Ecological and Mathematical Considerations on Self–Thinning in Even–Aged Pure Stands

I. Mean Plant Weight–Density Trajectory during the Course of Self–Thinning

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Ecological and mathematical considerations were made on Shinozaki's, Tadaki's and 3/2 power law models for the mean plant weight-density trajectory under self-thinning in even-aged pure stands, and interrelationships among these models were discussed. To overcome the discrepancy between the observed trajectory of the eastern white pine population and the one predicted from Tadaki's model, a new model was proposed. To construct the model the assumptions were made so as to incorporate the good properties of Tadaki's and Shinozaki's models in early stages of growth into those of the 3/2 power law model observed in later stages. Applicability of the model was tested for the pine population, which showed a good fit to the data. The growth analysis on the basis of the model revealed the growth curve of the pine followed a λw-type logistic cruve and suggested the existence of a lag time, a hyperbolic relationship between biological and physical time and a clear dependence of survivorship curves on initial density.

Self-thinnig, or successive decrease in plant density due to competitive interactions among individuals in a population, is considered as one of the most important plant demographic processes. Therefore, increasing attention has been paid to this remarkable phenomenon by ecologists (Braun-Blanquet, 1951; Koyama and Kira, 1956; Shinozaki and Kira, 1956; Ogawa and Koyama, 1957; Oshima *et al.*, 1958; Kuroiwa, 1959; Harper, 1960, 1961; Ando *et al.*, 1962; Harper and McNaughton, 1962; Shinozaki, 1962; Yoda *et al.*, 1963; Tadaki, 1963, 1964; Langer *et al.*, 1964; Ando, 1968; White and Harper, 1970; Sarukhán and Harper, 1973; Ellern, 1974; Kays and Harper, 1974; Harms and Langdon, 1976). The important parts of their works are reviewed by several authors (Harper, 1967; Hozumi, 1973; Harper and White, 1974; White, 1975).

Although we realize that many factors, whether they are biotic or abiotic, pertain to self-thinning in very complicated ways, we limit our consideration to even-aged pure populations without clonal growth. We assume furthermore in the present paper that the populations develop in the same environmental conditions and that their initial densities are different.

If we pursue the time course of self-thinning of a population, whose initial density and mean plant weight are ρ_i and w_0, we can draw a curve or trajectory for the mean

Table 1. Nomenclature of variables, their explanations and units.

Symbols	Explanations	Units
A	Reciprocal of the asymptote of biomass at each τ as $\rho \to \infty$	[m²/g, acre/ft³]
B	Reciprocal of the asymptote of mean plant weight or mean stem volume per plant at each τ as $\rho \to 0$	[g⁻¹, ft⁻³]
K	Empirical constant	[g/m³, ft³/acre³/²]
RGR	Relative growth rate of mean plant weight	[year⁻¹, day⁻¹]
W	Asymptote of w	[g, ft³]
Y	Constant final yield	[g/m², ft³/acre]
a	Empirical constant	[m²/g, acre/ft³]
b	Empirical constant	[m⁴/g, acre²/ft³]
c	Empirical constant	[m⁻², acre⁻¹]
g	Empirical constant	[year⁻¹]
h	Empirical constant	[dimensionless]
m	Relative mortality rate	[year⁻¹, day⁻¹]
p	Empirical constant	[m², acre]
t	Years or days after planting	[year, day]
w	Mean plant weight or mean stem volume per plant	[g, ft³]
w_0	Initial mean plant weight or mean stem volume per plant	[g, ft³]
y	Realized biomass defined by $y = w\rho$	[g/m², ft³/acre]
α	Empirical constant	[dimensionless]
β	Empirical constant	[dimensionless]
γ	Empirical constant	[dimensionless]
ε	Reciprocal of the asymptote of density at each τ as $\rho_i \to \infty$	[m², acre]
λ	Intrinsic growth rate of the logistic growth curve	[year⁻¹, day⁻¹]
μ	Empirical constant	[year⁻¹, day⁻¹]
ρ	Realzied density	[m⁻², acre⁻¹]
ρ_i	Initial density	[m⁻², acre⁻¹]
τ	Biological time defined by Eq. (7)	[dimensionless]

plant weight-density *vs.* time, which corresponds to the Allen curve in animal ecology. Therefore, the analysis of the trajectory is interesting in view of comparative ecology. The present paper is especially concerned with the mean plant weight-density trajectory, whose study was pioneered by Ando *et al.* (1962), Shinozaki (1962), Yoda *et al.* (1963) and Tadaki (1963, 1964).

Basic variables to be considered in the present analysis of self-thinning are initial density (ρ_i), actually realized density (ρ), mean plant weight (w), biomass (y) and time (t). Their notations and units are given in Table 1 together with those of other parameters. When we can construct a mathematical model for the system composed of the following relationships

$$w = w(\rho_i, t),\qquad\qquad (1)$$

$$\rho = \rho(\rho_i, t),\qquad\qquad (2)$$

we can get the mean plant weight-density trajectory, or briefly w-ρ trajectory, by eliminating t from the equations. This is the basic idea for the analysis of the trajectory.

Examination of existing models*

Shinozaki's model (S-model): Shinozaki (1962) showed that quantitative aspects

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of self-thinning could be reasonably understood and treated by the logistic theory of plant growth (Shinozaki and Kira, 1956).

Analyzing the data concerning self-thinning experiments in artificial populations of *Erigeron canadensis* carried out by Yoda *et al.* (1963), Shinozaki proposed the following equations

$$1/\rho = 1/\rho_i + \varepsilon(t) , \tag{3}$$

$$\varepsilon(t) = p\,(e^{\mu t} - 1) . \tag{4}$$

Eq. (3), which was found originally by Shinozaki and Kira (1956), shows that if time is constant, and thus $\varepsilon(t)$ is constant, there is an asymptotic density ($1/\varepsilon(t)$) as ρ_i tends to infinity and also that there is a hyperbolic relationship between the realized densities and the initial ones. On the other hand, Eq. (4) shows $\varepsilon(t)$ increases nearly exponentially with time. Parameters p and μ, whose dimensions are reciprocals of density and time, should be determined for each experiment.

Assuming that the mean plant weight follows a logistic growth curve of the λ-type, Shinozaki (unpublished) proposed the following equations to describe the time course of self-thinning.

$$\frac{1}{w} = \frac{1 - e^{-\tau}}{Y}\,\rho + \frac{e^{-\tau}}{w_0} , \tag{5}$$

$$\frac{1}{\rho} = \frac{1}{\rho_i} + p\,(e^{\tau} - 1) . \tag{6}$$

Here Y is the asymptote of biomass which is constant irrespective of initial densities, τ is the biological time defined by

$$\tau = \int_0^t \lambda(t)\,dt \tag{7}$$

and in turn $\lambda(t)$ is related to the differential form of the logistic growth curve,

$$\frac{1}{w}\,\frac{dw}{dt} = \lambda(t)\left(1 - \frac{w}{W}\right) , \tag{8}$$

where W is the asymptote of w.
From Eq. (6) we have

$$e^{\tau} = 1 + \frac{1}{p}\left(\frac{1}{\rho} - \frac{1}{\rho_i}\right) . \tag{9}$$

Putting e^{τ} into Eq. (5), we can get finally

$$w = (1/\rho - 1/\rho_i + p)/(1/Y + p/w_0 - \rho/Y\rho_i) . \tag{10}$$

Eq. (10) is referred to as Shinozaki's model of the w-ρ trajectory (Hozumi, 1973). Using the definition

$$y \equiv w\rho , \tag{11}$$

we have

$$y = (1 + p\rho - \rho/\rho_i)/(1/Y + p/w_0 - \rho/Y\rho_i), \tag{12}$$

which is equivalent mathematically to Eq. (10) and represents y-ρ trajectories as a function of p, ρ_i, Y and w_0.

Tadaki's model (*T-model*): Tadaki (1963) proposed the following formula for the w-ρ trajectory in *Pinus strobus* (Spurr *et al.*, 1957) and *Pinus densiflora* (Ando *et al.*, 1962) populations,

$$1/\rho = aw + c, \tag{13}$$

where a and c are constants for each population; w tentatitively stands for mean stem volume per tree. Considering Eq. (11), we have the formula for the y-ρ trjajectory of the T-model as follows:

$$\frac{y}{1/a} + \frac{\rho}{1/c} = 1. \tag{14}$$

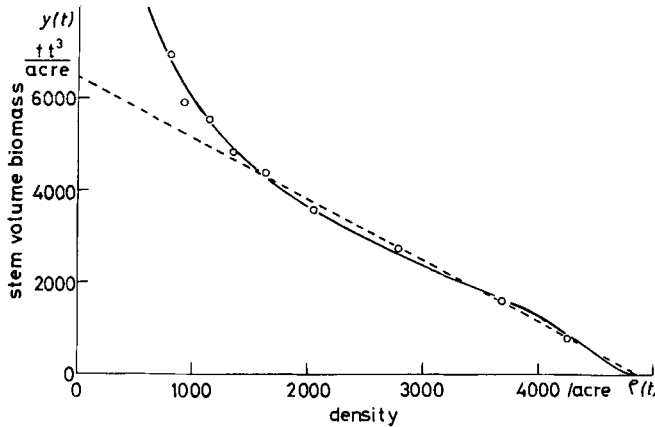Though this model is simple, it fits the data well at least in the early stages of growth, as shown in Fig. 1.

Fig. 1. The y-ρ trajectory of the eastern white pine population (Spurr *et al.*, 1957) under self-thinning. The dotted line denotes the y-ρ trajectory calculated by the T-model (Eq. (14)), showing good fit in the younger stages of growth. Discrepancy between observed and calculated trajectories becomes noticeable with time. The solid line denotes the trajectory after the present model. Its fit is good throughout the growth stages concerned.

The next problem to be considered is to clarify the relationship between the S- and the T-models. Setting

$$\left. \begin{array}{ll} 1/Y + p/w_0 = a \\ 1/Y\rho_i \quad\ \ = b \\ 1/\rho_i - p \quad = c \end{array} \right\} \tag{15}$$

in Eq. (10), we have

$$w = (1/\rho - c)/(a - b\rho) = \frac{1/\rho - c}{a(1 - b\rho/a)} \ .$$

If we can assume

$$1 \gg \frac{b}{a}\, \rho \ , \tag{16}$$

we have the approximation formula

$$w \simeq (1/\rho - c)/a \ ,$$

or
$$1/\rho \simeq aw + c = \left(\frac{1}{Y} + \frac{p}{w_0}\right) w + \left(\frac{1}{\rho_i} - p\right). \tag{17}$$

This procedure suggests that the T-model can be obtained from S-model under the assumption of Eq. (16) and that these two models are closely related to each other. And Eq. (17) gives biological meanings to the coefficients in the T-model.

Let us examine the biological meaning of Eq. (18)

$$\frac{b}{a}\, \rho = \frac{\rho}{\rho_i} \cdot \frac{w_0}{w_0 + Yp} \ . \tag{18}$$

Considering that in a self-thinning population

$$1 > \rho/\rho_i$$

and that since w_0, Y and p are all positive quantities,

$$1 > w_0/(w_0 + Yp) \ ,$$

we can always conclude

$$1 > \frac{b}{a}\, \rho \ .$$

But at present it is difficult to show

$$1 \gg \frac{b}{a}\, \rho \ ,$$

since the biological meaning of p is not clear enough.

Interrelationships among the S-model, the T-model and the 3/2 power law: The two models mentioned above have a common characteristic; if the density tends to zero with time, the biomass of the populations, or $y \equiv w\rho$, tends to a definite value irrespective of the initial densities.
For the S-model,

$$y]_{\rho \to 0} = 1/(1/Y + p/w_0) \ ,$$

while for the T-model,

$$y]_{\rho \to 0} = 1/a \ .$$

This property common to the two is quite contrary to the conclusion derived from the 3/2 power law of self-thinning (Yoda et al., 1963) given by Eq. (19)

$$w\rho^{3/2} = K \,, \tag{19}$$

where K is a constant for each species.

In this case, if we can assume that the law is valid for all t, then we have

$$w(t)\,\rho(t)^{3/2} = K \,,$$

or
$$y(t) = K\rho(t)^{-1/2} \,, \tag{20}$$

which generates another model for the w-ρ trajectory. In Eq. (20), for very small values of $\rho(t)$, which are reached inevitably by self-thinning after a long lapse of time, it is concluded that

$$y]_{\rho \to 0} \to \infty \,. \tag{21}$$

This is an important property intrinsic to the 3/2 power law.

As was suggested by several authors (Tadaki, 1963; Yoda et al., 1963; Yoda, 1971; Hozumi, 1973), the general features of the w-ρ trajectory fit the S- or T-model well in the early stages of growth, but in the later stages the 3/2 power law becomes a good model to describe the trajectory. Fig. 1 depicts the situation. The observed trajectory of the eastern white pine (Spurr et al., 1957) shows good agreement with the trajectory predicted by the T-model (Eq. (14)) until 36 years after planting. But afterwards the discrepancy between the two trajectories becomes increasingly noticeable with the progress of time.

New model for w-ρ trajectory

The next problem to be considered, therefore, is to overcome the discrepancy in Fig. 1, or to harmonize the 3/2 power law with the S-model or T-model. Since the former is established with the assumptions quite different from either of the latter, the harmonization is difficult in view of our present knowledge concerning self-thinning. A possible means to gain this end is to incorporate the good properties of the S- or T-model into those of the 3/2 power law.

Basic assumptions: To unify the S-model with the 3/2 power model and thus to construct a new model for a w-ρ trajectory, we made the following assumptions.

$$\frac{1}{\rho} = \frac{1}{\rho_i} + p(e^{\alpha\tau}-1) \,, \tag{22}$$

$$0 < a < 1 \,, \tag{23}$$

$$\frac{1}{w} = A\rho + B = A\rho + \frac{e^{-\tau}}{w_0} \,, \tag{24}$$

$$w(\tau)\,\rho(\tau)^\beta]_{\tau \to \infty} = K \,. \tag{25}$$

Eq. (22) is a modified form of Eq. (6), and p is an empirical constant. Also a is a constant to be determined for each experiment and acts as a factor to retard the

progress of the biological time defined by Eq. (7). If $a>1$, it acts as a promoting factor. The necessity of this factor is suggested by the fact that in *Erigeron* populations (Yoda *et al.*, 1963), the ratios of mean final weights to the initial weight range from 10^4 to 10^3, while the ratios of $1/\rho - 1/\rho_i$ during the early stages of growth to those at the final stage go from 10^3 to 10^2. Since the value of $1/\rho - 1/\rho_i$ should be always positive under self-thinning, α must be positive as shown in Eq. (23).

Eq. (24) is not only supported by the experimental data, but also a necessary condition to obtain the original form of Eq. (22), or Eq. (3). Furthermore, it means that there is a linear relationship between $1/w$ and ρ at every τ, where the gradient, A, and the intercept of the $1/w$-axis, B, are both functions of τ.

Eq. (25), a slightly modified from of the 3/2 power law, is introduced in view of its validity shown in the later stages of growth or at larger ranges of τ. The value of β is expected to vary within a limited range around 3/2 depending on the plant species.

Derivation of the new model: If we have the explicit form of A as a function τ, we can get the mathematical formulation of the present model.

Eq. (25) implies that the gradient of the w-ρ trajectory on log-log coordinates approaches $-\beta$ as τ tends to infinity

$$\beta = - \left. \frac{d \log w}{d \log \rho} \right]_{\tau \to \infty} . \tag{26}$$

On the otherhand, we can have Eq. (27) concerning the gradient

$$- \frac{d \log w}{d \log \rho} = - \frac{(dw/w)}{(d\rho/\rho)} = \frac{(dw/wd\tau)}{-(d\rho/\rho d\tau)} = \frac{(dw/wdt)}{-(d\rho/\rho dt)} = \frac{RGR}{m} , \tag{27}$$

where $dw/wd\tau$ and dw/wdt (RGR) stand for the relative growth rates with respect to the biological time τ and physical time t; $-d\rho/\rho d\tau$ and $-d\rho/\rho dt$ (m) denote relative mortality rates with respect to τ and t. Calculating the denominator and numerator of Eq. (27) from Eq. (22) and (24) and considering Eqs. (23) and (26), we have the following differential equation concerning $A(\tau)$,

$$\frac{dA(\tau)}{d\tau} + a(\beta-1) A(\tau) + \frac{p}{w_0} (\alpha\beta-1) e^{(\alpha-1)\tau} = 0 .$$

The solution is

$$A(\tau) = \frac{p}{w_0} e^{\alpha(1-\beta)\tau} \{1 - e^{(\alpha\beta-1)\tau}\} . \tag{28}$$

Considering Eq. (21) and $A(\tau) \geqq 0$, we can conclude

$$A(\tau)]_{\tau \to \infty} = 0 , \tag{29}$$

$$a < \frac{1}{\beta} , \quad \text{or} \quad \alpha\beta < 1 , \tag{30}$$
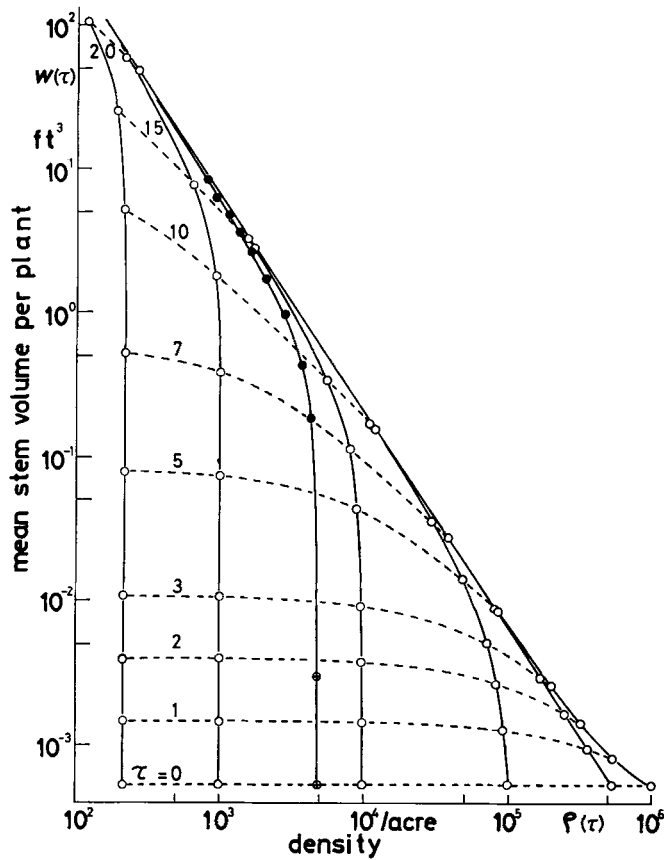
$$K = w_0/p^\beta . \tag{31}$$

Fig. 2. Diagramatic representation of the w-ρ relationship (Eq. (24) and (28)) and w-ρ trajectory (Eq. (32)) on log-log coordinates as assumed by the present model. Dotted lines show the w-ρ relationship at specific values of τ, while solid lines show w-ρ trajectories corresponding to different levels of ρ_i. Parameters of the model are determined to simulate the w-ρ trajectory of the eastern white pine population mentioned before. Open circles denote calculated values of the w-ρ relationship and w-ρ trajectory, solid circles and open circles including cross marks represent the observed and estimated values of w and ρ shown in Table 2.

Eliminating e^{τ} from Eqs. (22), (24) and (28), we get finally Eq. (32) showing the w-ρ trajectories of the model

$$\left.\begin{array}{l} \dfrac{1}{w} = \dfrac{p\rho}{w_0} Q^{1-\beta} [1 - Q^{\beta-1/\alpha}] + \dfrac{1}{w_0} Q^{-1/\alpha}, \\[12pt] Q = 1 + \dfrac{1}{p}\left(\dfrac{1}{\rho} - \dfrac{1}{\rho_i}\right). \end{array}\right\} \tag{32}$$

The applicability of Eq. (32) is tested for the w-ρ trajectory of the eastern white pine population shown in Fig. 2. Though it is difficult to determine suitable values of parameters in Eq. (32), we have obtained the followings after several trials.

$$\rho_i = 4840/\text{acre} \ (=11930/\text{ha}) , \qquad w_0 = 5.4 \times 10^{-4} ft^3 \ (=15.29 \text{ cm}^3)$$

$$\alpha = 0.38 , \qquad \beta = 3/2 , \qquad p = 1.86 \times 10^{-6} \text{ acre} \ (=7.546 \times 10^{-7} \text{ ha}) .$$

Here p is estimated from the linear relationship between y and ρ, y-ρ trajectory of T-model in Fig. 1, ρ_i and w_0 are estimated initial density and mean plant weight (stem volume) in 1904. The fit of the model to the observed w-ρ trajectory or y-ρ trajectory is good as shown in Figs. 1, 2 and Table 2. The dotted line in Fig. 2 represents the w-ρ relationship denoted by Eqs. (24) and (28) at some specified values of τ, while the solid line shows w-ρ trajectories including the trajectory given by the 3/2 power law. The shape of the trajectories, as shown in Fig. 2, is greatly affected by initial density or by the condition

$$\text{(a):} \quad \rho_i < \frac{1}{p} ; \qquad \text{(b):} \quad \rho_i = \frac{1}{p} ; \qquad \text{(c):} \quad \rho_i > \frac{1}{p} .$$

The trajectory under condition (b) follows the 3/2 power law from the initial stage of growth, namely

$$w(\tau) \, \rho(\tau)^\beta = K . \tag{33}$$

As τ increases, the trajectories under condition (a) and (c) gradually approach the curve denoted by Eq. (33) from the lower and upper sides of it.

The relationship between ρ and τ, or the survivorship curve of the present model (Eq. (22)) is shown in Fig. 3 for several levels of ρ_i. In the diagram we see the convergence of density, exponential decrease in density after a sufficient lapse of time and clear dependence of the survivorship curves on initial density. Under condition (b), density is expected to decrease exponentially with τ.
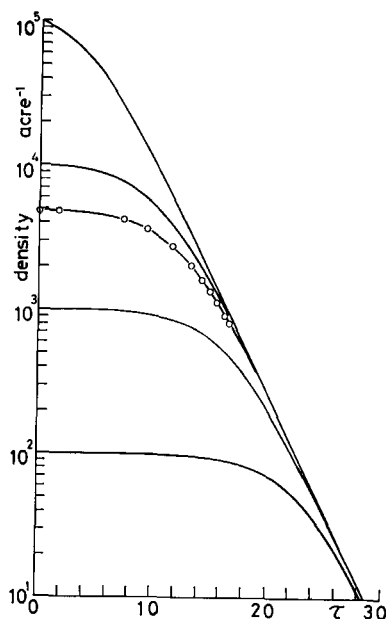

Fig. 3. Survivorship curves as related to initial density on the basis of the present model (Eq. (22)). Parameters are determined to simulate the observed curve of the eastern white pine, which is represented by open circles.

Table 2.   Comparison of the observed values of density, mean stem volume per plant
ones from the model, and the time trend of mean intrinsic growth rate.

Year	Years after planting	Observed density, mean stem volume per plant and stem volume biomass		
	t yr	ρ 1/acre[2]	w ft³ [3]	y ft³/acre[4]
1904	0	4840[5]	5.4×10^{-4} [5]	2.614 [5]
1908	4	4800	2.97×10^{-3} [5]	14.27 [5]
1916	12	4265	0.1829[5]	780
1920	16	3682	0.4364[5]	1607
1925	21	2786	0.9835[5]	2740
1930	26	2052	1.7519[5]	3595
1935	31	1630	2.6951[5]	4393
1940	36	1353	3.5713[5]	4832
1945	41	1144	4.8505[5]	5549
1950	46	925	6.3989[5]	5919
1955	51	815	8.5595[5]	6976

[1] Calculated density is omitted, since it is identical to the observed density.   [2] 1 acre≑
by the author.

Growth analysis: On the basis of the growth analysis established by Shinozaki
and Kira (1956), we can go far into the characteristics of this pine population growth.
   The A-τ diagram given by Eq. (28) shows that the pine population follows a
logistic growth curve of the λw-type. A reaches the maximum value ($A_{\max}$) at the
specific value of τ (τ^*).

$$A_{\max} = \frac{p}{w_0} \cdot \frac{1-\alpha\beta}{1-\alpha} \left\{ \frac{\alpha(\beta-1)}{1-\alpha} \right\}^{\frac{\alpha(1-\beta)}{\alpha\beta-1}} ,$$

$$\tau^* = \frac{1}{\alpha\beta-1} \cdot ln\, \frac{\alpha(\beta-1)}{1-\alpha} .$$

And A decreases exponentially with τ afterwards, as shown in Fig. 4.
   The A-B diagram shown in Fig. 5, or the trajectory of the A-B relationship with τ,
also shows that the growth curve of the pine follows the λW-type of logistic growth, and
resembles to some extent that of the soybean populations obtained by Shinozaki and
Kira (1956).   The diagram equated by

$$A = \frac{p}{w_0} \cdot \{(w_0 B)^{\alpha(\beta-1)} - (w_0 B)^{1-\alpha}\}$$

shows that A reaches $A_{\max}$ at the specific value of $B(B^*)$,

$$B^* = \frac{1}{w_0} \left[\frac{\alpha(\beta-1)}{1-\alpha} \right]^{1/(1-\alpha\beta)} ,$$

and that it decreases afterwards with the decrease in B or with the progress of growth.
But it should be noticed that the A-B relationship in the early stages of growth or at
relatively larger values of B can be approximated by a linear relationship, which

and stem volume biomass of the eastern white pine (Spurr *et al.*, 1957) to the calculated

| Calculated mean mean stem volume per plant and stem volume biomass[1] | | Biological time | | | Mean intrinsic growth rate |
| | | | | | $\lambda = \dfrac{\Delta\tau}{\Delta t}$ |
w ft³	y ft³/acre	τ	$\Delta\tau$	Δt yr	1/yr
5.4×10^{-4}	2.614	0			
2.97×10^{-3}	14.27	1.7244	1.7244	4	0.4311
0.2094	893	7.2923	5.5679	8	0.6960
0.4488	1652	9.4256	2.1333	4	0.5333
0.9404	2620	11.6252	2.1996	5	0.4399
1.7396	3570	13.2194	1.5942	5	0.3188
2.6374	4299	14.1908	0.9714	5	0.1943
3.6346	4918	14.8960	0.7051	5	0.1410
4.8124	5505	15.4889	0.5929	5	0.1186
6.8111	6300	16.1978	0.7089	5	0.1418
8.3497	6805	16.6031	0.4052	5	0.0810

4046.8 m².   [3] 1 ft³=28317 cm³.   [4] 1 ft³/acre≒6.98 cm³/m².   [5] Calculted or estimated
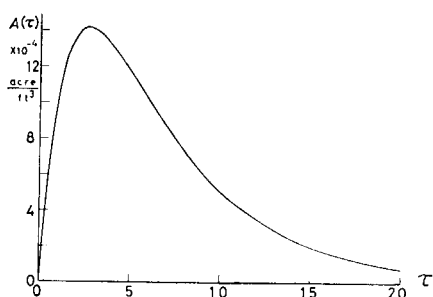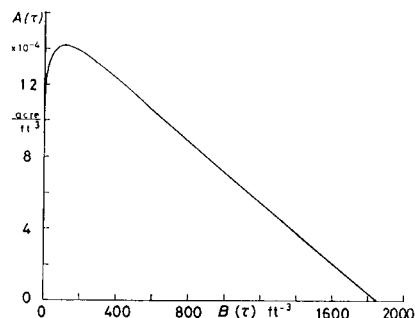

Fig. 4. $A(\tau)$–τ relation ((Eq. (28)) for the eastern white pine population after the present model, showing the growth curve follows the λw-type of logistic curve.

Fig. 5. $A(\tau)$–$B(\tau)$ diagram of the pine population.   The relationship can be approximated by linear relationship at larger ranges of $B(\tau)$, showing that the pine follows a λ-type of logistic growth curve.

shows the growth of the pine follows a λ-type of logistic growth.

We can calculate τ as related to t by the following procedures.   From Eq. (22) it follows that

$$\tau = \frac{1}{a}\,ln\left[\frac{1}{p}\left(\frac{1}{\rho} - \frac{1}{\rho_i}\right) + 1\right]. \tag{34}$$

Since the values of a, p and ρ_i are already determined and the value of ρ is given as a function of time in the report of Spurr *et al.* (1957), we have a τ-t relationship with other growth characteristics of the pine as summarized in Table 2.   As a whole, the relationship is approximated by a slightly sigmoidal curve.   If we introduce the lag
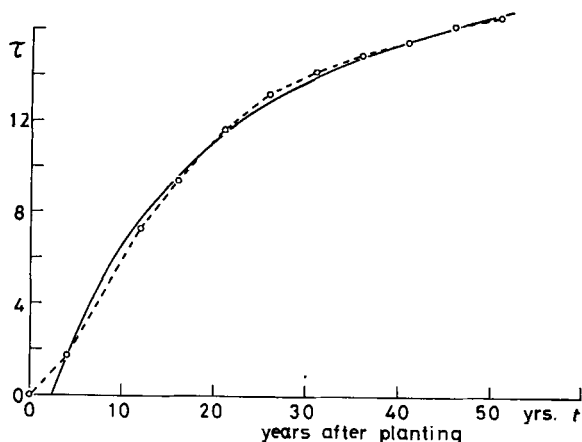
Fig. 6. The τ-t relation in the pine population. The observed relationship shows a slightly
sigmoidal curve, but it can be approximated by a hyperbolic curve with lag time of 2.5 years
(Eq. (35)).

time of 2.5 years presumably due to planting injury, the relationship is reasonably
formulated by Eq. (35), as shown in Fig. 6.

$$\frac{1}{\tau} = \frac{g}{t-2.5} + h\,. \tag{35}$$

Here $g=8.267\times10^{-1}$ years and $h=4.2637\times10^{-2}$. Differentiating both sides of Eq.
(35) with respect to t, we have

$$\lambda(t) \equiv \frac{d\tau}{dt} = \frac{g}{\{g+h(t-2.5)\}^2}\,. \tag{36}$$

Considering Eqs. (35) and (36), we conclude that the reciprocal of g denotes the
intrinsic growth rate at the initial stage, or at 2.5 years after planting and the reciprocal
of h denotes the ceiling value of τ as t tends to infinity. On the basis of the standard
method proposed by Shinozaki and Kira (1956), the mean intrinsic growth rate during
a given time interval is calculated by

$$\lambda \simeq \frac{\varDelta\tau}{\varDelta t}\,,$$

as shown in Table 2. The result of the comparison between λ-values obtained by the
two procedures is given in Fig. 7, showing good coincidence.

Discussion

Shinozaki (1962) proposed Eq. (37), assuming the growth curve follows the λw-
type logistic growth curve and the law of constant final yield is applicable to self-
thinning populations,

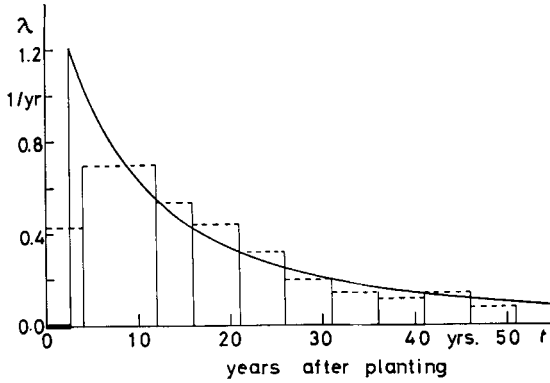$$\frac{1}{w} = e^{-\tau}\int_0^\tau \frac{\rho e^\tau}{Y(\tau)}\,d\tau + \frac{e^{-\tau}}{w_0}\,. \tag{37}$$

Fig. 7. The λ-t relationship in the pine population. The dotted line denotes the observed relationship (Table 2). The solid line shows the relationship calculated by Eq. (36) having lag time of 2.5 years, where λ is assumed to be zero as shown by a thick solid bar.

Here $Y(\tau)$ represents the final yield as being independent of ρ. The equation resembles Eq. (24) to some extent, but the difference between these equations deserves our notice. If we assume these two are identical, then we have

$$\int_0^\tau \frac{\rho e^\tau}{Y(\tau)}\, d\tau = A\rho e^\tau .$$

Differentiating both sides of this equation with respect to τ, we get

$$\frac{1}{Y} = A + \frac{dA}{d\tau} + A\,\frac{1}{\rho}\,\frac{d\rho}{d\tau} .$$

Since Y and A must be independent of ρ and populations are assumed to be self-thinning, we conclude

$$\frac{1}{\rho}\,\frac{d\rho}{d\tau} = \text{const.} = -\gamma \qquad (\gamma > 0) ,$$

or ρ decreases exponentially with τ. This conclusion is not exactly in harmony with Eq. (22). But it is not overlooked that Eq. (22) has the property

$$\frac{1}{\rho}\,\frac{d\rho}{d\tau} \simeq -\alpha ,$$

as τ tends to infinity, which is shown in Fig. 3. Therefore, if we want to estimate Y values, which are not defined in the present model, we may calculate them approximately by Eq. (38) at relatively larger values of τ,

$$\frac{1}{Y} \simeq (1-\alpha)\,A + \frac{dA}{d\tau} . \tag{38}$$

From the viewpoint of the logistic theory of plant growth, Eq. (37) should be considered as the most fundamental formula to show the w-ρ relationship of self-thinning populations. We should, therefore, conclude that Eq. (24) is an empirical formula, though it is useful to describe quantitative aspects of self-thinning as stated before.

The w-ρ trajectory given by the present model can be considered to show a kind of trajectory stability of the system converging to a particular state from a variety of starting positions (Orians, 1975). Furthermore, the assumptions made in Eqs. (22) and (25) are premised on a trajectory stability concerning both ρ-τ and w-ρ relationships. It should be noted that Fig. 2 is quite similar to the w-ρ diagram in the buckwheat experiment (Fig. 21, Yoda et al., 1963). This fact suggests the present model may have wider applicability to the growth analysis of self-thinning annual plant populations.

It is true that sometimes in overcrowded artificial populations composed of plants of relatively uniform size, catastrophic damages are observed after a heavy rain, wind, or snow, preventing the normal progress of self-thinning. Thus, self-thinning plays an important role as a self-regulatory mechanism for plant populations to assure sufficient seeds for the next generation (Yoda et al., 1963). Further studies should be made on the collapse mentioned above in relation to the stability of even-aged pure populations and to frequency distribution patterns of plant size (Koyama and Kira, 1956; Hozumi et al., 1968).

We consider fundamentally only four variables, among which initial density and time are independent and mean plant weight and realized density are dependent, to construct the model. But as stated before, many factors pertain to self-thinning. We should accordingly study the effect of these factors, especially of soil fertility, on the w-ρ trajectory and the survivorship curve, and construct the model to predict dead plant amounts due to self-thinning.

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