A Stochastic Model and the Moment Dynamics of the Growth and Size Distribution in Plant Populations

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A stochastic model for growth and size distribution in plant populations is proposed, which is described by the Kolmogorov forward equation (diffusion equation). The moments of size distribution are calculated based on the diffusion process. Theoretical analyses are made of the mechanisms and the dynamics of size distribution pattern of an even-aged plant population based on the experiemntal data of *Impatiens balsamina* L. Plant height, stem diameter and individual plant weight have their specific size-dependent growth pattern, and show almost normal, positively skewed and more positively skewed size distribution, respectively. The stochastic model incorporating size-dependence of individual growth explains these phenomena theoretically. The ecological meaning of the growth and size distribution patterns is discussed. The hypothesis that dry matter production by photosynthesis is first allocated to height growth and then to diameter growth is proposed.

1. Introduction

Size distribution in biological populations is a main concern to biologists, because it reflects the dynamics of population growth. Analyses of size distribution provide information on the structure and the function of biological populations.

Theoretical analyses of plant community growth have been made on mean plant size basis, i.e. from the populational level (e.g. Shinozaki & Kira, 1956; Hozumi, 1977, 1980), but Koyama & Kira (1956) pointed out the importance of studying plant size distributions. Many researchers followed this line of study (e.g. Kuroiwa, 1959, 1960a, b; Obeid, Machin & Harper, 1967; White & Harper, 1970; Ford, 1975; Mohler, Marks & Sprugel, 1978).

I carried out a field experiment with even-aged annual plants to investigate the dynamics of plant population growth. Based on these experimental data, I propose a stochastic model for individual plant size growth in a population, and start with the Kolmogorov forward equation (diffusion equation) as a

basic equation. I determine the coefficients involved in the equation from the experimental data, and present the actual growth pattern of individual plant size. The growth pattern is size-dependent; plant height (H), stem diameter (D) and individual plant weight (W) have their specific growth pattern. Next, I calculate the moments of size distribution based on the diffusion process, and make theoretical analyses of the mechanisms and the dynamics of size distribution pattern based on the experimental data.

Size distribution pattern is divided into three types, i.e. symmetrical (or normal), negatively skewed and positively skewed distribution. Out of these distributions, the positively skewed one is often met with in biological phenomena (Koch, 1966, 1969). Koyama & Kira (1956) made an attempt to explain how positive skewness appears in individual plant weight distribution. Ford (1975) claimed that size distributions of intensively self-thinning plant populations are biomodal. Gates (1978) and Ford & Diggle (1980) explained this phenomenon with theoretical models. A strict test of bimodality is a very difficult and a subtle problem. In many cases, size distribution can be roughly approximated by a unimodal curve. If we assume unimodality, we immediately know the shape of the size distribution curve from some moments. For simplicity, I assume unimodality and ignore the question of biomodality for the moment.

The main concerns of this paper are the mechanisms and the dynamics of size distribution pattern. For this purpose, the dynamics of some moments are analyzed.

The stochastic model which is described by the Kolmogrov forward equation and incorporates size-dependence of individual growth reveals that the size-dependent growth pattern determines its size distribution pattern. Therefore, we can explain by this model the phenomenon that D and W have positively skewed distribution while H has an almost normal distribution.

I discuss the ecological meaning of the growth and size distribution pattern as important factors in the competition for light, and present a hypothesis on the basic property of plant growth in a population.

2. Materials and Methods

I carried out a field experiment with *Impatiens balsamina* L. at the Botanical Garden, Faculty of Science, Kyoto University, in 1977. Seeds were sown randomly on a 3×6 m plot on 3 September. All plants within three randomly distributed 30×30 cm quadrats were marked and their individual growth in height and diameter at ground level was recorded. The initial density was 833 m^{-2} and five measurements were made at 10-day

intervals; the first measurment on 27 September (t_1), and the last on 6 November (t_5). Flowering commenced at t_4-t_5. At each measurement time, twenty plants were randomly sampled outside the quadrats and their heights, stem diameters at ground level, and dry (80°C for two days) weights of stem and leaf were measured. Dry weights of stem and leaf of all marked plants were estimated by the allometric relationships derived from the data of twenty sampled plants.

3. A Basic Equation

We consider how size distribution changes as a population grows. Let us consider the growth of individual size as a diffusion process $\{X_t\}$, $t \in T = [0, \infty)$. Denote the distribution density of X_t by $f(t, x)$. The total number at time t, $N(t)$, is given by

$$N(t) = N_0 \int_E f(t, x)\, dx, \tag{1}$$

where N_0 is the total number at $t = 0$ and $E = [A, B]$ is the state space.

The diffusion process $\{X_t\}$ is associated with the following Kolmogorov forward equation (diffusion equation) (Kolmogoroff, 1931; Gnedenko, 1962; Dynkin, 1965; Cox & Miller, 1972; Karlin & Taylor, 1981):

$$\frac{\partial}{\partial t} f(t, x) = \frac{1}{2} \frac{\partial^2}{\partial x^2} [D(t, x) f(t, x)]$$

$$- \frac{\partial}{\partial x} [G(t, x) f(t, x)] - M(t, x) f(t, x),$$

$$x \in E = [A, B], \qquad t \in T = [0, \infty). \tag{2}$$

$G(t, x)$ is the drift coefficient or the infinitesimal mean, and $D(t, x)$ is the diffusion coefficient or the infinitesimal variance. They are written as follows:

$$\lim_{h \downarrow 0} \frac{1}{h} E[\Delta_h X_t \,|\, X_t = x] = G(t, x), \tag{3}$$

$$\lim_{h \downarrow 0} \frac{1}{h} V[\Delta_h X_t \,|\, X_t = x] = D(t, x), \tag{4}$$

where $\Delta_h X_t = X_{t+h} - X_t$. $M(t, x)$ is the termination coefficient, and represents the instantaneous mortality per unit time. If the diffusion process is conservative, then $M(t, x) = 0$.

I use equation (2) as a basic equation for the analysis. By solving equation (2), we can get $f(t, x)$ and simulate the dynamics of size distribution pattern.

Generally, we cannot have the analytical solution to equation (2). We can only solve it numerically.

To solve equation (2), we first determine the coefficients $G(t, x)$, $D(t, x)$ and $M(t, x)$. To clarify the actual growth pattern of individual size, I employ the empirical way, i.e. determine these coefficients from the experimental data. We approximate infinitesimal $G(t, x)$, $D(t, x)$ and $M(t, x)$ by finite time interval.
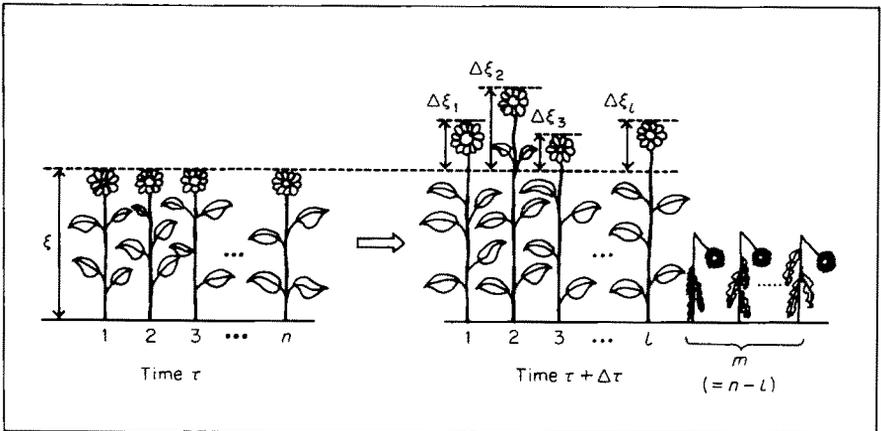
FIG. 1. Diagrammatic explanation how to determine $G(t, x)$, $D(t, x)$ and $M(t, x)$ from the experimental data. Plant height is taken as size. For the details, see the text.

Take plant height as size, for example (Fig. 1). Let n be the number of plants of size ξ at time τ. These plants grow or die after $\Delta\tau$, and let l and m be the numbers of the live and the dead plants at time $\tau + \Delta\tau$, respectively. When individual plants $1, 2, 3, \ldots, l$ grow in size respectively by $\Delta\xi_1$, $\Delta\xi_2$, $\Delta\xi_3, \ldots, \Delta\xi_l$ during $\Delta\tau$, quantities of $G(\tau, \xi)$, $D(\tau, \xi)$ and $M(\tau, \xi)$ are given as follows:

$$G(\tau, \xi) = \frac{1}{\Delta\tau}\overline{\Delta\xi} = \frac{1}{\Delta\tau}\frac{1}{l}\sum_{i=1}^{l}\Delta\xi_i, \tag{5}$$

$$D(\tau, \xi) = \frac{1}{\Delta\tau}\frac{1}{l}\sum_{i=1}^{l}(\Delta\xi_i - \overline{\Delta\xi})^2$$

$$= \frac{1}{\Delta\tau}\left\{\frac{1}{l}\sum_{i=1}^{l}(\Delta\xi_i)^2 - (\overline{\Delta\xi})^2\right\}, \tag{6}$$

$$M(\tau, \xi) = \frac{1}{\Delta\tau}\frac{m}{n} \qquad (n = l + m). \tag{7}$$

Calculating for every ξ and τ, we obtain $G(t, x)$, $D(t, x)$ and $M(t, x)$.

$G(t, x)$ is mean growth of size x at time t per unit time. $D(t, x)$ is variance of growth of size x at time t per unit time, which is generated by the fluctuation of growth. $M(t, x)$ is mortality of size x at time t per unit time due to self-thinning. If all plants of the same size grow by the same quantities, $D(t, x)$ is equal to zero. In this case, the Kolmogorov forward equation (2) reduces to the continuity equation,

$$\frac{\partial}{\partial t}f(t, x) + \frac{\partial}{\partial x}[G(t, x)f(t, x)] = -M(t, x)f(t, x). \tag{8}$$

Many researchers have applied the continuity equation to ecological problems, mainly age and size structures of cell and animal populations (see Okubo, 1980).

4. Results of the Experiment

(A) ESTIMATION OF INDIVIDUAL PLANT WEIGHT

Allometric relationship between individual stem weight (y), plant height (x_1) and stem diameter (x_2) is given by

$$\log y = a_0 + a_1 \log x_1 + a_2 \log x_2, \tag{9}$$

where a_0, a_1 and a_2 are constants specific to each growth stage. These values were calculated by the multiple regression from the data of twenty sampled plants at each stage. Obtained a_1's and a_2's are nearly equal to 1 and 2, respectively, irrespective of growth stages. For simplicity, let stem weight stand for plant weight. Individual plant weights of all marked plants were estimated by equation (9) at each growth stage.

(B) GROWTH PATTERN

For the data analysis, I used all plants from two quadrats neglecting one for its poor growth. The number of plants was initially 145 and decreased successively to 96 in the final stage due to self-thinning. Figs 2, 3 and 4 show respectively $G(t, x) - x$, $D(t, x) - x$ and $M(t, x) - x$ relationships at each growth stage for plant height (H), stem diameter (D) and individual plant weight (W). Size-dependence is noted in all the results, but obviously H, D and W have different types of size-dependence. The condition $X_t = x$ in equations (3) and (4) is interpreted biologically as size-dependence of individual growth. The next growth of a plant is determined by its present size in a population. We can approximate all $G(t, x)$ and $D(t, x)$ by the
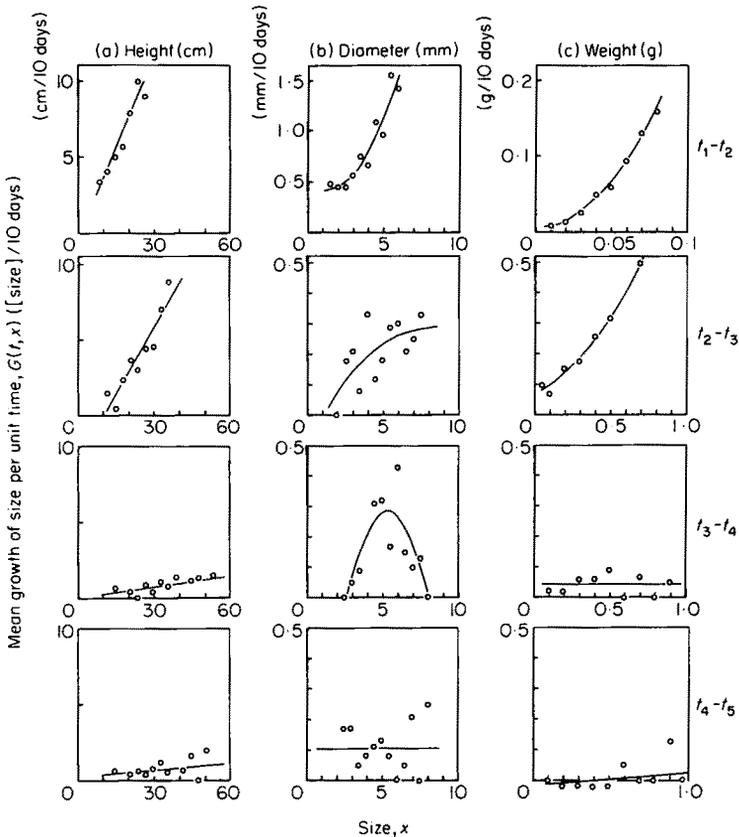
FIG. 2. Mean growth of size per unit time, $G(t, x) \sim$ size, x relationships at each growth stage empirically obtained from the experimental data of *Impatiens balsamina*. Subscripted t indicates successive growth stages when the measurements were made; t_1 is 24 days after sowing, and time interval between two successive growth stages is 10 days. (a) Plant height (cm); (b) stem diameter (mm) and (c) individual plant weight (g) are taken as size. $\bigcirc$, observed value; ——, regression by equation (10).

polynomial equations of at most degree two,

$$G(t, x) = a_g(t) + b_g(t)x + c_g(t)x^2, \tag{10}$$

$$D(t, x) = a_d(t) + b_d(t)x + c_d(t)x^2. \tag{11}$$

As to H, both $G(t, x) - x$ and $D(t, x) - x$ relationships show straight lines with positive slopes throughout the growth period, i.e. $c_g(t)$, $c_d(t) = 0$ and $b_g(t)$, $b_d(t) > 0$ for any t, and the slopes flatten gradually as a population grows. In the final stage, both $G(t, x)$ and $D(t, x)$ have almost constant values near zero irrespective of size x. In the case of $a_g(t) = 0$, mean growth
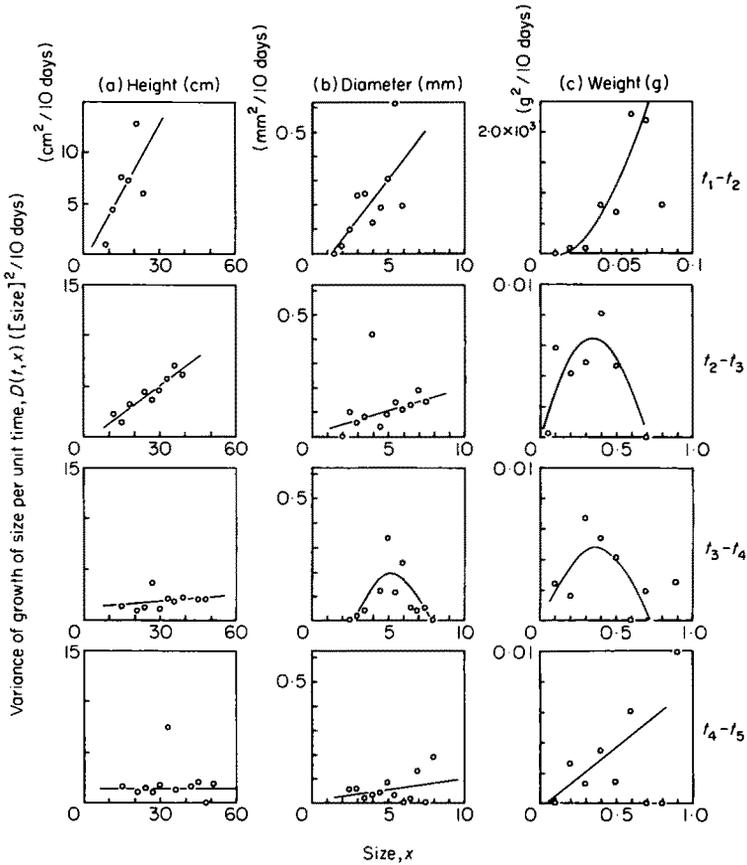
FIG. 3. Variance of growth of size per unit time, $D(t, x) \sim$ size, x relationships at each growth stage of *Impatiens balsamina*. The details are the same as in Fig. 2.

of H per unit time is proportional to its present size, i.e. H has constant RGR irrespective of size. The same $G(t, x) - x$ relationship of H is also found in Fig. 3 of Mohler *et al.* (1978) for natural stands of *Prunus pensylvanica*.

As to D, $G(t, x) - x$ relationship shows a complicated pattern. But it shows the same time trend as that of H. Values of $G(t, x)$ decrease as a population grows, and keep almost constant values in the final stage. In the first stage, $G(t, x) - x$ relationship is a convex curve, i.e. $c_g(t) > 0$. In the second and third stages, it is a concave curve, i.e. $c_g(t) < 0$. $G(t, x) - x$ relationship in the second stage can be also approximated by a hyperbolic curve, which was obtained by Nagano (1978) for Minamata forest stands.
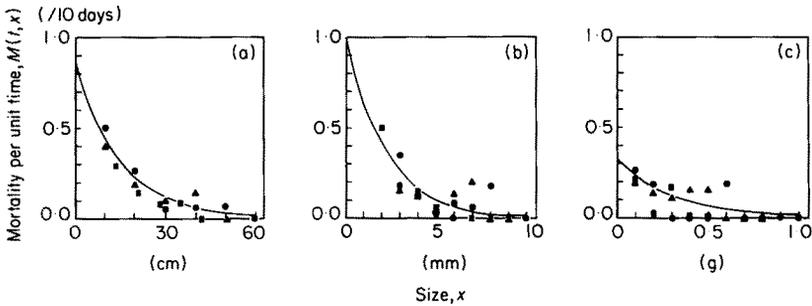
FIG. 4. Mortality per unit time, $M(t, x) \sim$ size, x relationships at each growth stage of *Impatiens balsamina*. The details are the same as in Fig. 2. Solid symbols indicate the observed values: ■, t_2-t_3; ▲, t_3-t_4; ●, t_4-t_5. Self-thinning does not occur at t_1-t_2. Solid curves indicate regression by equation (12). (a) Height (cm); (b) diameter (mm); (c) weight (g).

The same relationship and time trend are found in Fig. 2 of Mohler *et al.* (1978) for natural stands of *Prunus pensylvanica*.

As to W, $G(t, x) - x$ relationship is a convex curve (i.e. $c_g(t) > 0$) in the early stages, and almost a constant near zero in the later stages. The same relationship in the early stages is found in Fig. 3 of Kuroiwa (1960a) for *Abies* stands. In the case of $a_g(t) = 0$, this means that relative growth rate (RGR) $- x$ relationship of W is a straight line with positive slope. This is also found in Fig. 8 of Ford (1975) for *Tagetes patula*.

$D(t, x) - x$ relationships of D and W show somewhat scattered complicated pattern, but all $D(t, x)$'s can be approximated by equation (11). In the early stages, they are positively correlated with size x. Random environment, competition between neighbouring plants, etc. generate $D(t, x)$. Even plants of the same size cannot have the same growth rate. For example, even if two plants are of the same size, one with large neighbours has smaller growth rate than another with small neighbours due to the more intense suppression. This effect is expressed by $D(t, x)$, which is interpreted as fluctuation of growth.

$M(t, x)$'s of H, D and W take the same form, a convex curve such that $M(t, x) \to 0$ as $x \to +\infty$. I empirically employ the following equation,

$$M(t, x) = \exp(a + bx) \qquad (b < 0). \qquad (12)$$

5. Moment Dynamics of Size Distribution

Let $g(t, x)$ be any twice continuously differentiable function defined on $T \times E$. Denote $\langle g(t, x) \rangle$, expectation of $g(t, x)$, by

$$\langle g(t, x) \rangle = \int_E g(t, x) f(t, x) \, dx \bigg/ \int_E f(t, x) \, dx. \qquad (13)$$

Let m_k and μ_k be the kth moments about the origin and about the mean respectively given as follows:

$$m_k = \langle x^k \rangle, \tag{14}$$

$$\mu_k = \langle (x - \langle x \rangle)^k \rangle. \tag{15}$$

This paper deals with growth only in the vegetative stage, and I impose the boundary conditions

$$f(t, A) = f(t, B) = 0, \tag{C1}$$

to distinguish vegetative stage from reproductive one. Neither inflow nor outflow of probability occur at the boundaries $x = A, B$ until X_t first reaches them. Therefore, until the first passage time (i.e. during the vegetative stage) the probability current $J = G(t, x)f(t, x) - (1/2)\partial[D(t, x)f(t, x)]/\partial x$ is equal to zero at $x = A, B$.

Now, we can calculate the time rate of change in m_k and μ_k during the vegetative stage from equation (2) as follows:

$$\frac{\mathrm{d}}{\mathrm{d}t} m_k = \tfrac{1}{2} k(k-1) \langle x^{k-2} D(t, x) \rangle$$

$$+ k \langle x^{k-1} G(t, x) \rangle - \mathrm{Cov}\{x^k, M(t, x)\}, \tag{16}$$

$$\frac{\mathrm{d}}{\mathrm{d}t} \mu_k = \tfrac{1}{2} k(k-1) \langle (x - \langle x \rangle)^{k-2} D(t, x) \rangle$$

$$+ k \, \mathrm{Cov}\{(x - \langle x \rangle)^{k-1}, G(t, x)\}$$

$$- \mathrm{Cov}\{(x - \langle x \rangle)^k, M(t, x)\}$$

$$+ k \langle (x - \langle x \rangle)^{k-1} \rangle \, \mathrm{Cov}\{x, M(t, x)\}. \tag{17}$$

In this paper, I deal with plant populations where, for simplicity of analysis self-thinning does not occur. Low intensity of self-thinning observed in the experiment with *Impatiens balsamina* L. hardly affects the shape of size distribution curves (Fig. 8). Therefore, I set $M(t, x) = 0$ in this paper. We want to know how size distribution pattern changes as a population grows or time t passes. For this purpose we have only to get the time rate of changes in at least $\langle x \rangle$ (mean), μ_2 (variance) and μ_3. We can know the approximate shape of size distribution curve from the value of skewness γ given by

$$\gamma = \mu_3 / \mu_2^{3/2}. \tag{18}$$

Positive γ represents L-shaped distribution, negative γ J-shaped distribution, and zero γ symmetrical distribution.

If $G(t, x)$ is given as equation (10) with $c_g(t) = 0$ and $D(t, x)$ as equation (11), we have skewness in the explicit form as a function of time t:

$$\gamma = \{\dot{\mu}_3 + F_2(t)\} \, e^{(3/2)B(t)} / \{\dot{\mu}_2 + F_1(t)\}^{3/2}, \tag{19}$$

where

$$A(t) = \int_{t_0}^{t} b_g(s) \, ds, \qquad B(t) = \int_{t_0}^{t} c_d(s) \, ds,$$

$$\langle x \rangle(t) = \left\{ \langle \dot{x} \rangle + \int_{t_0}^{t} e^{-A(s)} a_g(s) \, ds \right\} e^{A(t)}, \qquad \langle \dot{x} \rangle = \langle x \rangle(t_0),$$

$$F_1(t) = \int_{t_0}^{t} e^{-(2A(s)+B(s))} D(s, \langle x \rangle(s)) \, ds,$$

$$\mu_2(t) = \{\dot{\mu}_2 + F_1(t)\} \, e^{2A(t)+B(t)}, \qquad \dot{\mu}_2 = \mu_2(t_0),$$

$$F_2(t) = 3 \int_{t_0}^{t} e^{-3(A(s)+B(s))} D_x(s, \langle x \rangle(s)) \mu_2(s) \, ds,$$

$$\mu_3(t) = \{\dot{\mu}_3 + F_2(t)\} \, e^{3(A(t)+B(t))}, \qquad \dot{\mu}_3 = \mu_3(t_0).$$

In the simplest case where $D(t, x) = 0$ (no fluctuation in growth), we have $\gamma = \dot{\mu}_3 / \dot{\mu}_2^{3/2} \equiv \dot{\gamma}$. Therefore, the initial skewness $\dot{\gamma}$ is kept throughout the growth process. In the case where $D(t, x) = a_d(t)$, if $\dot{\gamma} = 0$, then $\gamma = 0$; if $\dot{\gamma} > 0$, then γ decreases toward zero; if $\dot{\gamma} < 0$, then γ increases toward zero. Further, we see that $D(t, x)$ positively (negatively) correlated with size x, i.e. $D_x(t, \langle x \rangle) > 0$ (<0), promotes positive (negative) skewness. Note that in these cases the initial zero skewness is not kept.

If $c_g(t) \neq 0$ in equation (10), we cannot have skewness in the explicit form as a function of t. However, we can know the sign of skewness. We see that

$$\mu_3(t) = \left[\dot{\mu}_3 + 3 \int_{t_0}^{t} e^{-C(s)} \{D_x(s, \langle x \rangle(s)) \mu_2(s) \right.$$
$$\left. + c_g(s) V[(x - \langle x \rangle)^2]\} \, ds \right] e^{C(t)}, \tag{20}$$

where

$$C(t) = 3 \int_{t_0}^{t} \{c_d(s) + G_x(s, \langle x \rangle(s))\} \, ds, \qquad \dot{\mu}_3 = \mu_3(t_0)$$

In the simplest case where $D(t, x) = 0$, if $\dot{\mu}_3 \geq 0$ and $c_g > 0$, then $\mu_3 > 0$; if $\dot{\mu}_3 \leq 0$ and $c_g < 0$, then $\mu_3 < 0$. Note that from the initial zero skewness positive c_g generates positive skewness, and negative c_g negative skewness, even if $D(t, x) = 0$. Further, we see the same effect of $D(t, x)$ on skewness

as in equation (19). Fluctuation of growth positively (negatively) correlated with size promotes postive (negative) skewness.

The analyses made in this section give the interrelationship between the shape of size distribution curve and the growth pattern $G(t, x)$ and the variance of growth $D(t, x)$.

6. Discussion

As has been reported by many researchers (e.g. Koyama & Kira, 1956; Kuroiwa, 1959, 1960b; White & Harper, 1970; Ford, 1975; Mohler *et al.*, 1978), H-, D-, and W-distributions of even-aged plant populations show almost zero, positive, and greater positive skewness respectively. Figures 5, 6 and 7 show these features clearly. The experimental data of *Impatiens balsamina* L. show that H, D, and W have their specific size-dependent
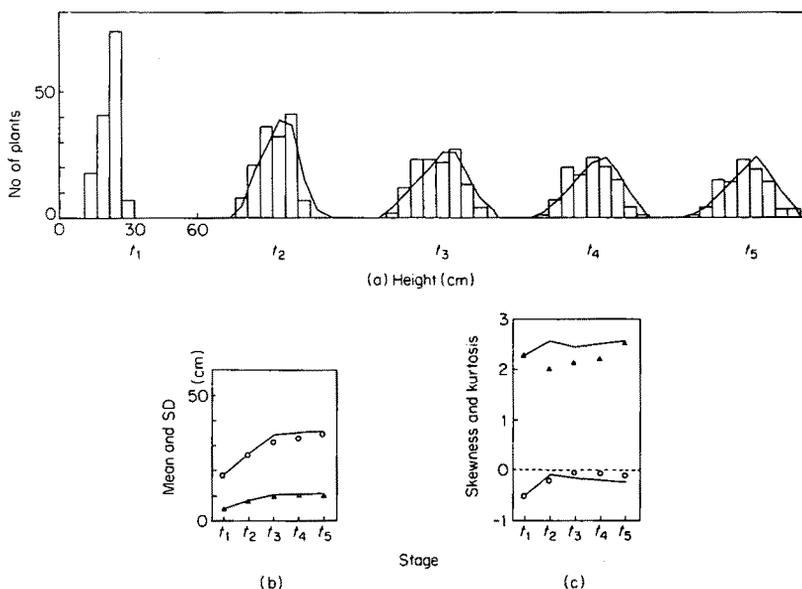
FIG 5. (a) Plant height distribution of *Impatiens balsamina* L. at each growth stage. Histogram, the observed; full line, the calculated by equation (2). Interval of histograms is 6 cm for all growth stages. Subscripted t indicates successive growth stages when the measurements were made (see Fig. 2). N_{obs} and N_{cal} indicate the observed and calculated total numbers of plants respectively. t_1, $N_{obs} = 145$; t_2, $N_{obs} = N_{cal} = 145$; t_3, $N_{obs} = 126$, $N_{cal} = 127$; t_4, $N_{obs} = 109$, $N_{cal} = 113$; t_5, $N_{obs} = 96$, $N_{cal} = 102$. (b) Observed mean (O) and standard deviation (△) of the above distribution. Full line indicates those values calculated by equation (2). (c) Observed skewness (O) and kurtosis (△) of the above distribution. Full line indicates those values calculated by equation (2).
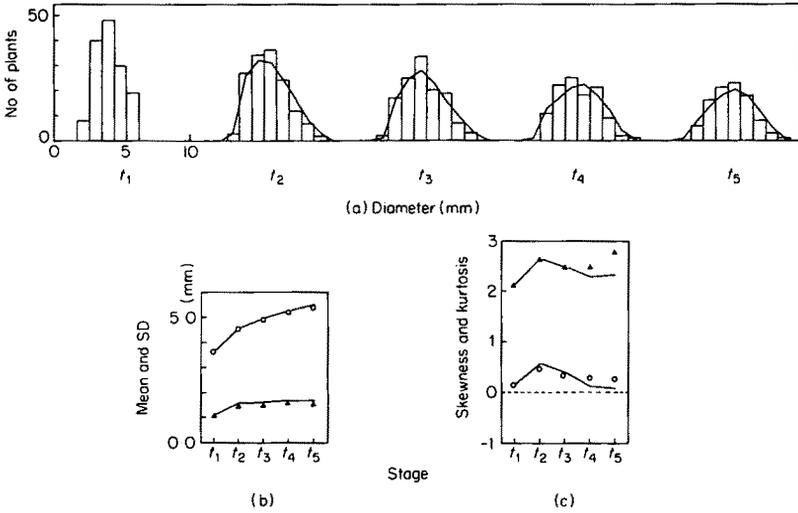
FIG. 6. (a) Stem diameter distribution of *Impatiens balsamina* L. at each growth stage t_1, $N_{obs} = 145$; t_2, $N_{obs} = N_{cal} = 145$; t_3, $N_{obs} = 126$, $N_{cal} = 124$, t_4, $N_{obs} = N_{cal} = 109$; t_5, $N_{obs} = N_{cal} = 96$. Symbols as in Fig. 5. Interval of histograms is $1 \cdot 0$ mm for all growth stages. (b), (c) As in Fig. 5.

growth pattern (Figs 2, 3 and 4). The model proposed in this paper reveals the close interrelationship between these two phenomena. Size distribution pattern is determined by size-dependent growth pattern, mainly $G(t, x)$. In the case where fluctuation of growth, i.e. $D(t, x)$ is strongly correlated with size x, $D(t, x)$ affects size distribution pattern. The effect of $D(t, x)$ can also generate positive or negative skewness. Note that $D(t, x)$ independent of size x does not affect μ_3. We can explain by the fluctuation of growth or $D(t, x)$ the part that cannot be explained only by the continuity equation (8).

The fundamental condition for a diffusion process is the Markov property. It states that the future state is determined only by the present state and independent of the previous states. It is a question whether this property rigorously holds in the case of individual plant growth in a stand. The whole growth period of *Impatiens balsamina* L. in this experiment was about 70 days, and the time interval between two successive measurements was 10 days. I asume that the size 10 days later is determined almost solely by the present size but hardly affected by the size 10 days before. This assumption needs further investigation, but I think it is reasonable as a first approximation. Therefore, we can assume the Markov property and get the Kolmogorov forward equation as a first approximation. This is also supported by the good agreement between the calculated results and the experimental data (Figs 5, 6 and 7).
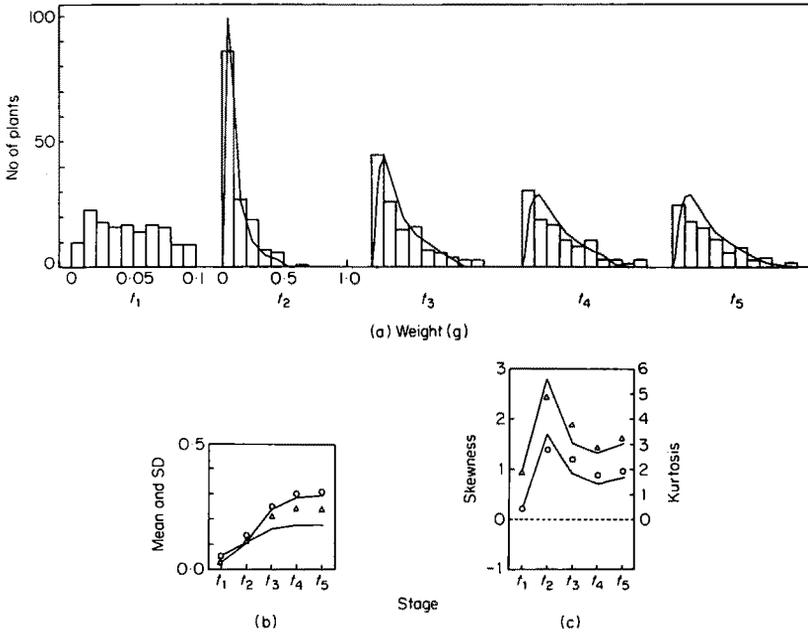
FIG. 7. (a) Individual plant weight distribution of *Impatiens balsamina* L. at each growth stage. Symbols as in Fig. 5. Interval of histograms is 0·01 g for t_1 and 0·1 g for t_2–t_5 t_1, $N_{obs} = 145$; t_2, $N_{obs} = 145$, $N_{cal} = 144$; t_3, $N_{obs} = 126$, $N_{cal} = 120$, t_4, $N_{obs} = 108$, $N_{cal} = 105$; t_5, $N_{obs} = 94$, $N_{cal} = 105$. A few individuals greater than 1·0 g are excluded from the calculation. Therefore, N_{obs}s do not coincide with those of Figs 5 and 6. (b), (c) As in Fig. 5.

(A) SIMULATION OF THE DYNAMICS OF SIZE DISTRIBUTION PATTERN

We solve equation (2) numerically to simulate the dynamics of size distribution pattern by using the explicit functions of $G(t, x)$, $D(t, x)$ and $M(t, x)$ (equations (10), (11) and (12), respectively) obtained from the experimental data. We scale size x and time t to dimensionless $0 \le x \le 1·0$ and $0 \le t \le 4·0$, and employ the implicit finite difference method with $\Delta x = 0·025$ and $\Delta t = 0·001$. The initial conditions are the observed distributions of the first stage, and the boundary conditions are $f(t, 0) = 0$ and $f(t, 1·0) = 0$ for any $t \ge 0$. Calculated size distributions and some statistics agree well with the observed ones (Figs 5, 6 and 7).

(B) MOMENT DYNAMICS IN THE EXPERIMENT

In my experiment with *Impatiens balsamina* L. t_1, time period of the first measurement, was 24 days after sowing. Considering the whole growth

period (about 70 days), it is rather the early middle stage. Skewness of H-distribution is negative at t_1, first increases to zero, and then keeps a constant value, zero (Figs 5, 8). The increase of skewness at $t_1 - t_3$ is explained
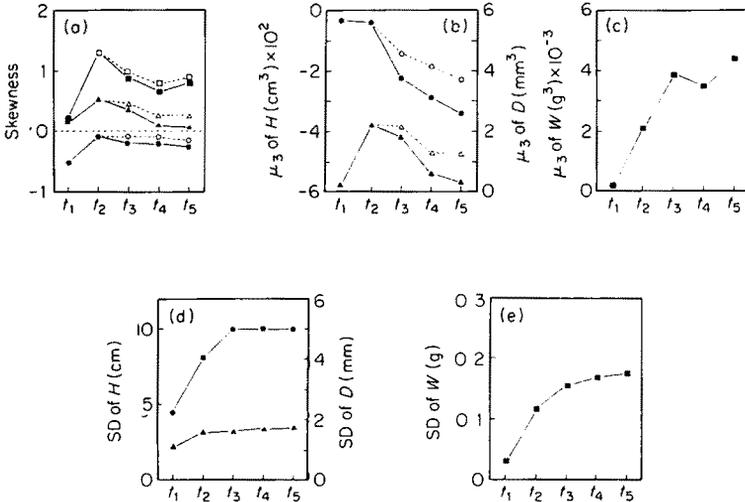
FIG. 8. Effect of mortality rate $M(t, x)$ on skewness, SD and μ_3. ——— with solid symbols indicates those values for self-thinning population calculated by equation (2) with the same coefficients, $G(t, x)$, $D(t, x)$ and $M(t, x)$ as in Figs 2, 3 and 4 (the same results as in Figs 5, 6 and 7); – – – with open symbols indicates those values for non-self-thinning population calculated in the same way but with $M(t, x) = 0$. Subscripted t indicates successive growth stages. At t_1-t_2, self-thinning does not occur. Circle, plant height (H); triangle, stem diameter (D); square, individual plant weight (W). (a) Skewness of H, D and W; (b) μ_3 of H and D; (c) μ_3 of W; (d) SD of H and D; (e) SD of W. In (c), (d) and (e), closed and open symbols are almost indistinguishable graphically.

only by $D(t, x)$ which is positively correlated with size x, because $G(t, x)$ with $c_g(t) = 0$ keeps skewness constant (Figs 2 and 3). This is generated by the stochastic factor $D(t, x)$, not by the deterministic one $G(t, x)$, therefore, this is not explained by the continuity equation (8). The constant skewness, zero, at $t_3 - t_5$ is attributed to $G(t, x)$ with $c_g(t) = 0$ and $D(t, x)$ independent of size x (Figs 2 and 3). D- and W-distribution show the same time trend of change in skewness, though W has greater skewness than D. Both D and W show increase in positive skewness from the initial zero skewness in the first stage. This is explained by the growth pattern $G(t, x)$ with positive $c_g(t)$. In the following stages, their skewnesses decrease. This phenomenon was reported by Mohler *et al.* (1978) and Kohyama & Fujita (1981) for self-thinning populations. Mohler *et al.* (1978) claimed that intensive self-thinning brings about this phenomenon. I attribute this decrease in my

experiment to equation (10) with negative $c_g(t)$ and to equation (11) with negative $c_d(t)$ for D, and to equation (10) with $b_g(t)$, $c_g(t) = 0$ and equation (11) with negative $c_d(t)$ for W (Figs 2 and 3).

(C) THE EFFECT OF SELF-THINNING ON THE MOMENTS

Mortality rate $M(t, x)$ obtained from my experimental data are almost independent of time t. Whether this relationship is general or not is a question, because the intensity of self-thinning was very low in this experiment (from 145 to 96 plants). I think more intensive self-thinning will generate time-dependent $M(t, x)$. This low mortality rate $M(t, x)$ hardly affects skewness (Fig. 8). But a non-self-thinning population has slightly greater skewness than a self-thinning one. Difference is markedly clear in μ_3, while the time trend is parallel. Standard deviation is hardly affected by $M(t, x)$. Set $k = 2$ in equation (17), and the last term vanishes. Thus, the standard deviation $(=\sqrt{\mu_2})$ is less affected than μ_3 by $M(t, x)$. I think intensive self-thinning, i.e. high mortality rate $M(t, x)$ affects the growth and size distribution pattern and reduces skewness. It is clear from equations (16) and (17) that $M(t, x)$ independent of size x does not affect the moments.

(D) NON-INTERACTING POPULATIONS

Consider a population where individuals are located so far apart that they do not interact with each other. For the simplest growth equation for an individual size x, we employ the exponential equation,

$$\frac{dx}{dt} = r(t)x, \tag{21}$$

where $r(t)$ is relative growth rate (RGR) dependent on time t. Let $\xi(t)$ be random perturbation approximated by the Gaussian white noise subject to the conditions,

$$\langle \xi(t) \rangle = 0, \qquad \langle \xi(t + \tau)\xi(t) \rangle = \delta(\tau), \tag{C2}$$

where $\langle \ \rangle$ indicates average taken over a suitable ensemble.

If RGR fluctuates in equation (21), we have the fluctuation equation,

$$\frac{dx}{dt} = \{\bar{r}(t) + \sigma\xi(t)\}x, \tag{22}$$

We get the Kolmogorov forward equation corresponding to equation (22)

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(the Stratonovich calculus is used); its coefficients are

$$D(t, x) = \sigma^2 x^2,$$ (23)

$$G(t, x) = \{\bar{r}(t) + \tfrac{1}{2}\sigma^2\}x.$$ (24)

where $\bar{r}(t) = \langle r(t) \rangle$, and σ^2 is the intensity coefficient.

The growth pattern given by equation (24) does not generate positive skewness from the initial zero skewness, but it keeps the initial skewness throughout the growth period. The presence of $D(t, x)$ given by equation (23) generates positive skewness. If $\bar{r}(t) = r = $ constant, the solution to this Kolmogorov forward equation is analytically obtained as follows:

$$f(t, x) = \frac{1}{\sigma x \sqrt{2\pi t}} \exp\left[-\frac{1}{2\sigma^2 t}(\log x - \log x_0 - rt) \right],$$ (25)

under the initial condition $f(0, x) = \delta(x_0)$.

Equation (25) is a log-normal distribution showing positive skewness,

$$\gamma = [\exp(\sigma^2 t) - 1]^{3/2} + 3[\exp(\sigma^2 t) - 1]^{1/2}.$$ (26)

Large values of σ generates large positive skewness; skewness increases as time t passes. Koyama & Kira (1956) showed the appearance of positively skewed distribution in a non-interacting population by the model calculation (their C–N complex model). Their model calculation can be interpreted as the model described by equation (22).

If growth rate (dx/dt) fluctuates in equation (21), we have the fluctuation equation,

$$\frac{dx}{dt} = r(t)x + \sigma\xi(t).$$ (27)

Coefficients of the corresponding Kolmogorov forward equation are

$$D(t, x) = \sigma^2,$$ (28)

$$G(t, x) = r(t)x.$$ (29)

In the growth process governed by the Kolmogorov forward equation with equations (28) and (29), the initial zero skewness is kept, or skewness converges toward zero from the initial non-zero skewness.

Note that fluctuation of RGR generates positive skewness, but that fluctuation of growth rate does not. We saw that the growth pattern $G(t, x)$ with positive $c_g(t)$ generates positive skewness, and that $D(t, x)$ positively correlated with size x can also generate positive skewness. There are two independent factors generating positive skewness; one is the deterministic

(growth pattern $G(t, x)$) in the interacting populations, and another the stochastic (variance of growth $D(t, x)$) in the non-interacting populations.

(E) A BASIC PROPERTY OF PLANT GROWTH IN A STAND

H shows almost normal distribution, which is generated by the growth pattern specific to H. Roughly speaking, RGR of H is almost a constant independent of size. The most important factor in the intraspecific competition is light (Kuroiwa, 1960a, b). Individual plant height is crucial for the competition, because tall plants can obtain more light for photosynthesis than short ones. Normal distribution of H is the natural outcome of equal chance for obtaining light. I present the following hypothesis about the basic property of individual plant growth in a stand: dry matter production by photosynthesis, which is partitioned to stem, is first allocated to height growth after equation (10) with $c_g(t) = 0$, i.e. to maintain a normal H-distribution, and then to diameter growth. Short plants must consume their small dry matter production, which is caused by the shorts of light, for height growth at the cost of diameter growth. Tall plants which obtain more dry matter production can have the surplus for diameter growth in addition to height growth. Thus, short plants are very small in stem diameter or plant weight as compared to tall ones. This method of dry matter allocation will generate normal H-distribution and positively skewed D- and W-distribution which are made up of a large number of small plants and a few large plants. I suggest such size distribution patterns are the outcome of the basic property of individual growth in the interacting plant populations.

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