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Time-trajectory of Mean Phytomass and Density in Self-thinning Plant Populations

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Abstract

Reconciling the competition-density (C-D) effect observed at a particular moment in time with the 3/2 power law of self-thinning observed over time, a model for describing the time-trajectory of mean phytomass w and density ρ (briefly, the w - ρ trajectory) during the course of self-thinning is theoretically derived. The model gives a consistent, full explanation of the w - ρ trajectories of populations starting with any initial density. The larger value of the relative mortality rate with respect to biological time of a population, which is governed by the 3/2 power law of self-thinning, plays an important role in relieving the C-D effect, so that the w - ρ trajectories asymptotically approach the self-thinning line on logarithmic coordinates at the earlier stage of growth. The survivorship curve is divided into three types owing to initial density: logistic, exponential and cologistic types of decrease. All populations tend to decrease exponentially in number at the same rate of relative mortality after a sufficient lapse of time, irrespective of their initial density. The populations decreasing exponentially in number follow the 3/2 power law of self-thinning. The carrying capacity of yield is explicitly defined as a function of biological time, so that it is concluded that the carrying capacity increases exponentially with increasing biological time. An approximated expression of the model for the w - ρ trajectory is proposed and is confirmed to mimic well the time-trajectories of mean stem volume and density during the development of eastern white pine (*Pinus strobus* L.) plantations.

Introduction

The competition-density (C-D) effect refers to the relationship between mean phytomass and density at a particular moment in time among a set of populations grown at a wide range of densities. Self-thinning, on the other hand, refers to the time-trajectory of mean phytomass w and density ρ (briefly, the w - ρ trajectory) of any given population over time. It is well-known that overcrowded populations are governed by the 3/2 power law of self-thinning (Yoda et al. 1963). The w - ρ trajectories of populations starting with initial densities below the full density asymptotically approach the self-thinning line on logarithmic coordinates and then travel along this line as the populations grow with the progress of self-thinning (e.g. Tadaki and Shidei, 1959; Ando, 1962; Tadaki, 1963; Kays and Harper, 1974; Westoby, 1984; White, 1981; Norberg, 1988). This process may be formulated in terms of mathematical equations (Minowa, 1982; Hara, 1984; Naito, 1984, 1992; Firbank and Watkinson, 1985; Smith and Hann, 1986; Tang et al., 1994).

Merging the 3/2 power law of self-thinning into the logistic theory of the C-D effect (Shinozaki and Kira, 1956) or the logistic theory of plant growth (Shinozaki, 1961), Hozumi (1977, 1980) succeeded to a considerable extent in explaining the w - ρ trajectory over the development of self-thinning populations. However, Minowa (1982) and Naito (1992) pointed out that there would be a theoretical limit in reconciling the C-D effect and self-thinning within the framework of the logistic theory, because density does not change in the populations considered in the theory.

In a previous paper (Hagihara, 1999), a model for describing the C-D effect occurring in self-thinning populations was reconstructed in line with the logistic theory of the C-D effect. On the basis of that model and the 3/2 power law of self-thinning, the present paper firstly intends to derive a model for describing the w - ρ trajectory of populations starting with any initial density. The derivation is based on the ideas presented by Hozumi (1977, 1980). Secondly, the carrying capacity of yield, which was an unknown function, is explicitly defined as a function of biological time. Next, an approximated expression of the newly derived model is proposed as a convenient and practical model for describing the w - ρ trajectory. Finally, the applicability of the approximated model is examined with the data obtained by Spurr et al. (1956) in eastern white pine (*Pinus strobus* L.) plantations.

The C-D effect and the 3/2 power law

The C-D effect in self-thinning populations

In a previous paper (Hagihara, 1999), a theory of the C-D effect in self-thinning populations was reconstructed in line with the logistic theory (Shinozaki and Kira, 1956; Shinozaki, 1961), which focuses on the C-D effect in nonself-thinning populations, on the basis of the following assumptions:

1) The growth of yield y per unit area follows the general logistic equation proposed by Shinozaki (1953a).

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

where λ is the growth coefficient and Y is the carrying capacity of y , and both λ and Y are allowed to be functions of time t .

2) The growth coefficient λ is independent of initial density ρ_i .

$$\frac{\partial \lambda}{\partial \rho_i} = 0. \quad (2)$$

3) The carrying capacity Y is independent of initial density ρ_i , i. e. the law of constant final yield is realized (Kira et al., 1953; Hozumi et al., 1956).

$$\frac{\partial Y}{\partial \rho_i} = 0. \quad (3)$$

4) Initial mean phytomass w_0 is constant irrespective of initial density ρ_i .

$$y_0 = w_0 \rho_i \quad (y|_{t=0} = y_0) \quad (4)$$

$$\frac{\partial w_0}{\partial \rho_i} = 0. \quad (5)$$

5) There exists a functional relationship between the density of survivors ρ and initial density ρ_i at any given time (Shinozaki and Kira, 1956).

$$\frac{1}{\rho} = \frac{1}{\rho_i} + \varepsilon \quad \left(\rho \Big|_{\rho_i \rightarrow \infty} = \frac{1}{\varepsilon} \right). \quad (6)$$

$$\frac{\partial \varepsilon}{\partial \rho_i} = 0 \quad \left(= \frac{\partial \varepsilon}{\partial \rho} \right). \quad (7)$$

The five assumptions above lead to the equation describing the relationship between mean phytomass w ($= y/\rho$) and density ρ being expressed as

$$\frac{1}{w} = \left(e^{-\tau} \int_0^{\tau} \frac{e^{\tau}}{Y} d\tau - \frac{e^{-\tau}}{w_0} \varepsilon \right) \rho + \frac{e^{-\tau}}{w_0}, \quad (8)$$

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

$$\tau = \int_0^t \lambda dt. \quad (9)$$

If the value of ε is zero, eqn (8) is synonymous with the equation theoretically reached by Shinozaki and Kira (1956), which describes the relationship between w and ρ in nonself-thinning populations.

With abbreviations of

$$A_t = e^{-\tau} \int_0^{\tau} \frac{e^{\tau}}{Y} d\tau - \frac{e^{-\tau}}{w_0} \varepsilon \quad (10)$$

and

$$B = \frac{e^{-\tau}}{w_0}, \quad (11)$$

eqn (8) can be rewritten in the form,

$$\frac{1}{w} = A_t \rho + B. \quad (12)$$

The coefficients A_t and B are functions of time, but are independent of density ρ . Equation (12) describes the C-D effect at a particular moment in time among a set of populations grown at different levels of density.

Equation (12) is considered a generalization of the reciprocal equation of the C-D effect occurring in not only nonself-thinning, but also self-thinning populations (Shinozaki and Kira, 1956). The validity of eqn (12), i. e. eqn (8), is supported with a great deal of experimental data (e. g. Shinozaki and Kira, 1956; 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 stem volume) w and density ρ is discernible in not only nonself-thinning populations, but also self-thinning populations.

The 3/2 power law of self-thinning

Yoda et al. (1963) discovered that the mortality of overcrowded self-thinning populations occurs in the following way,

$$w = K\rho^{-\alpha}, \quad (13)$$

where K is a constant that varies from species to species and α has a value of approximately 3/2 for a wide range of species (White, 1985). On the other hand, Tadaki and Shidei (1959), Ando (1962) and Tadaki (1963) found that mortality can also occur in less crowded populations and the w - ρ trajectory asymptotically approaches the self-thinning line given by eqn (13) on logarithmic coordinates.

Although there has been considerable debate over the universality of the 3/2 power law of self-thinning (e.g. Weller, 1987, 1990, 1991; Zeide, 1987; Osawa and Sugita, 1989; Lonsdale, 1990), what is clear is that eqn (13) can be used to describe the w - ρ trajectory of an overcrowded self-thinning population (Hamilton et al., 1995; Watkinson, 1997).

The time-trajectory of mean phytomass and density

Unification of the C-D effect and the 3/2 power law

The time-trajectory of mean phytomass w and density ρ on logarithmic coordinates (briefly, the w - ρ trajectory) moves upward on points on the C-D curves given by eqn (12) as populations develop. A series of the points creates the w - ρ trajectory of any self-thinning population starting with initial density ρ_i (e.g. White, 1981; Westoby, 1984; Norberg, 1988; Osawa and Sugita, 1989). In other words, eqn (8), i.e. eqn (12), involves the relationship between $w(\tau)$ and $\rho(\tau)$ of any population over biological time τ .

Hozumi (1977) pointed out that the slope of the w - ρ trajectory takes the form,

$$\frac{d \log w}{d \log \rho} = - \frac{\frac{1}{w} \frac{dw}{d\tau}}{-\frac{1}{\rho} \frac{d\rho}{d\tau}}. \quad (14)$$

Therefore, considering eqns (11) and (14), the slope of the reciprocal equation of the C-D effect in self-thinning populations, i.e. eqn (12), over time on logarithmic coordinates is expressed in the form,

$$\frac{d \log w}{d \log \rho} = - \frac{A_i \left(-\frac{1}{\rho} \frac{d\rho}{d\tau} \right) + \frac{B}{\rho} - \frac{dA_i}{d\tau}}{\left(A_i + \frac{B}{\rho} \right) \left(-\frac{1}{\rho} \frac{d\rho}{d\tau} \right)}. \quad (15)$$

On the other hand, the slope of the power equation, i.e. eqn (13), on logarithmic coordinates is

$$\frac{d \log w}{d \log \rho} = -\alpha. \quad (16)$$

The w - ρ trajectory approaches the self-thinning line with a slope of $-\alpha$, i.e. eqn (13), and then travels along this line. That is, the slope given by eqn (15) becomes the same as the slope given by eqn (16) as biological time τ tends to be finitely large. Therefore, the following equality holds,

$$\frac{dA_i}{d\tau} = \frac{B(1-\alpha m)}{\rho} - (\alpha - 1)A_i m, \quad (17)$$

where

$$m = -\frac{1}{\rho} \frac{d\rho}{d\tau}. \quad (18)$$

Since both A_t and τ are independent of density ρ , the term $dA_t/d\tau$ on the left-hand side of eqn (17) is also independent of ρ , i. e.

$$\frac{\partial}{\partial \rho} \left(\frac{dA_t}{d\tau} \right) = 0. \quad (19)$$

Therefore, the derivative of the terms on the right-hand side of eqn (17) with respect to ρ must be zero. This leads to the following relationship in consideration of eqn (6),

$$\frac{B(1-\alpha m)}{\rho_i^2} \frac{d\rho_i}{d\rho} + \left[(\alpha - 1)A_t + \frac{\alpha B}{\rho} \right] \frac{dm}{d\rho} = 0. \quad (20)$$

If both

$$\frac{d\rho_i}{d\rho} = 0 \quad (21)$$

and

$$\frac{dm}{d\rho} = 0, \quad (22)$$

then the realization of eqn (20) is ensured. Equations (21) and (22) indicate respectively that the initial density ρ_i and the relative mortality rate m of any population become constant irrespective of ρ as τ tends to be finitely large, i. e.

$$\rho_i = \rho_i^* \quad (23)$$

and

$$m = -\frac{1}{\rho} \frac{d\rho}{d\tau} = \mu. \quad (24)$$

The solution to eqn (24) with the initial condition of eqn (23) is

$$\rho(= \rho^*) = \rho_i^* e^{-\mu\tau}. \quad (25)$$

Equation (25) denotes that the density ρ of any population tends to decrease exponentially against biological time τ irrespective of initial density ρ_i after a sufficient lapse of time. The ρ_i^* is regarded as the initial density of a population which obeys the 3/2 power law of self-thinning from the start of an experiment, i. e. $\tau = 0$. Hozumi (1980) designated the population as ρ_i^* -population and assumed eqn (25) for the survivorship curve of the ρ_i^* -population. The derivation of eqn (25) gives a theoretical background to this assumption.

Survivorship curve

All populations follow eqn (6). The ρ_i^* -population is also governed by eqn (6), so that the following relationship is concluded,

$$\varepsilon \left(= \frac{1}{\rho} - \frac{1}{\rho_i} \right) = \frac{1}{\rho^*} - \frac{1}{\rho_i^*}. \tag{26}$$

Considering eqns (25) and (26), the unknown function ε is explicitly defined as a function of biological time τ as follows,

$$\varepsilon = \frac{1}{\rho_i^*} (e^{\mu\tau} - 1). \tag{27}$$

Inserting eqn (27) into eqn (6), the following equation is reached,

$$\frac{1}{\rho} = \frac{1}{\rho_i} + \frac{1}{\rho_i^*} (e^{\mu\tau} - 1). \tag{28}$$

This equation is the same as what Hozumi (1980, 1983) presupposed in deriving the w - ρ trajectory.

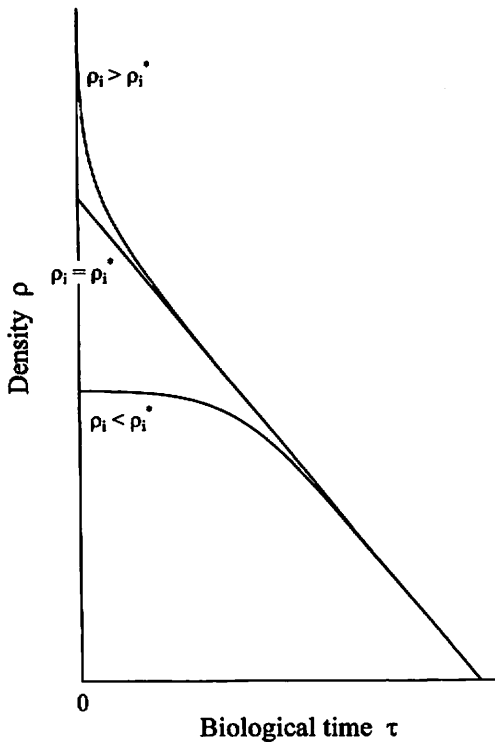


Fig. 1. Survivorship curves relative to initial density ρ_i on semi-logarithmic coordinates. The curves are given by eqn (28), where $\mu=0.6$. The ρ_i^* is the initial density of the ρ_i^* -population (see text). $\rho_i < \rho_i^*$, a logistic type of decrease; $\rho_i = \rho_i^*$, an exponential type of decrease; $\rho_i > \rho_i^*$, a cologistic (Shinozaki, 1953b) type of decrease.

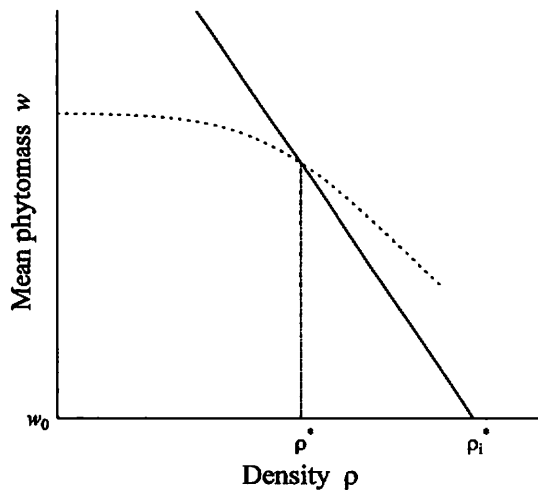


Fig. 2. Interrelationship between the C-D curve and the self-thinning line on logarithmic coordinates. When density ρ becomes equal to ρ^* , the C-D curve given by eqn (12) intersects the self-thinning line given by eqn (13). The ρ_i^* is the initial density of the ρ_i^* -population (see text) and w_0 is initial mean phytomass.

Equation (28) describes the survivorship curve of any population starting with initial density ρ_i . As shown in Fig. 1, in the case of $\rho_i = \rho_i^*$, the survivorship curve displays an exponential type of decrease. If $\rho_i > \rho_i^*$, the survivorship curve displays a logistic type of decrease, whereas if $\rho_i < \rho_i^*$, the survivorship curve displays a cologistic (Shinozaki, 1953b) type of decrease. The survivorship curve of any population tends to the exponential type of decrease irrespective of ρ_i after a sufficient lapse of time. Xue and Hagihara (1998) analyzed the data obtained by Tadaki et al. (1979) in self-thinning stands of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) and reported that the survivorship curve tended to converge to the same density level after a sufficient lapse of time, even if the stands started with different initial densities.

Explicit form of the coefficient A_t

When density ρ becomes equal to density ρ^* of the ρ_i^* -population, as depicted in Fig. 2, the C-D curve, i.e. eqn (12), intersects the self-thinning line, i.e. eqn (13). That is, the following equality is concluded,

$$A_t \rho_i^* + \frac{e^{-\tau}}{w_0} = \frac{1}{K \rho_i^{*\alpha}}, \quad (29)$$

where in consideration of eqn (13) the coefficient K is expressed in terms of the initial density ρ_i^* of the ρ_i^* -population and initial mean phytomass w_0 , i.e.

$$K = w_0 \rho_i^{*\alpha}. \quad (30)$$

Considering eqn (25), eqn (29) is arranged in the following way,

$$A_t = \frac{1}{w_0 \rho_i^*} \left(e^{-(\alpha-1)\mu\tau} - e^{-(1-\mu)\tau} \right). \quad (31)$$

Since the value of the coefficient A_t is not negative because of the nature of the C-D curve created by eqn (12) (Shinozaki and Kira, 1961), the value of the coefficient μ is restricted to the following range,

$$0 < \mu < \frac{1}{\alpha}. \quad (32)$$

As shown in Fig. 3, the value of A_t increases up to its maximum in the earlier stage of growth and then decreases gradually with increasing biological time τ . This trend is consistent with the results obtained by Xue and Hagihara (1998) in analyzing the data of the *Pinus densiflora* stands. As the value of μ becomes larger, A_t takes on a smaller value.

The w - ρ trajectory

The w - ρ trajectory can be obtained basically by eliminating time from both of the equations of mean phytomass w and density ρ as functions of time (Hozumi, 1977). Equation (12), i.e. eqn (8), determines the growth pattern of w of a population starting with initial density ρ_i over time. The growth pattern has now been explicitly obtained as a function of biological time τ through the explicit forms of A_t , i.e. eqn. (31), and ρ , i.e. eqn (28), which in turn determines the mortality pattern of the population over time. The τ appears in the explicit forms of the coefficients A_t and B (i.e. eqn (11)) in eqn (12) in the form of $e^{-\tau}$. On the basis of eqn (28), the $e^{-\tau}$ can be expressed as a function of ρ ,

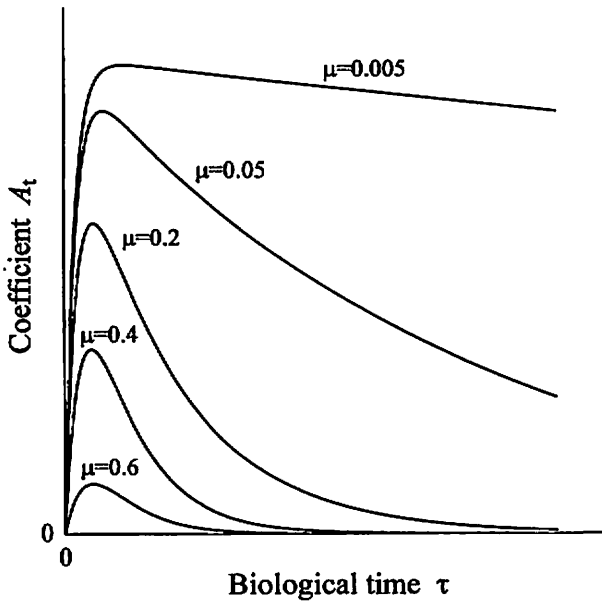


Fig. 3. Transitions of the value of the coefficient A_t with biological time τ . The curves are given by eqn (31), where $\alpha = 3/2$. The value of A_t decreases with increasing rate of relative mortality μ .

$$e^{-\tau} = \left(\frac{\rho_i^*}{\rho} - \frac{\rho_i^*}{\rho_o} \right)^{-\frac{1}{\mu}}, \quad (33)$$

where

$$\frac{1}{\rho_o} = \frac{1}{\rho_i} - \frac{1}{\rho_i^*}. \quad (34)$$

Eliminating $e^{-\tau}$ from eqns (11) and (31) using eqn (33), and in consideration of eqn (30), the reciprocal equation of the C-D effect, i. e. eqn (12), can be rewritten in the form,

$$w = \frac{K\rho^{-\alpha} \left(1 - \frac{\rho}{\rho_o} \right)^{\alpha-1}}{1 + \frac{\rho_i^*}{\rho_o} \left(\frac{\rho_i^*}{\rho} - \frac{\rho_i^*}{\rho_o} \right)^{-\left(\frac{1}{\mu} - \alpha + 1 \right)}} \quad (35)$$

Equation (35) describes the time-trajectory of mean phytomass w and density ρ during the course of self-thinning in any population starting with initial density ρ_i . In the case of $\rho_i = \rho_i^*$, eqn (35) is the same as the power equation of self-thinning, i. e. eqn (13). As ρ becomes much smaller than ρ_i , eqn (35) also becomes identical to eqn (13).

As illustrated in Fig. 4, eqn (35) gives a consistent, full explanation of the w - ρ trajectory of any population starting with initial density ρ_i . When the value of the relative mortality rate μ of the ρ_i^* -population is low, the C-D effect occurs intensely from the earlier stage of growth and

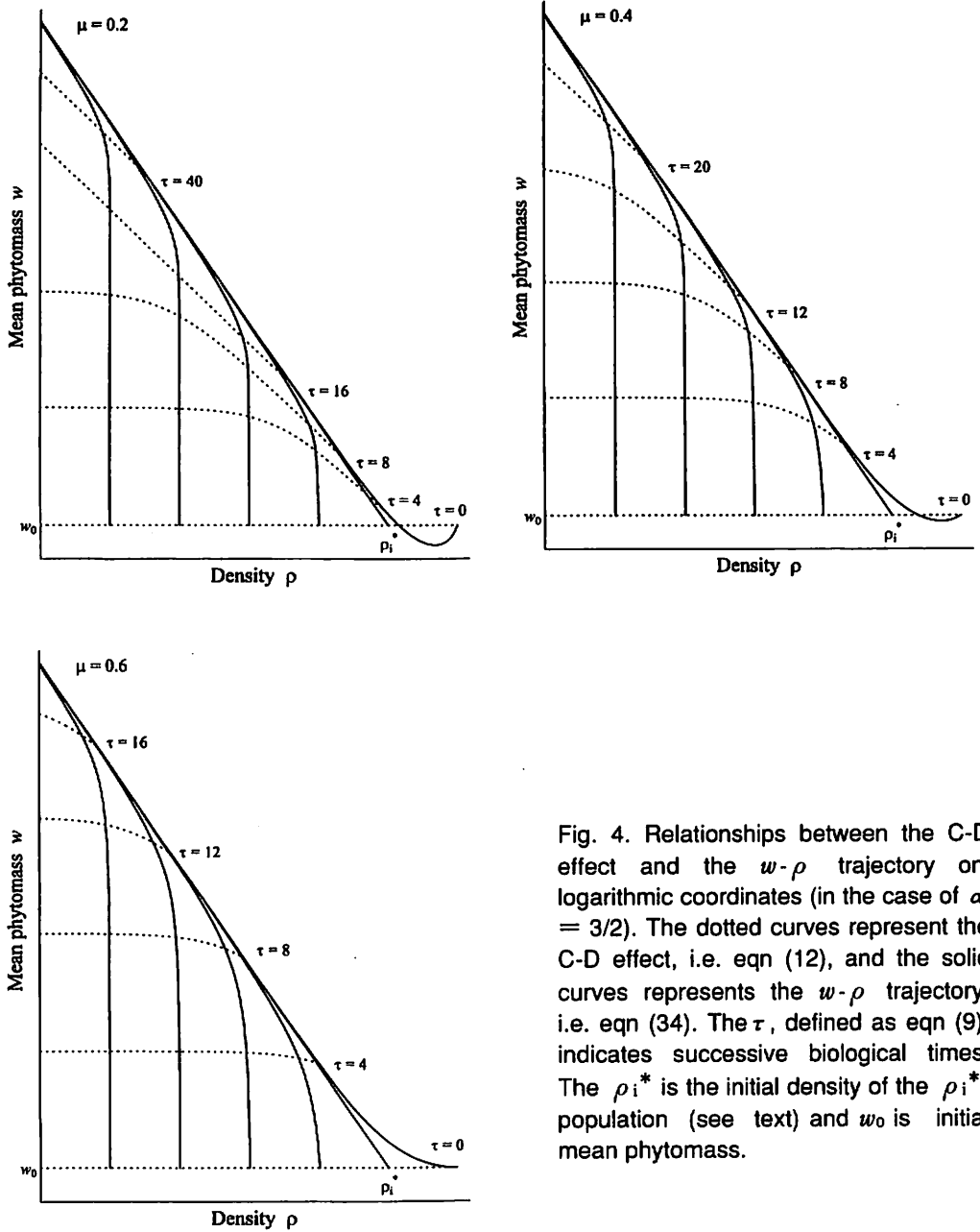


Fig. 4. Relationships between the C-D effect and the w - ρ trajectory on logarithmic coordinates (in the case of $\alpha = 3/2$). The dotted curves represent the C-D effect, i.e. eqn (12), and the solid curves represents the w - ρ trajectory, i.e. eqn (34). The τ , defined as eqn (9), indicates successive biological times. The ρ_i^* is the initial density of the ρ_i^* -population (see text) and w_0 is initial mean phytomass.

the w - ρ trajectory approaches the self-thinning line at the later stage of growth. On the other hand, as the value of μ increases, the C-D effect occurs moderately in the earlier stage of growth, gradually rising in intensity at the later stage of growth, and the w - ρ trajectory approaches the self-thinning line at the earlier stage of growth. This means that the value of μ plays an important role in relieving or intensifying intraspecific competition. It can be seen in Fig. 4 that a population starting with ρ_i higher than ρ_i^* decreases its mean phytomass at the

initial stage of growth. This would explain the phenomenon observed by Yoda et al. (1963) in the spacing experiment of buckwheat (*Fagopyrum esculentum* Moench), where the mean phytomass of the highest initial density plot (5×10^4 seeds m^{-2}) decreased at the first sampling (21 days after sowing).

Discussion

Explicit form of the carrying capacity Y

Since the coefficients ϵ and A_t have been defined respectively by eqns (27) and (31) as functions of biological time τ , the carrying capacity Y of yield y is the only unknown function left in eqn (10). Differentiating both sides of eqn (10) with respect to τ , Y is explicitly obtained as a function of τ , i. e.

$$Y = \frac{w_0 \rho_i}{1 - (\alpha - 1)\mu} e^{(\alpha - 1)\mu\tau} \tag{36}$$

It is concluded from eqn (36) that Y increases exponentially with increasing τ . This trend is consistent with the result confirmed by Xue and Hagihara (1998) in the *Pinus densiflora* stands that Y tended to increase gradually with increasing stand age.

Density-dependent mortality

In consideration of eqn (34), eqn (28) can be rewritten in the following differential form,

$$m = -\frac{1}{\rho} \frac{d\rho}{d\tau} = \mu \left(1 - \frac{\rho}{\rho_i} \right) \tag{37}$$

If initial density ρ_i is equal to ρ_i^* , which is the initial density of the ρ_i^* -population, eqn (37)

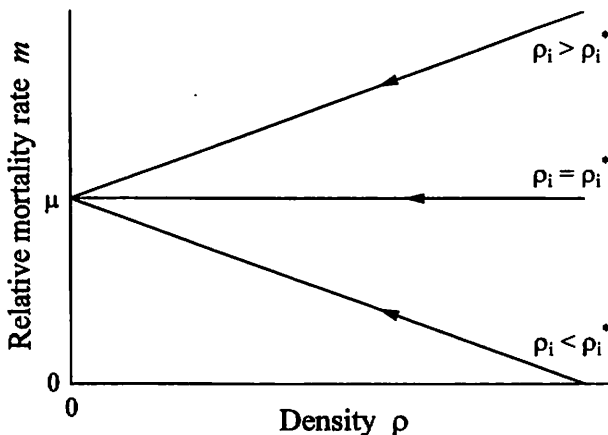


Fig. 5. Linear relationships of relative mortality rate m to density ρ . The straight lines are given by eqn (37). The ρ_i means the initial density of any population and the ρ_i^* means the initial density of the ρ_i^* -population (see text). The arrows stand for the progress of time. $\rho_i < \rho_i^*$, a logistic type of decrease; $\rho_i = \rho_i^*$, an exponential type of decrease; $\rho_i > \rho_i^*$, a cologistic (Shinozaki, 1953b) type of decrease.

is the same as eqn (24). Figure 5 shows the relationships of relative mortality rate m to density ρ (so-called $s-n$ diagram (Shinozaki, 1953b)) based on eqn (37). The m of populations starting with ρ_i^* is constant at μ throughout the mortality process, i. e. an exponential type of decrease. The m of populations starting with ρ_i smaller than ρ_i^* is smaller than μ and increases linearly toward μ as ρ decreases, i. e. a logistic type of decrease. On the other hand,

the m of populations starting with ρ_i larger than ρ_i^* is larger than μ and decreases linearly toward μ as ρ decreases, i. e. a cologistic type of decrease.

Approximated expression of the w - ρ trajectory

The value of the coefficient μ in eqn (35) is in the range given by eqn (32). As the value of μ tends to the lower limit of zero, eqn (35) can be written in the form (Hagihara, 1998),

$$w = K\rho^{-\alpha} \left(1 - \frac{\rho}{\rho_0}\right)^{\alpha-1} \tag{38}$$

On the other hand, as the value of μ tends to the upper limit of $1/\alpha$, eqn (35) can be written in the form,

$$w = K\rho^{-\alpha} \left(1 - \frac{\rho}{\rho_0}\right)^{\alpha} \tag{39}$$

To first approximation, therefore, the w - ρ trajectory given by eqn (35) may follow the equation,

$$w = K\rho^{-\alpha} \left(1 - \frac{\rho}{\rho_0}\right)^{\beta} \quad (\alpha - 1 < \beta < \alpha) \tag{40}$$

The results of fitting the data, which were obtained by Spurr et al. (1957) in eastern white

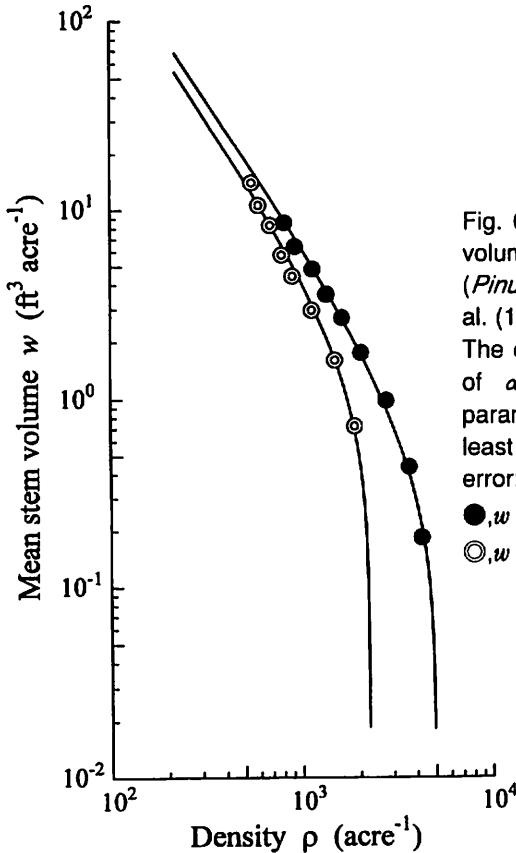


Fig. 6. Time-trajectories of mean phytomass (stem volume) w and density ρ in eastern white pine (*Pinus strobus* L.) plantations examined by Spurr et al. (1957). Unit: 1 acre = 4047 m²; 1 ft³ = 28.32 dm³. The curves are given by eqn (40), where the value of α was assumed to be 3/2 and the other parameters were determined on the basis of the least square method with respect to the relative error:

- , $w = 2.30 \times 10^5 \rho^{-3/2} (1 - \rho/4980)^{0.703} (r^2 = 0.992)$;
- , $w = 1.90 \times 10^5 \rho^{-3/2} (1 - \rho/2240)^{0.651} (r^2 = 0.975)$.

pine (*Pinus strobus* L.) plantations, to eqn (40) are shown in Fig. 6. It is apparent from the figure that eqn (40) accurately mimics the time-trajectories of mean phytomass (stem volume) w , which increases, and density ρ , which decreases, with the development of the plantations. This provides evidence that eqn (40) can be a convenient and practical model for describing the w - ρ trajectory during the course of self-thinning in even-aged populations.

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