996; Shibuya et al., 1997) showing that the reciprocal relationship between yield (or mean phytomass) and density is discernible in not only nonself-thinning populations, but also self-thinning populations.

It has been so far impossible to systematically interpret the interrelationships between the density effect observed at a time constant and the self-thinning observed along a time continuum (see Figs. 1 and 2) within the scheme of the logistic theory of the C-D effect (Hozumi, 1977, 1980, 1983; Minowa, 1982; Naito, 1992). The present model, applicable to the density effect occurring in self-thinning populations, is expected to give us a clue for solving the problem. A detailed account of the systematic interpretation will be published elsewhere.

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Appendix

Differentiating both sides of Eq. (4), i.e.,

$$\frac{1}{\rho}=\frac{1}{\rho_{\rm i}}+\varepsilon(t) ,$$

with respect to initial density ρ_i gives

$$\frac{\partial \rho}{\partial \rho_{\rm i}} = \frac{\rho^2}{\rho_{\rm i}^2} \,. \tag{A1}$$

Considering Eq. (A1), Eqs. (5), (6) and (8) can be rewritten respectively in the forms,

$$\frac{\partial \lambda(t)}{\partial \rho_{i}} = \frac{\partial \lambda(t)}{\partial \rho} \frac{\rho^{2}}{\rho_{i}^{2}} = 0 , \qquad (A2)$$
$$\frac{\partial Y(t)}{\partial \rho_{i}} = \frac{\partial Y(t)}{\partial \rho} \frac{\rho^{2}}{\rho_{i}^{2}} = 0 \qquad (A3)$$

and

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$$\frac{\partial w_0}{\partial \rho_i} = \frac{\partial w_0}{\partial \rho} \frac{\rho^2}{\rho_i^2} = 0 .$$
 (A4)

Here, it is apparent that $\rho^2/\rho_1^2 \neq 0$, so that the following are concluded from Eqs. (A2), (A3) and (A4), respectively,

$$\frac{\partial \lambda(t)}{\partial \rho} = 0 , \qquad (A5)$$

$$\frac{\partial Y(t)}{\partial \rho} = 0 \tag{A6}$$

and

$$\frac{\partial w_0}{\partial \rho} = 0 \ . \tag{A7}$$

The $\lambda(t)$ has been verified to be independent of actual density ρ , which in turn means that the biological time τ defined as Eq. (13), i.e.,

$$\tau=\int_0^t\lambda(t)dt\;,$$

is independent of ρ . Since τ , Y(t) and w_0 have been known to be independent of actual density ρ and in addition $\varepsilon(t)$ is also known to be independent of ρ from Eq. (9), the coefficients A_1 and B are demonstrated to be independent of ρ .