論 文

A Simple and Practical Model for Mean Size-Density Trajectories of Tree Stands

Masato SHIBUYA*

SHIBUYA, M.: **A simple and practical model for mean size-density trajectories of tree stands. J. Jpn. For. Soc. 77: 247～253, 1995** A simple and practical model for mean size-density trajectories derived from TADAKI's model by reparameterizing of the density term is proposed and examined for fitnesses to actual trajectories of monospecific. even-aged tree stands. The model is recognized to be a special case of NAITO's model. Various mean volume-density trajectories of coniferous stands are simulated by the model very closely, and fitness of the model comparison to those of NAITO's model. The present model did not deviate from an actual trajectory in the later self-thinning stages as found in TADAKI's model, and it is considered to be appropriate for the mean size-density trajectories. It was confirmed by examinations of ecological meanings of parameters that the model consisted of a full-density line of a species concerned and the term which describes the approaching process to that line according to the stand initial state. Also, the model can be manipulated like the C-D rule according to the density of the stand initial state when the full-density line already is fixed.

渋谷正人：**林分の平均サイズ-密度トラジェクトリーの単純で実用的なモデル 日林誌 77：247～253, 1995** 同齢単純林の平均サイズ-密度トラジェクトリーについて単純で実用的なモデルを提唱した。このモデルは只木のモデルを変形することで導くことができ，内藤モデルの1特殊形にあたる。本モデルは針葉樹同齢単純林の様々な平均材積-密度トラジェクトリーに精度よくあてはまり，只木モデルで指摘されている自己間引き後期段階における逸脱はみられなかった。あてはまりの精度は，内藤モデルと比べても遜色なかった。結果として，本モデルは平均サイズ-密度トラジェクトリーモデルとして適当であると考えられた。パラメータの生態学的な意味について検討し，このモデルは対象とする種の最多密度線と，初期密度に応じて最多密度線へ漸近する過程を記述する項から構成されることがわかった。さらに最多密度線が明らかな場合，C-D曲線と同様に扱うことができることが示された。

I. Introduction

Stand dynamics of monospecific, even-aged tree stands were described as mean size-density trajectories frequently (TADAKI and SHIDEI, 1959; ANDO, 1962; HOZUMI, 1977). The mean size-density trajectory is a very important factor for stand yield estimations (ANDO, 1968). TADAKI's model (TADAKI, 1963, 1964) has been often employed for mean volume (w)-density (N) relationships of tree stands in forestry studies as follows:

$$1/N = Aw + B \tag{1}$$

where A and B are constants determined by the trajectory. HOZUMI (1977) pointed out that this model approximates the mean volume-density relationship in the earlier stages of the self-thinning of a stand. However, it increasingly deviates from that in the later self-thinning stages. This deviation is considered to be peculiar to the model because its gradient is different from the full-density line on which the trajectory travels in the later self-thinning stages. Because the trajectory approximated by TADAKI's model was assumed to shift to the full-density line when it came to that line (TADAKI, 1963), this disadvantage of the model was not conspicuous.

In the recent ten or more years, MINOWA (1983), HAYASHI (1985) and SMITH and HANN (1986) derived mean size-density trajectories that moved vertically on the log (mean size)-log (density) plot in the initial

* Fac. of Agric., Hokkaido Univ., Sapporo 060 北海道大学農学部

stand development stages and approached the full-density line very smoothly with self-thinning. These models seemed to be more appropriate than TADAKI's model, although parameter determinations for them are more or less difficult. It is desired that the model for the mean size-density trajectory easily determines parameters and applies them to harvest estimations.

In this paper, a simple and practical model for mean size-density trajectories of monospecific, even-aged tree stands is proposed and fitted to actual data obtained from various studies, and it is examined on ecological meanings of the parameters.

II. Mean Size-Density Trajectory Data

Mean size-density trajectories of coniferous tree species (Table 1) were employed for simulations by a model proposed later. Although tree species of KHILMI's data (KHILMI, 1957) were not identified, other trajectories consisted of five species of various shade tolerances and stand development stages. All stands had not or hardly had been thinned artificially. Mean size of the stands is mean volume in this paper. Dimensions of tree volume and area are converted into m^3 and ha, respectively.

Chamaecyparis obtusa (SIEB. et ZUCC.) ENDL. data obtained from TAKEUCHI (1980) covered stand ages from 25 to 70 years old. This plantation is located in the Tokyo University Forest in Chiba Prefecture and was investigated for tree diameters on a 0.02 ha-plot. Because stand stock decreased during the 65～70 years old, data for the 70 years old was omitted from the analysis.

An *Abies sachalinensis* MASTERS plantation was established in 1929 in the Ikeda District in Hokkaido (Hokkaido Prefectural Forest Office, 1982). Initial stand density was 4,200/ha, and diameter measurements were continued from 1948 at 2～5-year intervals. Stand density decreased from 3,990 to 2,174/ha in the investigating period. This stand was analyzed for frequency distributions of individual volumes by KIKUZAWA (1981).

A *Pinus strobus* LINN. stand reported by SPURR *et al.* (1957) was in southeastern Michigan, United States. Many Japanese workers (*e.g.* TADAKI and SHIDEI, 1959; HOZUMI, 1977; HAYASHI, 1985) studied the mean volume-density relationship of this stand. Stand density after initial mortality was about 11,900/ha. Stand stock and density were investigated nine times during 1916～1955, at 13～52-year-old stand ages. The range of stand density decrease was larger than those of *C. obtusa* and *A. sachalinensis* stands (Fig. 1).

KHILMI's data (KHILMI, 1957) was taken from yield tables prepared by Professor TYURIN. These data are supposed to be based on the dynamics of stands that were conducted as cultural works. He indicated stand

Table 1. Results of fittings of the present mean volume-density trajectory model

Species	Parameters of the trajectories			R^2	Data sources
	$\log_{10}a$	k	b		
*Chamaecyparis obtusa**	4.869	1.470	0.118	0.8857	TAKEUCHI (1980)
*Abies sachalinensis**	4.958	1.556	0.162	0.9609	Hokkaido Prefectural Forest Office (1982)
*Pinus strobus**	4.473	1.537	0.0115	0.9965	SPURR *et al.* (1957)
Pine, Site Quality I**	4.477	1.545	0.0663	0.99992	KHILMI (1957)
Pine, Site Quality IV**	4.332	1.529	0.0258	0.9998	KHILIM (1957)
Spruce, Site Quality I**	4.656	1.526	0.0846	0.9978	KHILMI (1957)
Spruce, Site Quality IV**	4.317	1.462	0.0337	0.9948	KHILMI (1957)
Pinus taeda(1)***	2.408	1.321	0.048	0.9998	PEET and CHRISTENSEN (1980)
Pinus taeda(2)***	2.596	1.362	0.0146	0.9735	PEET and CHRISTENSEN (1980)
Pinus taeda(3)***	2.505	1.328	0.0514	0.9889	PEET and CHRISTENSEN (1980)
Pinus taeda(4)***	2.274	1.230	0.0930	0.9551	PEET and CHRISTENSEN (1980)
Picea mariana(1)***	5.797	1.791	0.0120	0.9562	CARLETON and WANNAMAKER (1987)
Picea mariana(2)***	5.899	1.767	0.0446	0.9447	CARLETON and WANNAMAKER (1987)
Picea mariana(3)***	5.850	1.843	0.0434	0.9354	CARLETON and WANNAMAKER (1987)

* Artificial stand. ** Stand origin was indistinct. *** Natural stand.

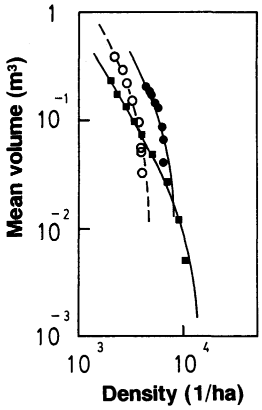

Fig. 1. Mean volume-density trajectories of coniferous plantations

Legend: Black and white dots, and black squares are trajectories of *Chamaecyparis obtusa* and *Abies sachalinensis*, and *Pinus strobus* stands, respectively.

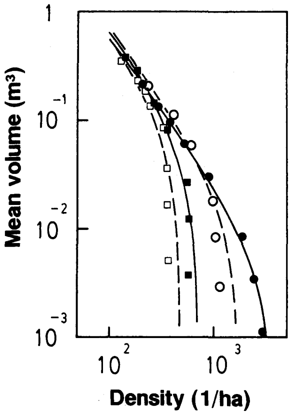

Fig. 3. Mean volume-density trajectories of *Pinus taeda* stands

Legend: Black and white dots, and black and white squares indicate Stand (1)〜(4) (Table 1) in that order.

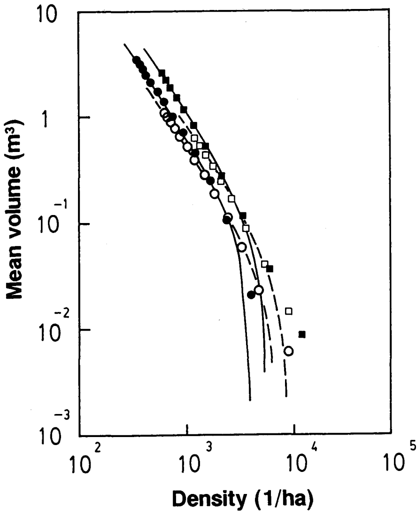

Fig. 2. Mean volume-density trajectories of pine and spruce stands on sites of different qualities

Legend: Black and white dots, and black and white squares correspond to pine site-I, pine site-IV, spruce site-I, and spruce site-IV, respectively.

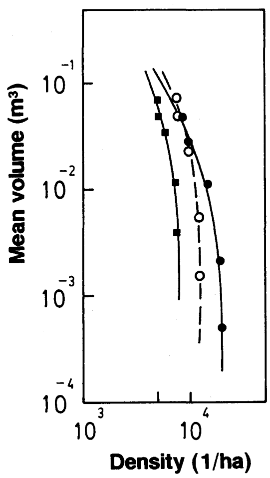

Fig. 4. Mean volume-density trajectories of *Picea mariana* stands

Legend: Black and white dots, and black squares are Stand (1)〜(3) (Table 1), respectively.

stocks of pine and spruce for six site qualities. Trajectories for Site Qualities I and IV of each tree are tested in this paper (Fig. 2).

Even-aged *Pinus taeda* LINN. stands regenerated naturally on sites abandoned from agricutural cultivation were surveyed in a succession study of tree communities by PEET and CHRISTENSEN (1980). These stands are located in North Carolina's Piedmont area, United States. Investigated plots were established in the early 1930's and measured for diameter and height of each tree. Initial densities of Stands (1)〜(4) in the first survey when stand age was 8 years old were 2,896, 1,065, 578 and 368/ha, respectively (Fig. 3). These plots were remeasured 7〜9 times until 1978. Mean volume-density trajectories of all stands were more curvilinear than linear in the stages where self-thinning had progressed considerably as the authors pointed out. Especially, the last data for each stand showed an obvious different trend from the other points, and they were excluded from analyses.

Picea mariana (MILL.) B.S.P. stands also invaded naturally after forest fires as even-aged cohorts. CARLETON and WANNAMAKER (1987) reconstructed mean volume-density trajectories through research on tree ages and growth patterns of live and standing dead stems. Although they tried to restore the trajectories exactly, underestimation of density may be inevitable in the earliest growth stage of an old stand. Three stands that had large initial densities were selected for this study from ten of their stands. The authors asserted that these trajectories were rotated sigmoid-shaped (Fig. 4).

III. Model

A model for mean size-density trajectory is empirically proposed by the reparameterizing of the power term of density in Eq. (1):

$$w = aN^{-k} - b \qquad (2)$$

where a, b, and k are parameters for each trajectory (a, b, $k>0$). This model is a kind of reciprocal equation. In this study, the parameters of Eq. (2) are determined by the non-linear least squares method, employing the quasi-Newton method, and the coefficient of determination is the ratio of the explained sum of squares to the total sum of squares.

The trajectory by the model moves vertically in stand establishment stages and along the line expressed by $w=aN^{-k}$ in stand mature stages. Trajectory shape is similar to MINOWA's (1983) and HAYASHI's models (1985). NAITO (1983) also suggested that the same type function as Eq. (2) could be derived when the stand density decrease and the mean size growth followed the RICHARDS function. Furthurmore, NAITO (1984) explicitly proposed a more general trajectory model than the present one as follows:

$$w = (aN^{-\beta} - \gamma)^{\delta} \qquad (3)$$

The present model is recognized as a special case of NAITO's model when the parameter δ is assumed to be 1. I examined the fitnesses of both models (Eqs. (2) and (3)) to the trajectory data.

IV. Results

The results of the fittings of the present model to stand data are given in Table 1 and Figs. 1~4. Coefficients of determination are larger than 0.935 in all stands except for a *C. obtusa* stand, and this model simulated sufficiently these trajectories. NAITO's model (Eq. (3)) showed larger coefficients of determination than those in the present model for six trajectories out of 14 sets of stand data (Table 2), in spite of repetitive trials of regressions with various initial values of the parameters. NAITO's model is considered to

Table 2. Results of fittings of NAITO's mean volume-density trajectory model*

Species	Parameters of NAITO's trajectory model				R^2
	α	β	γ	δ	
Chamaecyparis obtusa	40.197	0.479	−0.039	5.811	0.8530
Abies sachalinensis	124.055	0.595	0.703	1.615	0.9567
Pinus strobus	105.940	0.687	0.080	2.024	0.9960
Pine, Site Quality I	145.633	0.726	0.183	1.951	0.99991
Pine, Site Quality IV	42.005	0.538	0.267	2.194	0.9999
Spruce, Site Quality I	62.417	0.570	0.191	2.609	0.9999
Spruce, Site Quality IV	57.726	0.577	0.121	2.604	0.99997
Pinus taeda (1)	5.511	0.384	0.137	2.754	0.9996
Pinus taeda (2)	4.399	0.274	0.424	2.685	0.9773
Pinus taeda (3)	6.306	0.326	0.579	2.414	0.9870
Pinus taeda (4)	4.801	0.215	0.958	3.138	0.9366
Picea mariana (1)	1.038×10^3	0.861	−0.243	7.477	0.9741
Picea mariana (2)	5.969×10^2	0.776	−0.179	9.547	0.9569
Picea mariana (3)	28.353	0.368	0.570	6.475	0.9272

* Analyzed trajectory data are the same as in Table 1.

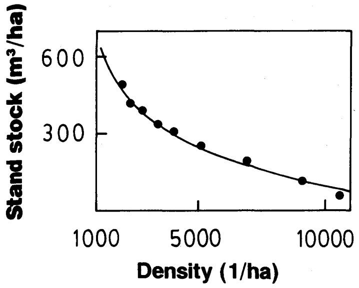

Fig. 5. Relationship between stand stock and density of a *Pinus strobus* plantation (SPURR *et al*., 1957)

Note: Trajectory curve was obtained from that of the present mean volume-density model for this stand (Fig. 1).

be more flexible than the present model, although the results shown in Table 2 indicate that the fitting of Eq. (3) to the mean size-density trajectory of a tree stand is more or less difficult. NAITO (1984) reduced the difficulties of fitting Eq. (3) to trajectories by the assumption of $\beta\delta=3/2$ based on the 3/2 power law of self-thinning (YODA *et al*., 1963). Consequently, fitnesses of Eq. (2) to the trajectories compares with those of Eq. (3), and Eq. (2) is recognized to be suitable and applicable to mean size-density trajectories. Parameter k modifies the trajectory shape, and the deviation of the trajectory from actual data in the later self-thinnig stages observed in TADAKI's model as pointed out by HOZUMI (1977) was not found (Fig. 5).

It is notable that parameter values of $\log_{10} a$ and k are restricted within narrow ranges, the former between 4.3 and 5.0, and the latter between 1.46 and 1.56, excepting data in irregular trends of *P. taeda* and *P. mariana* stands. Their ranges are approximately comparable with those of the full-density lines of coniferous tree species (TADAKI, 1969).

V. Discussion

Ecological meanings of the parameters of Eq. (2) are examined here.

The gradient of Eq. (2) on the double-logarithmic plot is

$$\frac{d \log w}{d \log N}=-\frac{k}{1-(b/a)N^k} \qquad (4)$$

The gradient of a mean size-density trajectory just after stand establishment is hypothesized generally to be a very large negative value excepting for the stand of extremely large density. When $(d \log w/d \log N)$ approaches negative infinity, $1-(b/a)N^k \to 0$ in Eq. (4). Therefore, $N \fallingdotseq (a/b)^{1/k}$ is satisfied in this case. The stage of stand development when the mean size-density trajectory shifts vertically is defined as the initial state, and density in this state is expressed as N_0, then $N_0 \fallingdotseq (a/b)^{1/k}$. As understood from this definition, N_0 is not always equivalent to an actual initial density. Equation (2) is rewritten by substituting $b=aN_0^{-k}$ as

$$w=aN^{-k}\{1-(N/N_0)^k\} \qquad (5)$$

In the later growth stages, stand density decreased considerably, N is assumed to be fairly small compared with N_0. Consequently, $w \fallingdotseq aN^{-k}$ is held in these stages. Since TADAKI and SHIDEI (1959) and YODA *et al.* (1963), a concept that monospecific, even-aged stands with various initial densities and site qualities, tend to converge on the full-density line specific to species after sufficient growth periods, has been supported (HOZUMI, 1977, 1980). When this concept is agreed to, parameters a and k in the trajectory model are regarded as the intercept and the thinning exponent of the full-density line, respectively. Therefore, a and k are determined by species, and N_0 is determined by each trajectory, theoretically. On the right side of Eq. (5), the term aN^{-k} expresses the full-density state for the species concerned, and the term $1-(N/N_0)^k$ determines the approaching process to the full-density line according to the initial state of the stand.

It is natural that the ranges of $\log_{10} a$ and k in Table 1 are moderate for coniferous tree species, excluding stands with trajectories of irregular tendencies. Site quality is presumed not to affect the position of the full-density line (YODA *et al*., 1963); however, trajectories of the poorer site qualities located themselves below those of the more favorable sites in the later growth stages (Fig. 2). More careful examinations are needed about this problem. Parameters k for *P. taeda* and *P. mariana* trajectories are different from the 1.5 assumed by the 3/2 power law of self-thinning (YODA *et al*., 1963); nevertheless, parameters a and k are approximately similar within each species (Table 1).

Each parameter influences the trajectory in different ways (Fig. 6). Increased parameter a shifts the

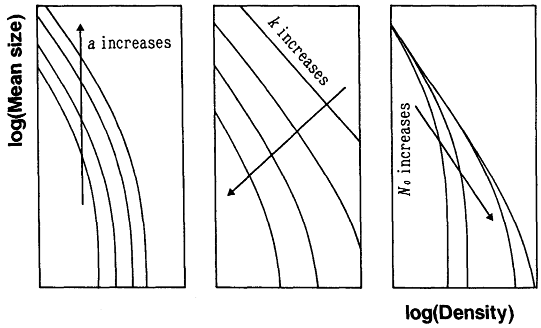

Fig. 6. Influences of parameters of the present model on mean size-density trajectories

Notes: Increased parameter a causes the vertical ascending of the trajectory (left figure). Parameter k determines the trajectory shape (middle figure). The trajectory moves along the full-density line with increases of parameter N_0 (right figure).

trajectory upward. Parameter k decides the trajectory shape. When density of the initial state N_0 increased, the trajectory moves downward parallel along the full-density line. If k is fixed, we can treat this trajectory model like the C-D curve (SHINOZAKI and KIRA, 1961). It must be examined whether or not shapes of mean size-density trajectories with various initial densities are considered to be the same within a species. However, statistical analyses on mean size-density trajectories of pure tree stands by PUETTMANN *et al.* (1993) concluded that trajectory shapes were not affected by stand initial density and stand origin within a species. Parameters in Eq. (2) must be determined by non-linear regression, although in the case of a species for which the full-density line is already fixed, the mean size-density trajectory is able to be settled roughly by only the manipulation of the N_0-value. Thus the present model is very practical in this characteristic like the C-D curve and easy determinations of the parameters.

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