Self-Thinning Boundary Line and Dynamic Thinning Line in Prince Rupprecht's Larch (*Larix principis-rupprechtii* Mayr) Stands

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The self-thinning boundary line and the dynamic thinning line were determined to investigate the characteristics of self-thinning in Prince Rupprecht's larch (*Larix principis-rupprechtii* Mayr) stands. The self-thinning boundary line for 56 sample stands showed a slope of -1.75, which was significantly steeper than the conventional value of $-3/2$. The mean stem volume (ν)−density (ρ) trajectories examined in three sample stands gradually approached their own dynamic thinning lines, which have respective slopes of -1.74, -1.75 and -1.70 with increasing stand age. The $\nu-\rho$ trajectories were well fitted with Hagihara's model, so that this model was considered to be suitable for describing the $\nu-\rho$ trajectory during the course of self-thinning. The dynamic thinning lines lay below the self-thinning boundary line and they were almost parallel to each other.

Key words: dynamic thinning line, Hagihara's model, mean stem volume−density trajectory, Prince Rupprecht's larch, self-thinning boundary line, $-3/2$ power law

Introduction

As individual trees in a stand grow, they begin to compete with each other for limited resources, which circumstances finally cause some individuals to die. The self-thinning law, or the $-3/2$ power law of self-thinning (Yoda *et al.* 1963), states the relationship between mean stem volume (ν) and plant density (ρ) as,

$$\nu = K\rho^{-\alpha}, \qquad (1)$$

where K is a coefficient, which varies with species, and $-\alpha$ is the slope of the self-thinning line on logarithmic coordinates, the value of which is close to $-3/2$ regardless of species, ages and site conditions. This law suggests that the mean stem volume of surviving plants increases with decreasing density in a stand suffering from self-thinning. Evidence in favour of the self-thinning law has been accumulated from experimental data for more than 30 years (*e.g.* White and Harper 1970; Gorham 1979; White 1981; Hutchings and Budd 1981; Westoby 1981, 1984; Hamilton *et al.* 1995). However, there are empirical examples to suggest that mortality due to self-thinning can occur before the $\nu-\rho$ trajectory approaches the self-thinning line (*e.g.* Tadaki and Shidei 1959; Tadaki 1963; Hozumi 1977, 1980).

Hagihara (1995, 1996) suggested that the mean stem volume (ν)−tree density (ρ) trajectory during the course of self-thinning in a stand is described as,

$$\nu = K\rho^{-\alpha}\left(1 - \frac{\rho}{\rho_0}\right)^{\alpha-1} \qquad \left(\frac{1}{\rho_0} = \frac{1}{\rho_1} - \frac{1}{\rho_1^*}\right), \qquad (2)$$

where K and α are coefficients, ρ_1 is the initial density of the stand and ρ_1^* is the initial density of the ρ_1^*-population (Hozumi 1980), which follows the $-3/2$ power law of self-thinning from the initial growth stage. The $\nu-\rho$ trajectory given by Eq. (2) gradually approaches the self-thinning line given by Eq. (1), and eventually moves along this self-thinning line.

Recently, the concept of the self-thinning line has been divided into the self-thinning boundary line and the dynamic thinning line. The self-thinning boundary line is the upper boundary of possible $\nu-\rho$ combinations, whereas the dynamic thinning line is asymptotically approached and followed by the time trajectory of ν and ρ in a given stand, and the two lines do not always coincide (Osawa and Allen 1993; Hamilton *et al.* 1995), because environmental limitations or stand's genetic compositions are different between stands (Weller 1990).

Although studies on herbaceous plants have provided many examples of the time trajectory of self-thinning (*e.g.* Yoda *et al.* 1963; White and Harper 1970; Hutchings 1979; Lonsdale and Watkinson 1983; Morris and Myerscough 1991), there have been relatively few studies on the time trajectory of self-thinning with the development of forest stands (*e.g.* Tadaki 1963, 1964;

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Hozumi 1977, 1980; Shibuya 1995; Hagihara 1995, 1996; Xue *et al.* 1997) and on the self-thinning boundary line (Weller 1990; Osawa and Allen 1993; Osawa 1995).

Prince Rupprecht's larch (*Larix principis-rupprechtii* Mayr) is naturally distributed in North China and is one of the mainstays of industry in China. This species is a relatively fast growing tree with good quality. However, the self-thinning characteristics of the species have not yet been well understood. Such information is necessary for not only understanding the basic $\nu - \rho$ relationship of the species, but also managing the forest stands. The purpose of this study is: (1) to inspect the self-thinning boundary line of the Prince Rupprecht's larch stands; (2) to analyse the $\nu - \rho$ trajectory of self-thinning in the larch stands; (3) to examine the relationship between the self-thinning boundary line and the dynamic thinning line of the larch stands.

Materials and Methods

Site description

The field study was conducted in the Guanqin Mountains (39° 04′ N, 112° 18′ E), Shanxi Province, China, at altitudes between 1600 m and 1900 m. This altitude range was focused on the distribution of the larch. The climate had long cold winter and short cool summer. Mean annual temperature was 0.1°C, with the mean monthly minimum temperature of -13.6°C in January and mean monthly maximum temperature of 13.1°C in July. Mean annual frostless period was 107 days and mean annual precipitation was 537 mm. The soil was brownish with a depth of over 50 cm, and had a pH-value of 7.0 to 7.9.

Plant materials

Originally the study area supported dense natural Prince Rupprecht's larch (*Larix principis-rupprechtii* Mayr) forests, but this area was destroyed by continuous clear cutting for timber. At the onset of this study, the study area was covered with naturally regenerated larch.

To investigate the self-thinning line for the larch, it was necessary to select the stands under the upper boundary condition of the mean stem volume (ν)-density (ρ) relationship resulting from undergoing natural thinning. The selected larch stands satisfied the following criteria: (1) closed overstory canopy; (2) extremely dense condition for a given tree size; (3) undergoing density dependent mortality. A total of 47 stands was selected to analyse the $\nu - \rho$ relationship. Another nine

densest stands, which seemed to construct the upper boundary of the $\nu - \rho$ relationship, were used to determine the self-thinning boundary line. Within each stand, a 0.1-ha plot was established in 1995. For all trees, stem diameter at breast height was measured, and tree height was measured for 50 randomly selected trees. Stem volume of each tree was estimated from a larch volume table (Forestry Exploration and Design Institute of Shanxi Province 1984).

In order to analyse the $\nu - \rho$ trajectory of the larch, three 0.1-ha plots with different initial densities established in 1957 were selected on the naturally regenerated stands, namely, Site I, Site II and Site III. The stand age was 26, 25 and 24 years for Site I, II and III, respectively (as of 1957). The canopies were closed, and there were some standing dead and dying trees. The plots were kept unthinned. The sample plots were located at about 130 m intervals. To understand dynamics of the stand growth, tree height and stem diameter at breast height were measured five times on all trees in each plot: at the ages of 26, 31, 41, 51 and 58 for Site I, 25, 30, 40, 50 and 57 for Site II, and 24, 29, 39, 49 and 56 for Site III. Stem volume of each tree was estimated from the larch volume table.

Model fitting

The self-thinning boundary line was estimated by fitting the data of the nine densest stands to Eq. (1), while the $\nu - \rho$ trajectories were estimated by fitting the data of the three stands with different initial densities to Eq. (2). The $\nu - \rho$ trajectory given by Eq. (2) gradually approaches the dynamic thinning line, which is written in the form of Eq. (1). Therefore, the values of the coefficients K and α of the dynamic thinning line are the same as those of Eq. (2). The coefficients K and α in Eq. (1) and the coefficients K, α and ρ_0 in Eq. (2) were determined using a nonlinear least squares method.

Results

Figure 1 shows scatterplots of the mean stem volume (ν, m³ per tree) and density (ρ, trees ha^{-1}) on logarithmic coordinates for the 56 sample stands of larch. The open squares represent the stands at the uppermost boundary of self-thinning. The nine stands were selected visually according to Osawa and Allen (1993) and Osawa (1995). The $-\alpha$ value of the self-thinning boundary line given by Eq. (1) was -1.75 ± 0.10 (SE), which was significantly steeper than the slope of $-3/2$ ($p < 0.05$).
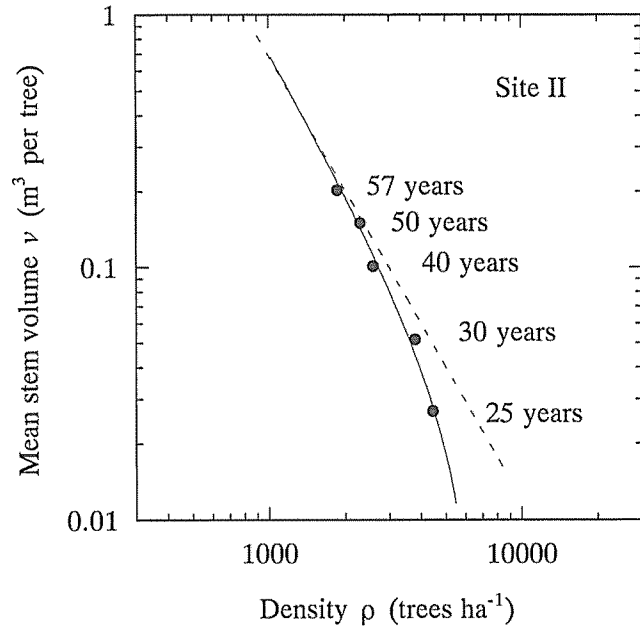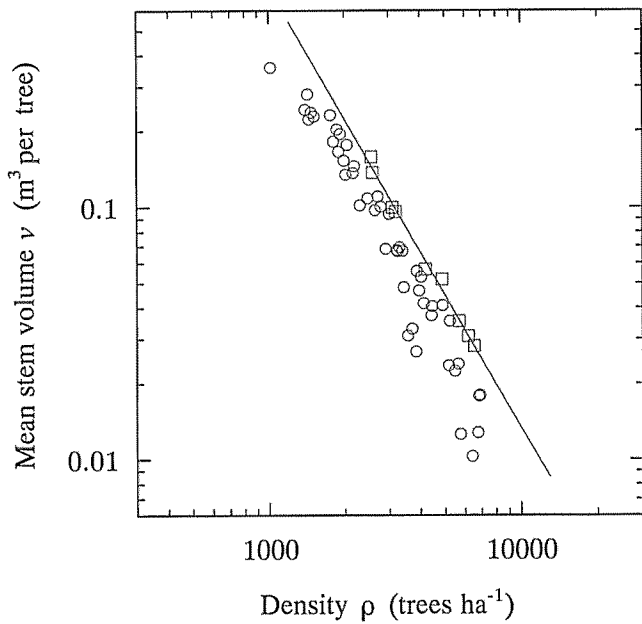
Fig. 1. Scatterplots of mean stem volume (v, m³ per tree) to density (ρ, trees ha⁻¹) for 56 sample larch stands on logarithmic coordinates. Open square (□) indicates the nine stands assumed to represent the uppermost limit of the $v-\rho$ relationship. Open circle (○) indicates the 47 stands which lie below the self-thinning boundary line given by Eq. (1), which is shown by the straight line: $v = 130010\rho^{-1.75}$.

As shown in Fig. 2, the mean stem volume (v, m³ per tree) increased with decreasing density (ρ, trees ha⁻¹) during the study period. With increasing stand age, the $v-\rho$ data points of each site moved upwards along the trajectory given by Eq. (2), and asymptotically approa-
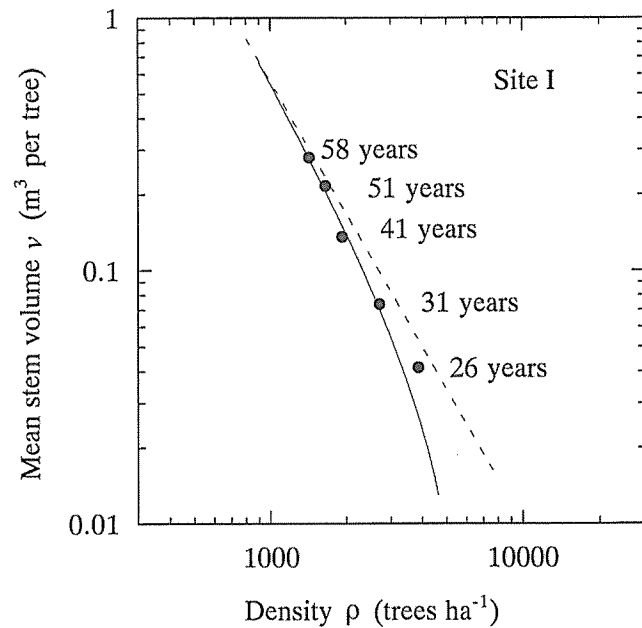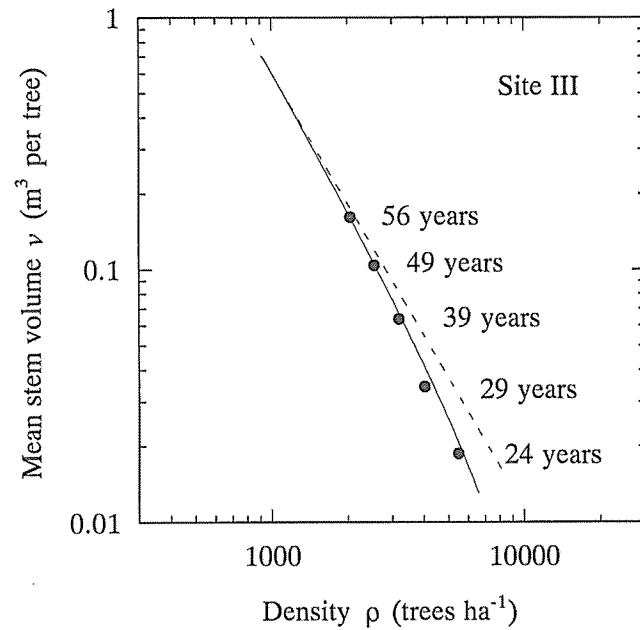

Fig. 2. Mean stem volume (v, m³ per tree)–density (ρ, trees ha⁻¹) trajectories for three sample larch stands with different initial densities. The solid line denotes the $v-\rho$ trajectory fitted with Eq. (2): $v = 104370\rho^{-1.74}\left(1-\dfrac{\rho}{6709}\right)^{0.74}$ for Site I; $v = 116800\rho^{-1.75}\left(1-\dfrac{\rho}{6964}\right)^{0.75}$ for Site II; $v = 91744\rho^{-1.70}\left(1-\dfrac{\rho}{6544}\right)^{0.70}$ for Site III. The data points gradually approached their own dynamic thinning line (broken line) given by Eq. (1): $v = 104370\rho^{-1.74}$ for Site I; $v = 116800\rho^{-1.75}$ for Site II; $v = 91744\rho^{-1.70}$ for Site III.

ched their own dynamic thinning line with a slope almost equal to the slope of the self-thinning boundary line. The curvilinear given by Eq. (2) showed a good agreement with the $\nu-\rho$ data of Site I ($p<0.01$, $r^2=0.997$), Site II ($p<0.01$, $r^2=0.995$) and Site III ($p<0.01$, $r^2=0.998$). The $-\alpha$, K and ρ_0 values in Eq. (2) were respectively estimated to be -1.74 ± 0.09 (SE), 104370 ± 2732 (SE) m³ ha⁻¹·⁷⁴ and 6709 ± 1737 (SE) trees ha⁻¹ for Site I, -1.75 ± 0.07 (SE), 116880 ± 2411 (SE) m³ ha⁻¹·⁷⁵ and 6964 ± 1829 (SE) trees ha⁻¹ for Site II and -1.70 ± 0.19 (SE), 91744 ± 2371 (SE) m³ ha⁻¹·⁷⁰ and 6544 ± 2100 (SE) trees ha⁻¹ for Site III. Therefore, the $-\alpha$ and K values of the dynamic thinning line given by Eq. (1) was respectively -1.74 and 104370 m³ ha⁻¹·⁷⁴ for Site I, -1.75 and 116880 m³ ha⁻¹·⁷⁵ for Site II and -1.70 and 91744 m³ ha⁻¹·⁷⁰ for Site III.

The relationship between the self-thinning boundary line (solid line) and the dynamic thinning lines (other lines) for the larch stands is shown in Fig. 3. The dynamic thinning lines lay below the self-thinning boundary line and they were almost parallel to each other.
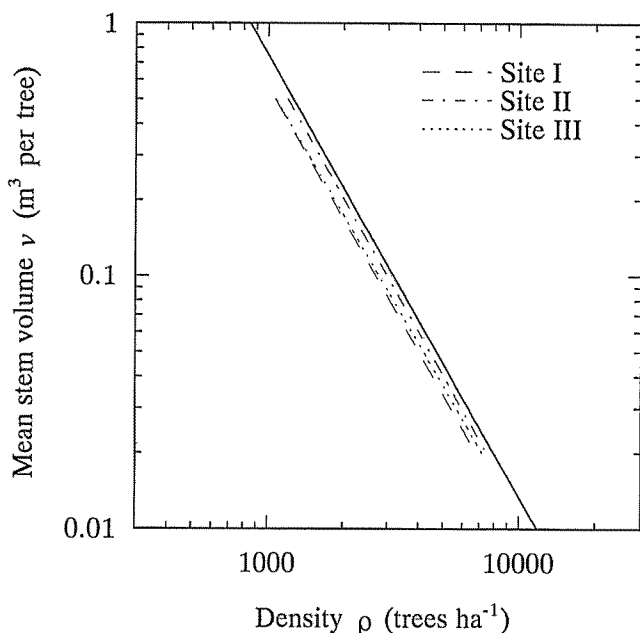

Fig. 3. Relationship between the self-thinning boundary line and the dynamic thinning lines of larch stands. The solid line shows the self-thinning boundary line (Fig. 1) and the broken (Site I), chained (Site II) and dotted (Site III) lines show the dynamic thinning lines (Fig. 2). The self-thinning boundary line stands for the uppermost limit of the mean stem volume (ν, m³ per tree) and density (ρ, trees ha⁻¹) combinations. The dynamic thinning lines are gradually approached and followed by the $\nu-\rho$ trajectories of respective three sample larch stands.

Discussion

The slope of the self-thinning boundary line was estimated to be -1.75 (Fig. 1), which was significantly different from a value of $-3/2$ expected from the $-3/2$ power law of self-thinning (Yoda *et al.* 1963). Osawa (1995) examined the self-thinning boundary line of four woody species; Jack pine (*Pinus banksiana* Lamb.), Japanese red pine (*Pinus densiflora* Sieb. et Zucc.), Japanese cedar (*Cryptomeria japonica* (Linn. fil.) D. Don) and mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole) showed their slopes of the self-thinning boundary line to be -1.42, -1.49, -1.56 and -1.13, respectively. Therefore, the slope of the self-thinning boundary line may take values other than $-3/2$. The slope of the self-thinning boundary line may be related to trends in slenderness (mean plant height divided by the square root of mean ground area occupied) and biomass packing (mean dry weight divided by spatial volume occupied) across stands (Weller 1990). Weller (1987) proposed the allometric model as,

$$w=K\rho^{-\frac{1}{2\varphi}}, \tag{3}$$

where α in Eq. (1) corresponds to $1/(2\varphi)$, φ reflecting changes in shape with size. Assuming that height (H), area occupied (A) (A is proportional to the reciprocal of density ρ) and biomass packing (d) ($=w/(AH)$) vary with plant weight (w) according to allometric power relationships: $H\propto w^\theta$, $d\propto w^\delta$ and $R\propto w^\varphi$, where R is the radius of the occupied area A, the following relationship is derived,

$$\varphi\left(=\frac{1}{2\alpha}\right)=0.5-0.5(\theta+\delta). \tag{4}$$

From Eq. (4) α equals $3/2$ only if $\varphi=1/3$, namely, $\theta+\delta=1/3$. Because θ and δ vary with species, the slope of the self-thinning boundary line can differ from $-3/2$. For the same density stands of different species, the species holding a higher tree height shows a higher slenderness (higher θ), resulting in a steeper slope of the self-thinning boundary line. Likewise, the species holding a higher stem volume packing (higher δ) yields a steeper slope.

The mean stem volume-density trajectories of three stands (Fig. 2) were more curvilinear rather than linear during the course of self-thinning ($p<0.01$). The mortality occurred in stands before the dynamic thinning line was reached, so that the $\nu-\rho$ data points of Site I, Site II and Site III gradually approached their own dynamic thinning lines with respective slopes of -1.74, -1.75 and -1.70. Equation (2) may be objective in

describing the $\nu-\rho$ trajectory of stands compared with Eq. (1), in which the $\nu-\rho$ trajectory is proposed as a straight line with a slope of ca. $-3/2$ on logarithmic coordinates. In self-thinning stands, the $\nu-\rho$ trajectory gradually approaches their own dynamic thinning line with a slope of $-\alpha$ and then progresses along it. The dynamic thinning line will not in general coincide with the self-thinning boundary line. If a stand of a species follows the $\nu-\rho$ trajectory which reaches the maximum dynamic thinning line for the species (Hamilton *et al*. 1995), the dynamic thinning line of the stand may coincide with the self-thinning boundary line. All the $\nu-\rho$ data for a species can scatter below or on the self-thinning boundary line, but can not transgress it. The $\nu-\rho$ trajectory of a given stand of the species may follow its own dynamic thinning line below or on the self-thinning boundary line after a sufficient lapse of time (Weller 1990; Hamilton *et al*. 1995). The results of the present study agree with this self-thinning viewpoint.

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落葉松林の自己間引き

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　落葉松林の自己間引きのバウンダリーラインとダイナミックラインを，それぞれ56林分と3林分で調べた。56林分で調べた落葉松林の自己間引きのバウンダリーラインの傾きは−1.75であった。この値は一般的に報告されている−3/2より有意に小さかった。林分の成育につれて，平均材積と密度の軌跡は，徐々にそれぞれ−1.74，−1.75，−1.70の傾きを持つ自己間引きのダイナミックラインに近づいた。これらの軌跡は萩原のモデルで良く近似され，このモデルは自己間引きのモデルとして有用であると考えられた。自己間引きのダイナミックラインは自己間引きのバウンダリーラインより下に位置し，お互いに平行関係にあった。

キーワード：ダイナミックライン，萩原モデル，平均材積−密度の軌跡，落葉松，バウンダリーライン，−3/2乗則