Res Popul Ecol (1999) 41:151–159

ORIGINAL ARTICLE

Akio Hagihara

Theoretical considerations on the C-D effect in self-thinning plant populations

Received: August 5, 1998 / Accepted: January 7, 1999

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

Key words General logistic equation · Reciprocal equation · Mean phytomass · Mortality · Population density · Law of constant final yield

A. Hagihara
Laboratory of Ecology and Systematics, Faculty of Science, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan
Tel. +81-98-895-8546; Fax +81-98-895-8546
e-mail: amyh@sci.u-ryukyu.ac.jp

Introduction

The competition–density (C-D) effect refers to the relationship at a particular moment in time between mean phytomass per plant and the number of plants per unit area among populations grown at different levels of density. On the other hand, self-thinning refers to the time trajectory of mean phytomass and population density, i.e., how mean phytomass increases as density decreases in a population over time. It is well known that overcrowded populations follow the 3/2 power law of self-thinning, which was first formulated by Yoda et al. (1963) (e.g., Harper 1977; Charles-Edwards et al. 1986; Silvertown and Doust 1993; Niklas 1994; Perry 1994; Begon et al. 1996; Watkinson 1997).

The reciprocal equations for describing the C-D effect (Bleasdale and Nelder 1960; Shinozaki and Kira 1961; Nelder 1962; Bleasdale 1967; Farazdaghi and Harris 1968; Watkinson 1980; Vandermeer 1984) originate in the logistic theory of the C-D effect established by Shinozaki and Kira (1956). On the basis of the reciprocal equation of the C-D effect or the basic equation of self-thinning (Shinozaki 1961), Hozumi (1977, 1980, 1983) succeeded to a considerable extent in explaining the time trajectory of mean phytomass and population density during the course of self-thinning. However, because density does not change in the populations considered in the logistic theory of the C-D effect, there would be a theoretical limit in reconciling the C-D effect and self-thinning within the framework of the logistic theory of the C-D effect (Minowa 1982; Naito 1992).

The objective of this article is to formulate the C-D effect in self-thinning populations grown at different levels of density, holding growth factors other than space constant. Successive decreases in density, i.e., self-thinning, occur as the result of competitive interactions among individual plants in populations over time. The mean phytomass w at any given time can only be calculated from yield per unit area y and the number of surviving plants (i.e., actual population density ρ) (Shinozaki 1979; Weller 1987). Namely, these three variables have the following relationship:

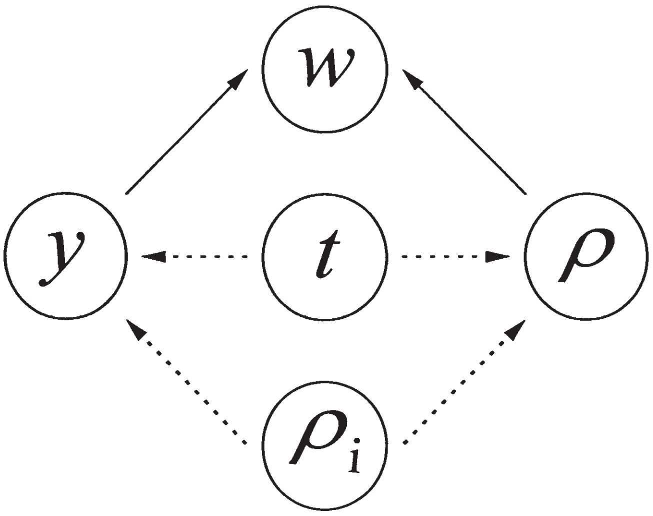

Fig. 1. Interrelationships among the fundamental variables to be considered in self-thinning (based on the diagram by Hozumi 1973). y, yield; ρ, actual population density; w, mean phytomass; ρ_i, initial population density (independent variable); t, time (independent variable)

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

As a result, the mean phytomass w is a function of the yield y and the actual population density ρ, both of which are in turn functions of the number of plants at the beginning of an experiment (i.e., initial population density ρ_i) and the period of growth (i.e., time t):

$$w = w(y, \rho)$$

$$y = y(\rho_i, t)$$

and

$$\rho = (\rho_i, t)$$

The interrelationships among the variables are diagrammatically shown in Fig. 1.

Before proceeding with the C-D effect in self-thinning populations, an overview of the logistic theory of the C-D effect is given and the derivation of the reciprocal equation of the C-D effect reached by Shinozaki and Kira (1956) is retraced. In addition, the model of the functional relationship between actual and initial population densities formulated by Shinozaki and Kira (1956) is reconfirmed. Then, a model applicable to the C-D effect in self-thinning populations is developed in line with the logistic theory of the C-D effect. Finally, the interrelationships between the logistic theory of the C-D effect and the present model are discussed.

The C-D effect in nonself-thinning populations

Shinozaki and Kira (1956) established the logistic theory of the C-D effect, in which they succeeded in formulating the functional relationship between mean phytomass and population density on the basis of the following assumptions.

Assumption 1

The growth of mean phytomass w follows the general logistic equation

$$\frac{1}{w}\frac{dw}{dt} = \lambda(t)\left(1 - \frac{w}{W(t)}\right) \tag{2}$$

where $\lambda(t)$ is the growth coefficient and $W(t)$ is the asymptote of w. Both $\lambda(t)$ and $W(t)$ are allowed to be functions of time t (Shinozaki 1953a).

Assumption 2

The growth coefficient $\lambda(t)$ is independent of population density ρ.

$$\frac{\partial \lambda(t)}{\partial \rho} = 0 \tag{3}$$

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

Assumption 3

Final yield per unit area $Y(t)$ is independent of population density ρ (Kira et al. 1953); i.e., the law of constant final yield (Hozumi et al. 1956) holds:

$$W(t) = \frac{Y(t)}{\rho} \tag{4}$$

$$\frac{\partial Y(t)}{\partial \rho} = 0 \tag{5}$$

Assumption 4

Initial mean phytomass w_0 is constant irrespective of population density ρ.

$$\frac{\partial w_0}{\partial \rho} = 0 \tag{6}$$

This assumption is supported with the fact that seeds are sown simultaneously at $t = 0$ irrespective of population density ρ.

Using Eq. 4, Eq. 1 can be rewritten in the form (Shinozaki 1961):

$$\frac{1}{w} = e^{-\tau}\int_0^{\tau} \frac{\rho e^{\tau}}{Y(t)} d\tau + \frac{e^{-\tau}}{w_0} \tag{7}$$

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

$$\tau = \int_0^t \lambda(t)dt \tag{8}$$

Equation 7 was considered as the most fundamental formula to show the w–ρ relationship of self-thinning populations, i.e., the basic equation of self-thinning (Hozumi 1977, 1980).

If the population density ρ is maintained at a constant value ρ_c (i.e., in the state of initial population density ρ_i throughout the experiment), then Eq. 7 reduces to

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

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 of A and B in Eq. 9 are apparently functions of time t alone, regardless of the population density ρ_c from Eqs. 3, 5, and 6.

Equation 9 is called the reciprocal equation of the C-D effect (Shinozaki and Kira 1956), which describes the relationship between the mean phytomass w and the population density ρ_c at any given time among a set of nonself-thinning populations grown at different levels of density. Equation 9 gives an excellent fit to the data and has been applied with considerable success to the relationship of mean phytomass to population density for a very wide range of species, implying that a simple rule underlies the growth of populations (e.g., Harper 1977; Firbank and Watkinson 1990; Silvertown and Doust 1993).

Mortality pattern in self-thinning populations

In the time course of self-thinning, plant populations cannot be denser than an asymptote of population density, whose level becomes lower as time progresses. Figure 2 depicts the relationships at any given time between actual population density ρ and initial population density ρ_i in *Pinus densiflora* stands examined by Tadaki et al. (1979). The relationship can be well approximated with the following equation proposed by Shinozaki and Kira (1956):

$$\frac{1}{\rho} = \frac{1}{\rho_i} + \varepsilon(t) \tag{12}$$

where $\varepsilon(t)$ represents the reciprocal of the asymptote of ρ at time t as ρ_i tends to infinity, and is apparently independent of ρ and ρ_i, but is a function of t alone. From here on, we designate Eq. 12 as the ρ–ρ_i model.

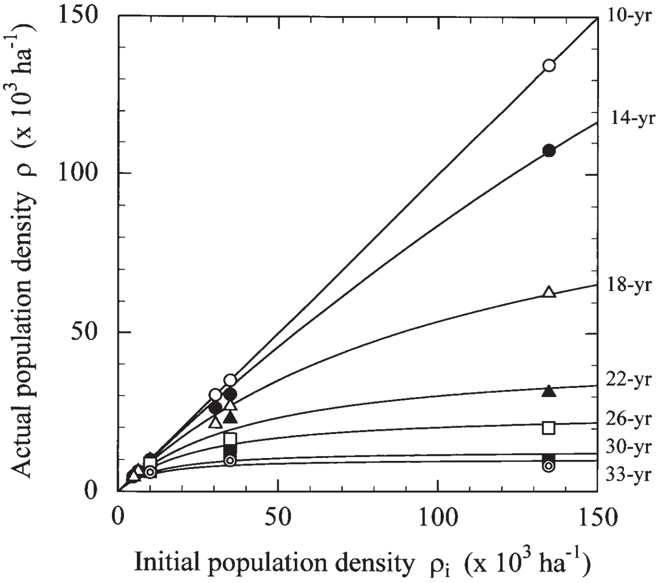

Fig. 2. Relationships between actual population density ρ and initial population density ρ_i at any give time in *Pinus densiflora* stands (data from Tadaki et al. 1979). The curves are given by Eq. 12

On the basis of experimental results in self-thinning populations, Shinozaki and Kira (1956) arrived at the ρ–ρ_i model from the following two assumptions, where an imaginary mean phytomass (Ikusima et al. 1955; Kira et al. 1956), defined as

$$w_i = \frac{y}{\rho_i} \tag{13}$$

is considered.

Assumption 1

There exists a reciprocal relationship between imaginary mean phytomass w_i and initial population density ρ_i at any given time in self-thinning populations.

$$\frac{1}{w_i} = A_i\rho_i + B_i \tag{14}$$

where A_i and B_i are time-dependent coefficients.

Assumption 2

There exists a reciprocal relationship between mean phytomass w and actual population density ρ at any given time in self-thinning populations.

$$\frac{1}{w} = A'\rho + B' \tag{15}$$

where A' and B' are time-dependent coefficients.

Under situations with extremely low population densities, populations are not overcrowded, so that the following equality is realized:

$$w_i\big|_{\rho_i \to 0} = w\big|_{\rho \to 0}$$

This equality means that B_i in Eq. 14 and B' in Eq. 15 agree with each other. As the following relationships are obvious from Eqs. 1 and 13

$$\frac{1}{y} = \frac{1}{w_i \rho_i} = \frac{1}{w\rho}$$

we have

$$\frac{1}{\rho} = \frac{1}{\rho_i} + \frac{A_i - A'}{B_i}$$

Here, let us denote the second term $(A_i - A')/B_i$ on the right-hand side by $\varepsilon(t)$, then the ρ–ρ_i model (Eq. 12) is reached.

Yoda et al. (1963) reconfirmed the validity of the ρ–ρ_i model on the basis of spacing experiments of *Sesame vulgaris* and *Fagopyrum esculentum* populations. Watkinson (1980) also reported that the ρ–ρ_i model fits extremely well to data collected from populations of *Agrostemma githago* and *Raphanus sativus*. Firbank and Watkinson (1985, 1990) and Watkinson (1986) recognized that the ρ–ρ_i model is useful in describing the density-dependent mortality pattern in plant populations.

Interrelationships among yield, mean phytomass, and population density in self-thinning populations

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

$$\frac{1}{w}\frac{dw}{dt} = \frac{1}{y}\frac{dy}{dt} + \left(-\frac{1}{\rho}\frac{d\rho}{dt}\right) \tag{16}$$

Equation 16 states that the relative growth rate of mean phytomass $(1/w)(dw/dt)$ is not equal to the relative growth rate of yield $(1/y)(dy/dt)$ in self-thinning populations.

If the growth of mean phytomass w is assumed to follow the general logistic equation (Eq. 2) and no self-thinning occurs in populations $(-(1/\rho)(d\rho/dt) = 0)$, then Eq. 16 reduces to the following equation (Shinozaki 1979):

$$\frac{1}{y}\frac{dy}{dt} = \lambda(t)\left(1 - \frac{y}{Y(t)}\right) \tag{17}$$

Equation 17 states that the growth of yield y follows a general logistic equation with the growth coefficient of $\lambda(t)$ and the asymptote of $Y(t)$. As a result, the law of constant final yield is successfully reflected in the growth equation of yield y. Therefore, it follows that the assumption of the logistic growth of w is equivalent to that of the logistic growth of y, so far as nonself-thinning populations are concerned.

However, if the growth of mean phytomass w is assumed to follow the general logistic equation (Eq. 2) and self-thinning does occur in populations $(-(1/\rho)(d\rho/dt) > 0)$, Eq. 16 reduces to the following equation:

$$\frac{1}{y}\frac{dy}{dt} = \lambda(t)\left(1 - \frac{y}{W(t)\rho}\right) - m \qquad \left(m = -\frac{1}{\rho}\frac{d\rho}{dt}\right) \tag{18}$$

Equation 18 is identical with a model proposed by Shinozaki (1976) for describing linear removal from a logistic growing system, so that the growth of yield y is regarded to follow a kind of logistic equation with the growth coefficient of $\lambda(t) - m$ and the asymptote of $(1 - m/\lambda(t))W(t)\rho$. Because the asymptote is apparently

$$\left(1 - \frac{m}{\lambda(t)}\right)W(t)\rho \neq Y(t)$$

Eq. 4 in assumption 3 of the logistic theory of the C-D effect

$$W(t) = \frac{Y(t)}{\rho}$$

does not hold. In addition, the asymptote depends on population density ρ because the relative mortality rate m is density dependent. Therefore, it follows that the law of constant final yield cannot be reflected in the resultant growth equation of yield y, so far as self-thinning populations are concerned.

When the logistic theory of the C-D effect is applied to the density effect in self-thinning populations, assumptions 1 and 3 of the theory are in conflict. In this context, it is concluded that Eq. 7 cannot function as the basic equation for describing the C-D effect in self-thinning populations.

The C-D effect in self-thinning populations

Conspecific individual plants are integrated into a higher level of biotic components, i.e., plant populations, which grow in a manner similar to that of a whole plant. Decreases in yield caused by mortality are most likely matched with increases in phytomass caused by the accelerated growth of survivors. The yield increases to approach asymptotically a carrying capacity for the environment. Realization of the constant final yield regardless of population density (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 (Eq. 17), whether self-thinning occurs or does not occur in populations.

Although the general logistic equation does not give a specifically determined curve, we can assume that it offers a general principle for describing population growth. Any change in actual population growth could be reasonably traced with the general logistic equation in which two arbitrary parameters are adequately modified as functions of time (Shinozaki 1953a,b).

In light of Eq. 16, the assumption of the logistic growth of yield y (Eq. 17) inevitably determines the growth of mean phytomass w as follows:

$$\frac{1}{w}\frac{dw}{dt} = \lambda(t)\left(1 - \frac{w}{Y(t)/\rho}\right) + m \qquad \left(m = -\frac{1}{\rho}\frac{d\rho}{dt}\right) \tag{19}$$

Equation 19 is also regarded as a kind of logistic equation (cf. Eq. 18), whose growth coefficient is $\lambda(t) + m$ and asymptote $W(t)$ is

$$W(t) = \left(1 + \frac{m}{\lambda(t)}\right)\frac{Y(t)}{\rho} \tag{20}$$

Equation 20 is quite different from Eq. 4 in assumption 3 of the logistic theory of the C-D effect. Conclusively speaking, it follows that the asymptote $W(t)$ of mean phytomass w is

$$W(t) \neq \frac{Y(t)}{\rho}$$

so far as self-thinning populations are concerned ($m > 0$).

To develop a model applicable to the C-D effect in self-thinning populations, the following assumptions are set up in a manner similar to the logistic theory of the C-D effect.

Assumption 1

The growth of mean phytomass w is described with Eq. 19.

$$\frac{1}{w}\frac{dw}{dt} = \lambda(t)\left(1 - \frac{w}{Y(t)/\rho}\right) + m \qquad \left(m = -\frac{1}{\rho}\frac{d\rho}{dt}\right)$$

Assumption 2

The growth coefficient $\lambda(t)$ for yield y is independent of initial population density ρ_i.

$$\frac{\partial \lambda(t)}{\partial \rho_i} = 0 \tag{21}$$

Assumption 3

The final yield $Y(t)$ is independent of initial population density ρ_i.

$$\frac{\partial Y(t)}{\partial \rho_i} = 0 \tag{22}$$

Assumption 4

Initial mean phytomass w_0, defined as initial yield y_0 divided by initial population density ρ_i, is constant irrespective of ρ_i.

$$w_0 = \frac{y_0}{\rho_i} \tag{23}$$

$$\frac{\partial w_0}{\partial \rho_i} = 0 \tag{24}$$

Assumption 5

The functional relationship of actual population density ρ realized at any given time t to initial population density ρ_i is described with the ρ–ρ_i model (Eq. 12):

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

$$\frac{\partial \varepsilon(t)}{\partial \rho_i} = 0 \qquad \left(= \frac{\partial \varepsilon(t)}{\partial \rho}\right) \tag{25}$$

Assumption 1 is equivalent to the assumption that the growth of yield y follows the general logistic equation given by Eq. 17. The logistic theory of the C-D effect assumed that the growth of mean phytomass w follows the general logistic equation given by Eq. 2. The assumption of the logistic growth of mean phytomass w is not compatible with that of the logistic growth of yield y in self-thinning populations, as mentioned earlier. Assumptions 2 to 4 are basically the same as those adopted in the logistic theory of the C-D effect. However, because Eq. 4 in assumption 3 of the logistic theory of the C-D effect is not valid in self-thinning populations, Eq. 4 is necessarily excluded in the present theory. Assumption 5 is newly incorporated into the present theory.

The five assumptions just discussed lead to the reciprocal equation of the C-D effect in self-thinning populations being expressed (Appendix 1) as

$$\frac{1}{w} = \left(e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau - \frac{e^{-\tau}}{w_0}\varepsilon(t)\right)\rho + \frac{e^{-\tau}}{w_0} \tag{26}$$

With abbreviations of

$$A_t = e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau - \frac{e^{-\tau}}{w_0}\varepsilon(t) \tag{27}$$

and

$$B = \frac{e^{-\tau}}{w_0} \tag{28}$$

Eq. 26 can be rewritten in the form

$$\frac{1}{w} = A_t\rho + B \tag{29}$$

The coefficient B is common between Eqs. 9 and 29 (cf. Eq. 11). The coefficients A_t and B in Eq. 29 are independent of actual population density ρ (Appendix 2), but are dependent on time t alone. If no self-thinning occurs in populations (i.e., $\varepsilon(t)$ in Eq. 12 is zero under the situation of $\rho = \rho_i$, so that A_t becomes equal to A given by Eq. 10 from Eq. 27), then Eq. 29 is identical to the reciprocal equation of the C-D effect in nonself-thinning populations (Eq. 9).

Equation 29 is essentially the same as Eq. 15, which was assumed in the derivation of the ρ–ρ_i model. The details are discussed in the next section.

Discussion

Let us consider the imaginary mean phytomass defined as Eq. 13:

$$w_i = \frac{y}{\rho_i}$$

Differentiating both sides of Eq. 13 logarithmically with respect to time *t* leads to

$$\frac{1}{w_i}\frac{dw_i}{dt} = \frac{1}{y}\frac{dy}{dt} \tag{30}$$

Therefore, on the assumption that the yield y grows according to the general logistic equation (Eq. 17), the growth of the imaginary mean phytomass w_i can be written in the form:

$$\frac{1}{w_i}\frac{dw_i}{dt} = \lambda(t)\left(1 - \frac{w_i}{W_i(t)}\right) \tag{31}$$

where $W_i(t)$ $(= Y(t)/\rho_i)$ is the asymptote of w_i. Equation 31 represents a general logistic equation with the growth coefficient of $\lambda(t)$ and the asymptote of $W_i(t)$.

We shall now suppose that the logistic theory of the C-D effect is concerned with the imaginary mean phytomass w_i instead of the mean phytomass w, so that the assumptions of the theory are modified as follows.

Assumption 1

The growth of imaginary mean phytomass w_i follows Eq. 31:

$$\frac{1}{w_i}\frac{dw_i}{dt} = \lambda(t)\left(1 - \frac{w_i}{W_i(t)}\right)$$

Assumption 2

The growth coefficient $\lambda(t)$ is independent of initial population density ρ_i:

$$\frac{\partial \lambda(t)}{\partial \rho_i} = 0$$

Assumption 3

Final yield $Y(t)$ is independent of initial population density ρ_i:

$$W_i(t) = \frac{Y(t)}{\rho_i}$$

$$\frac{\partial Y(t)}{\partial \rho_i} = 0$$

Assumption 4

Initial mean phytomass w_0 is constant irrespective of initial population density ρ_i:

$$\frac{\partial w_0}{\partial \rho_i} = 0$$

From these assumptions, we have the following reciprocal equation:

$$\frac{1}{w_i} = A_i\rho_i + B_i \tag{32}$$

The coefficients A_i and B_i in Eq. 32 are respectively expressed in the forms

$$A_i = e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau \tag{33}$$

and

$$B_i = \frac{e^{-\tau}}{w_0} \tag{34}$$

where the biological time τ is defined as Eq. 8:

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

It is recognized that the coefficients A_i and B_i in Eq. 32 are the same, respectively, as the coefficients A and B in Eq. 9 (cf. Eqs. 10 and 11).

Equation 32 coincides with Eq. 14 assumed in the derivation of the ρ–ρ_i model (Eq. 12). When Eq. 14 was assumed, the biological meanings were not clear. However, as a result of the present interpretation for the logistic theory of the C-D effect, validity has been given to Eq. 14.

Let us now replace Eq. 15, i.e., one of the two assumptions for the ρ–ρ_i model, with the ρ–ρ_i model itself (Eq. 12) and start with the following two assumptions.

Assumption 1

Equation 14, or Eq. 32, holds in self-thinning populations:

$$\frac{1}{w_i} = A_i\rho_i + B_i$$

Assumption 2

The relationship between actual population density ρ and initial population density ρ_i is described with the ρ–ρ_i model (Eq. 12):

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

These assumptions conclude the following relationship:

$$\frac{1}{w} = A'\rho + B' \tag{35}$$

where

$$A' = A_i - B_i\varepsilon(t) \tag{36}$$

and

$$B' = B_i \tag{37}$$

Equation 35 is Eq. 15 itself. In other words, the assumption for the ρ–ρ_i model appears as the conclusion.

Because the coefficients A_i and B_i in Eqs. 36 and 37 have been known as Eqs. 33 and 34, respectively, Eqs. 36 and 37 can be respectively rewritten in the forms:

$$A' = e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau - \frac{e^{-\tau}}{w_0}\varepsilon(t) \tag{38}$$

and

$$B' = \frac{e^{-\tau}}{w_0} \tag{39}$$

Equations 38 and 39, respectively, conform to Eqs. 27 and 28. It is, therefore, recognized that Eq. 35, i.e., Eq. 15, is the same as Eq. 29, as concluded in the present paper. Although biological or mathematical interpretation for the coefficients A' and B' in Eq. 15 were obscure in the derivation of the ρ–ρ_i model, the definitions of Eqs. 38 and 39, respectively, give mathematical interpretation to the coefficients A' and B' to some extent.

The validity of Eq. 29, i.e., Eq. 15, is supported with many experimental data (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 mean phytomass (or mean stem volume) and population density is discernible in not only nonself-thinning populations but also in self-thinning populations.

Conclusion

Shinozaki and Kira (1956) were the first to establish the logistic theory of the C-D effect, which was constructed on the basis of the following two basic assumptions: (1) the growth of mean phytomass *w* follows the general logistic equation (Eq. 2); and (2) the law of constant final yield holds. As a result, they concluded that the reciprocal equation of the C-D effect (Eq. 9)

$$\frac{1}{w}\left(=\left(e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau\right)\rho_c + \frac{e^{-\tau}}{w_0}\right) = A\rho_c + B$$

is realized at any given time among nonself-thinning populations grown over a wide range of densities.

On the basis of the review of the logistic theory of the C-D effect, it has been revealed that Eq. 7

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

does not function as the basic equation for describing the relationship between mean phytomass *w* and actual population density ρ in self-thinning populations, because the assumption that the growth of mean phytomass *w* follows the general logistic equation (Eq. 2) is not consistent with the assumption of Eq. 4:

$$W(t) = \frac{Y(t)}{\rho}$$

so far as self-thinning populations are concerned.

To develop a model applicable to the C-D effect in self-thinning populations, a theory was constructed in a manner similar to the logistic theory of the C-D effect. The present theory consists of the following three basic assumptions: (1) the growth of mean phytomass *w* follows the general logistic equation (Eq. 19); (2) the law of constant final yield holds; and (3) the functional relationship between actual population density ρ and initial population density ρ_i is described with the ρ–ρ_i model (Eq. 12). The resultant conclusion is summarized with Eq. 26 (i.e., Eq. 29):

$$\frac{1}{w}\left(=\left(e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau - \frac{e^{-\tau}}{w_0}\varepsilon(t)\right)\rho + \frac{e^{-\tau}}{w_0}\right) = A_t\rho + B$$

Equation (29) is essentially the same as Eq. 15:

$$\frac{1}{w} = A'\rho + B'$$

which was assumed in the derivation of the ρ–ρ_i model (Eq. 12). Although biological or mathematical interpretation for the coefficients A' and B' in Eq. 15 was obscure, it has become clear that they are respectively defined as Eqs. 38 and 39:

$$A'(=A_t) = e^{-\tau}\int_0^{\tau}\frac{e^{\tau}}{Y(t)}d\tau - \frac{e^{-\tau}}{w_0}\varepsilon(t)$$

and

$$B'(=B) = \frac{e^{-\tau}}{w_0}$$

The reciprocal equation of the C-D effect realized in self-thinning populations (Eq. 29; i.e., Eq. 35) is the same in form as that realized in nonself-thinning populations (Eq. 9). The difference between Eqs. 9 and 29 results from the difference in mathematical interpretation between the coefficient A in Eq. 9 and the coefficient A_t in Eq. 29.

There have so far existed theoretical difficulties in harmonizing the C-D effect observed at a time constant with the 3/2 power law of self-thinning (Yoda et al. 1963) observed along a time continuum (Hozumi 1977, 1980, 1983; Aikman and Watkinson 1980; Minowa 1982; Firbank and Watkinson 1985; Naito 1992). The derivation of Eq. 26, which describes the C-D effect realized in self-thinning populations, gives us a clue for solving the problem. A detailed account of the systematic interpretation will be published elsewhere.

Acknowledgments I thank Emeritus Prof. Kazuo Hozumi and Prof. Takeo Umemura, Nagoya University, former Prof. Kichiro Shinozaki, Tezukayama University, and Prof. Takuo Yamakura, Osaka City University, for their valuable suggestions and criticisms.

References

Aikman DP, Watkinson AR (1980) A model for growth and self-thinning in even-aged monocultures of plants. Ann Bot 45:419–427

Ando T (1968) Ecological studies on the stand density control in even-aged pure stand (in Japanese with English summary). Bull Gov For Exp Stn 210:1–152

Ando T (1992) Forest management after thinning. In: Silviculture. Asakura-Shoten, Tokyo, pp 137–159 (in Japanese)

Begon M, Harper JL, Townsend CR (1996) Ecology: individuals, populations and communities. Blackwell, Oxford

Bleasdale JKA (1967) The relationship between the weight of a plant part and total weight as affected by plant density. J Hortic Sci 42:51–58

Bleasdale JKA, Nelder JA (1960) Plant population and crop yield. Nature (Lond) 188:342

Charles-Edwards DA, Doley D, Rimmington GM (1986) Modelling plant growth and development. Academic Press, Sydney

Donald CM (1951) Competition among pasture plants. I. Intra-specific competition among annual plants. Aust J Agric Res 2:355–376

Drew TJ, Flewelling JW (1977) Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. For Sci 23:517–534

Farazdaghi H, Harris PM (1968) Plant competition and crop yield. Nature (Lond) 217:289–290

Firbank LG, Watkinson AR (1985) A model of interference within plant monocultures. J Theor Biol 116:291–311

Firbank LG, Watkinson AR (1990) On the effects of competition: from monocultures to mixture. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego, pp 165–192

Harper JL (1977) Population biology of plants. Academic Press, London

Hozumi K (1973) Interactions among higher plants. Kyouritsu-Shuppan, Tokyo (in Japanese)

Hozumi K (1977) Ecological and mathematical considerations on self-thinning in even-aged pure stands. I. Mean plant weight-density trajectory during the course of self-thinning. Bot Mag Tokyo 90:165–179

Hozumi K (1980) Ecological and mathematical considerations on self-thinning in even-aged pure stands. II. Growth analysis of self-thinning. Bot Mag Tokyo 93:149–166

Hozumi K (1983) Ecological and mathematical considerations on self-thinning in even-aged pure stands. III. Effect of the linear growth factor on self-thinning and its model. Bot Mag Tokyo 96:171–191

Hozumi K, Asahira T, Kira T (1956) Intraspecific competition among higher plants. VI. Effect of some growth factors on the process of competition. J Inst Polytech Osaka City Univ D 7:15–34

Ikusima K, Shinozaki K, Kira T (1955) Intraspecific competition among higher plants. III. Growth of duckweed, with a theoretical consideration on the C-D effect. J Inst Polytech Osaka City Univ D 6:107–119

Kira T, Ogawa H, Sakazaki N (1953) Intraspecific competition among higher plants. I. Competition-yield-density interrelationship in regularly dispersed populations. J Inst Polytech Osaka City Univ D 4:1–16

Kira T, Ogawa H, Hozumi K, Koyama H, Yoda K (1956) Intraspecific competition among higher plants. V. Supplementary notes on the C-D effect. J Inst Polytech Osaka City Univ D 7:1–14

Minowa M (1982) A theoretical approach to forest growth model. I. The log-Mitscherlich theory (in Japanese with English summary). J Jpn For Soc 64:461–467

Naito K (1992) Studies on forest growth modeling (in Japanese with English summary). Bull Utsunomiya Univ For 28:1–95

Nelder JA (1962) New kinds of systematic designs for spacing experiments. Biometrics 18:283–307

Niklas KL (1994) Plant allometry: the scaling of form and process. University of Chicago Press, Chicago

Perry DA (1994) Forest ecosystems. John Hopkins University Press, Baltimore

Shibuya M (1994) Maximum yield and the C-D effects in natural white birch stands. Ecol Res 9:325–332

Shibuya M, Yajima T, Matsuda K (1997) A modified stand density control diagram for Japanese white birch based on a trend of mean volume-density relationships with stand growth (in Japanese with English summary). Res Bull Hokkaido Univ For 54:202–211

Shinozaki K (1953a) On the generalization of the logistic curve. I. General discussions (in Japanese). J Osaka City Med Sch 2:143–147

Shinozaki K (1953b) On the generalization of the logistic curve. II. Japanese population (in Japanese). J Osaka City Med Sch 2:259–264

Shinozaki K (1961) Logistic theory of plant growth. Doctoral thesis, Kyoto University, Kyoto (in Japanese)

Shinozaki K (1976) Effects of removal on a growing system (in Japanese with English summary). Physiol Ecol Jpn 17:101–107

Shinozaki K (1979) Density effect of plants. 3. Growth of yield (in Japanese). Chem Biol 17:536–538

Shinozaki K, Kira T (1956) Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. J Inst Polytech Osaka City Univ D 7:35–72

Shinozaki K, Kira T (1961) The C-D rule, its theory and practical uses. (Intraspecific competition among higher plants. X.) J Biol Osaka City Univ 12:69–82

Silvertown JW, Doust JL (1993) Introduction to plant population biology. Blackwell, Oxford

Tadaki Y (1996) Structure and productivity of young *Castanopsis cuspidata* forests growing in different stand densities (in Japanese with English summary). Bull Nagoya Univ For 14:1–24

Tadaki Y, Takeuchi I, Kawahara T, Sato A, Hatiya K (1979) Growth analysis on the natural stands of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.). III. Results of experiment (research note) (in Japanese). Bull For For Prod Res Inst 305:125–144

Thoranisorn S, Sahunalu P, Yoda K (1990) Density effects and self-thinning in even-aged pure stands of *Eucalyptus camaldulensis* Dehn. Bot Mag Tokyo 103:283–295

Vandermeer J (1984) Plant competition and yield-density relationship. J Theor Biol 109:393–399

Watkinson AR (1980) Density-dependence in single-species populations of plants. J Theor Biol 83:345–357

Watkinson AR (1986) Plant population dynamics. In: Crawley MJ (ed) Plant ecology. Blackwell, Oxford, pp 137–184

Watkinson AR (1997) Plant population dynamics. In: Crawley MJ (ed) Plant ecology, 2nd edn. Blackwell, Oxford, pp 359–400

Weller DE (1987) A reevaluation of the −3/2 power rule of plant self-thinning. Ecol Monogr 57:23–43

Yoda K, Kira T, Ogawa H, Hozumi K (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants. XI.) J Biol Osaka City Univ 14:107–129

Appendix 1

Setting $1/w = x$, Eq. 19

$$\frac{1}{w}\frac{dw}{dt} = \lambda(t)\left(1 - \frac{w}{Y(t)/\rho}\right) + m$$

is arranged as the linear first-order differential equation

$$\frac{dx}{dt} + \left(\lambda(t) + m\right)x = \frac{\rho}{Y(t)}\lambda(t) \qquad \text{(A1)}$$

The general solution of Eq. A1 is

$$x = \frac{1}{w} = e^{-\int_0^t(\lambda(t)+m)dt}\left[\int_0^t \frac{\rho}{Y(t)}\lambda(t)e^{\int_0^t(\lambda(t)+m)dt}dt + k\right] \qquad \text{(A2)}$$

where k is an arbitrary constant. In consideration of Eq. 8

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

and

$$\int_0^t m\,dt = \int_0^t \left(-\frac{1}{\rho}\frac{d\rho}{dt}\right)dt = -\int_{\rho_i}^{\rho} \frac{1}{\rho}d\rho = \log\frac{\rho_i}{\rho}$$

Eq. A2 can be rewritten in the form

$$\frac{1}{w} = \left(e^{-\tau}\int_0^{\tau} \frac{e^{\tau}}{Y(t)}d\tau\right)\rho + \frac{\rho}{\rho_i}e^{-\tau}k \tag{A3}$$

Here, considering the initial conditions of $w = w_0$ and $\rho = \rho_i$ at $t = 0$, i.e., $\tau = 0$, we have

$$k = \frac{1}{w_0}$$

Therefore, Eq. A3 becomes

$$\frac{1}{w} = \left(e^{-\tau}\int_0^{\tau} \frac{e^{\tau}}{Y(t)}d\tau\right)\rho + \frac{\rho}{\rho_i}\frac{e^{-\tau}}{w_0} \tag{A4}$$

Inserting Eq. 12:

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

into Eq. A4 leads to Eq. 26:

$$\frac{1}{w} = \left(e^{-\tau}\int_0^{\tau} \frac{e^{\tau}}{Y(t)}d\tau - \frac{e^{-\tau}}{w_0}\varepsilon(t)\right)\rho + \frac{e^{-\tau}}{w_0}$$

Appendix 2

Differentiating both sides of Eq. 12

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

with respect to initial density ρ_i gives

$$\frac{\partial \rho}{\partial \rho_i} = \frac{\rho^2}{\rho_i^2} \tag{B1}$$

Considering Eq. B1, Eqs. 21, 22, and 24, respectively, can be rewritten in the forms:

$$\frac{\partial \lambda(t)}{\partial \rho_i} = \frac{\partial \lambda(t)}{\partial \rho}\frac{\rho^2}{\rho_i^2} = 0 \tag{B2}$$

$$\frac{\partial Y(t)}{\partial \rho_i} = \frac{\partial Y(t)}{\partial \rho}\frac{\rho^2}{\rho_i^2} = 0 \tag{B3}$$

$$\frac{\partial w_0}{\partial \rho_i} = \frac{\partial w_0}{\partial \rho}\frac{\rho^2}{\rho_i^2} = 0 \tag{B4}$$

Here, it is apparent that $\rho^2/\rho_i^2 \neq 0$, so that the following are respectively concluded from Eqs. B2, B3, and B4:

$$\frac{\partial \lambda(t)}{\partial \rho} = 0 \tag{B5}$$

$$\frac{\partial Y(t)}{\partial \rho} = 0 \tag{B6}$$

$$\frac{\partial w_0}{\partial \rho} = 0 \tag{B7}$$

The $\lambda(t)$ has been verified to be independent of actual population density ρ, which in turn means that the biological time τ, defined as Eq. 8:

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

is independent of ρ. Because τ, $Y(t)$, and w_0 have been known to be independent of actual population density ρ and because $\varepsilon(t)$ is also known to be independent of ρ from Eq. 25, the coefficients A_t and B are demonstrated to be independent of ρ.