

Leaf biomass changes with stand development in hinoki cypress (*Chamaecyparis obtusa* [Sieb. et Zucc.] Endl.)

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Abstract We monitored a permanent plot of 3-year-old *Chamaecyparis obtusa* seedlings for 11 years after planting. As the stem cross-sectional area at the crown base can be regarded as a good predictor of leaf mass according to the pipe model theory, we measured this parameter to determine temporal trends in leaf biomass. The mean values showed asymptotic growth, maintaining a near-constant level after a stand age of 9 years. Peak values were found at 9 years, followed by a slight decrease because of a continuous reduction in stand density. This temporal trend suggests that the leaf biomass per unit land area attains a peak at an age of 9 years. As

the stand density changes with stand age, the relationship between stand stem cross-sectional area at the crown base and stand density showed an optimum curve in which the optimum density was around 9200 ha⁻¹. We propose hypothetical trends in primary productivity and biomass density with stand age, based on the results of measurements of stem cross-sectional area at the crown base and stand density under the assumption of the 3/2 power law of self-thinning.

Keywords Biomass density · *Chamaecyparis obtusa* · Leaf biomass · Primary productivity · Stem cross-sectional area at the crown base · 3/2 Power law of self-thinning

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Introduction

Foliage is the part of the tree that plays a key role in the primary production of forests. Therefore, the leaf biomass and the leaf area index of a forest community are the most important information required to analyze the capacity for production and production processes in the forest (Tadaki 1977; Satoo and Madgwick 1982).

Several researchers have demonstrated trends in leaf biomass changes associated with the development of even-aged pure stands (Kira and Shidei 1967;

Rauner 1976; Kira 1977; Tadaki 1977; Gower et al. 1996; Ryan et al. 1997, 2004). However, these data on leaf biomass were derived by sampling several different plots rather than monitoring the same permanent plots. Furthermore, the effects of stand density on temporal trends in leaf biomass were not taken into consideration, probably because these studies did not monitor the same permanent plot. As self-thinning usually occurs as the stand develops (cf. Perry 1994; Silvertown and Charlesworth 2001; Kimmins 2004; Schulze et al. 2005), the leaf biomass in the stand may be influenced by changes in stand density. In order to clarify the effect of stand density on leaf biomass, it is necessary to monitor the same permanent plot.

According to Yoda et al. (1963), the $3/2$ power law of self-thinning for crowded but actively growing even-aged plant populations predicts that the average mass (w) and stand density (ρ) are related by the simple power equation $w = K\rho^{-\alpha}$, where $\alpha = 3/2$ and K is a population constant. This law applies once the stand reaches the maximum density. However, it is not fully understood when the $3/2$ power law is applicable during stand development. Enquist and colleagues (West et al. 1997, 1999, 2001; Enquist et al. 1998) recently argued that plants have evolved to make full use of the resources available (the WBE theory). Therefore, following their argument, the expected slope of self-thinning (α) is $4/3$ rather than $3/2$ based on their WBE theory regarding the basis of resource allocation and fractal networks of transportation systems, as summarized by Begon et al. (2006), Niklas (1994), and Pretzsch (2009). Moreover, Ogawa (2009) suggested that one of the reasons why the $3/2$ power law has been rejected on a geometric basis (Yoda et al. 1963; Hutchings 1983) is because of uncertainty regarding whether the h/D value is constant in older trees.

In the present study, we monitored the same permanent plot of hinoki cypress (*Chamaecyparis obtusa* [Sieb. et Zucc.] Endl.) seedlings for 11 years after planting. Monsi and Saeki (1953) developed the stratified clip method to determine the aboveground stand structure by dividing the photosynthetic part (leaves) and non-photosynthetic parts (stems and branches) at a given stem length interval between the canopy top and the ground surface. Based on their measurement method for tree mass, Shinozaki et al. (1964a, b) found that the stem cross-sectional area at

the crown base can be regarded as a good predictor of the leaf mass of individual trees. Therefore, this parameter was measured in the present study to determine temporal trends in leaf biomass.

During the experimental period, self-thinning occurred in the observed stand; consequently, the effect of stand density on leaf biomass during stand development was quantitatively analyzed. We propose hypothetical trends in primary productivity and biomass density with stand age, based on the results of measurements of stem cross-sectional area at the crown base and stand density. Finally, we determined when the $3/2$ power law of self-thinning is applicable in the temporal trend of leaf biomass during stand development.

Materials and methods

Study site and plant materials

Three-year-old field-run seedlings of hinoki cypress (*Chamaecyparis obtusa* [Sieb. et Zucc.] Endl.), supplied by the Midorigaoka Nursery of Gifu District Forest Office at Minokamo, Gifu Prefecture, Japan, were planted with a 1×1 m spacing on an experimental dressed soil in a field of 19×9 m in size (total seedlings planted, 190) at the Graduate School of Bioagricultural Sciences, Nagoya University, Japan, in April 1986 (Ogawa et al. 1988). The even-aged hinoki cypress stand was established on a flat area at 50 m a.s.l. ($35^{\circ}09'N$, $136^{\circ}58'E$). The mean annual air temperature was $15.7 \pm 0.2^{\circ}C$, and the annual precipitation was 1496.5 ± 90.7 mm. These data were obtained from Nagoya Meteorological Station, which is located 1.0 km from the experiment site.

Census and stem volume measurements

A monthly census was carried out on all trees in the stand for 11 years, from when the stand was 3 years old (1986) until it was 13 years old (1996). From 1986 to 1988, when the stand was at the seedling stage, measurements were made of stem diameter at the crown base. From 1989 to 1996, measurements were made of stem girth at the crown base.

For the yearly estimation of stem volume from 1986 to 1988, measurements were made of seedling height (H) and stem diameter at 10% of the seedling height ($D_{0.1H}$). Ogawa (1989) examined the allometric relationship between stem volume, v ($\text{cm}^3 \text{ tree}^{-1}$), and seedling height times the square of the stem diameter at 10% of the seedling height, $D_{0.1H}^2 H$ (mm^3), for 254 destructively sampled hinoki cypress seedlings and found a strong relationship: $v = 0.000528(D_{0.1H}^2 H)^{0.955}$ ($R^2 = 0.969$, $P < 0.001$), as shown in Fig. 1. This relationship was used to estimate the stem volume of individual trees. From 1989 to 1996, measurements were made of stem height and stem girth at 50 cm intervals, starting from the base of the stem (Yokota et al. 1994; Yokota and Hagihara 1995, 1996, 1998; Adu-Bredu and Hagihara 1996, 2003; Adu-Bredu et al. 1996a, b, 1997a, b, c). From these measurements, the stem volume was calculated using Smalian's formula (e.g., Avery and Burkhart 1994), with the tree top regarded as a cone.

Predictor of leaf mass and harvest measurement

According to the pipe model theory (Shinozaki et al. 1964a, b), the leaf mass of individual trees is proportional to the stem cross-sectional area at the crown base

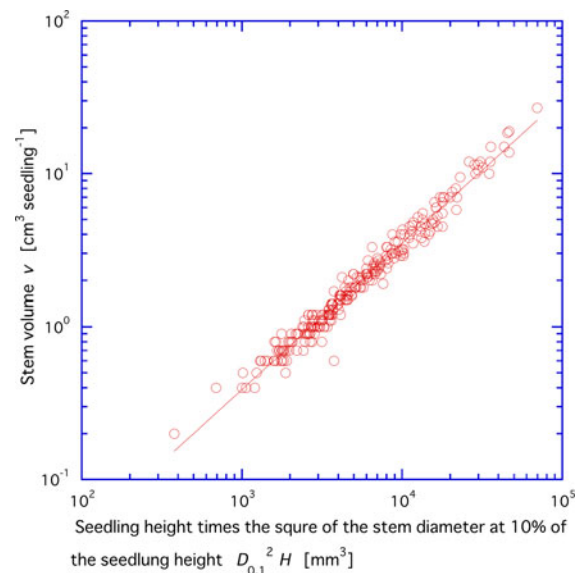


Fig. 1 Allometric relationship between stem volume (v) and seedling height times the square of the stem diameter at 10% of the seedling height $D_{0.1H}^2 H$ for 254 sampled seedlings. The regression line is given by $v = 0.000528(D_{0.1H}^2 H)^{0.955}$ ($R^2 = 0.969$, $P < 0.001$)

in any stand, regardless of its age or habitat. Since the stem cross-sectional area at the crown base can be regarded as a good predictor of the leaf mass of forest trees, we used it to determine the time course of leaf biomass changes in the present study.

In order to estimate the leaf mass and area, 14 trees were destructively sampled in 1996 (Adu-Bredu and Hagihara 1996). After measuring the stem girth at the crown base and the leaf fresh mass, leaf samples were taken to calculate the specific leaf area and the dry-to-fresh mass ratios. The leaf area was determined with an area meter (Hayashi AAC-100, Tokyo, Japan). The leaf samples were oven-dried at 85°C for 48 h and then weighed after desiccation for 24 h. These data from 1996 were combined with the data set for the 12–16-year-old hinoki cypress trees grown in the same experimental field (Hagihara et al. 1993) to analyze the allometric relationships.

Regression analysis

The coefficients in Eqs. 1 and 2 were determined by the least-squares method on log-transformed data, whereas the coefficients K , α , ρ_0 , n , and m of the non-linear equations (Eq. 3) were determined using a statistical analysis software package (KaleidaGraph version 4.02, Synergy Software, Reading, PA). Significance testing for the best-fit curvilinear equation was also performed, with the SPSS 17.0 statistical software package (SPSS, Chicago, IL).

Results

Allometric relationships between leaf mass and stem cross-sectional area at the crown base, and between leaf area and leaf mass

As shown in Fig. 2a, the allometric relationship between leaf dry mass (w_{Li}) and the stem cross-sectional area at the crown base (a_i) of individual trees is given by

$$w_{Li} = 0.0592a_i^{1.008}, \quad (1)$$

where the value of the allometric coefficient does not differ significantly from unity at the level of 1%. This indicates that leaf dry mass is proportional to stem

cross-sectional area at the crown base, consistent with the pipe model theory (Shinozaki et al. 1964a, b).

Leaf area (u_i) correlated well with w_{Li} on logarithmic coordinates (Fig. 2b). This relationship is approximated by

$$u_i = 4.640w_{Li}^{0.904}, \quad (2)$$

where the value of the allometric coefficient in Eq. 2 does not differ significantly from unity at the level of 1%, suggesting that the specific leaf area ($= u_i/w_{Li}$) is constant, irrespective of tree size.

Changes in stand density, mean stem volume, and mean stem cross-sectional area at the crown base

Since no mortality occurred at the seedling stage (3–5 years), the stand density maintained a constant level of 9796 ha⁻¹ (Fig. 3). Subsequent mortality meant that the stand density decreased annually to 7959 ha⁻¹ at the final stand age of 13 years.

The mean stem volume tended to increase exponentially with stand development (Fig. 4). However, the mean stem cross-sectional area at the crown base increased asymptotically, maintaining a more-or-less constant level after a stand age of 9 years. Therefore, according to the pipe model theory (Shinozaki et al. 1964a, b), the mean leaf mass per tree is constant after 9 years of age.

Relationship between mean stem volume and density

The relationship between the mean stem volume, v (dm³ tree⁻¹), and density, ρ (ha⁻¹), on logarithmic coordinates is shown in Fig. 5. The time trajectory of v and ρ was formulated as follows:

$$v = K\rho^{-\alpha} \left(1 - \left(\frac{\rho}{\rho_0} \right)^n \right)^m, \quad (3)$$

where K , ρ_0 , α , n , and m are coefficients (Ogawa 2005a, b). The values for K , ρ_0 , α , n , and m were calculated to be 1.0885 × 10⁷ dm³ tree⁻¹ ha⁻¹, 9815.6 ha⁻¹, 1.505, 7.308, and 1.084, respectively.

The time trajectory of v and ρ in Eq. 3 is characterized by the following three stages (Perry 1994). During the early stages of stand development, competition among the trees is insufficient to cause mortality,

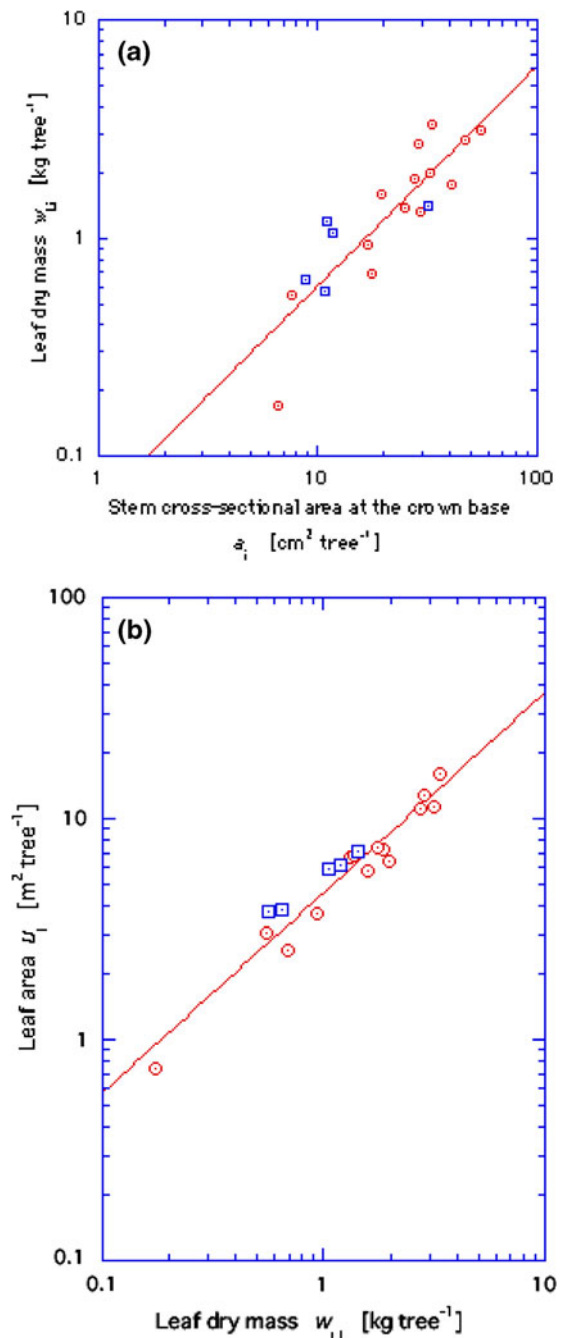


Fig. 2 **a** Allometric relationship between leaf dry mass (w_{Li}) and stem cross-sectional area at the crown base (a_i) of individual trees. *Circles* this study, *squares* Hagihara et al. (1993). The regression line is given by Eq. 1 ($R^2 = 0.71$, $P < 0.001$). **b** Allometric relationship between leaf area (u_i) and leaf dry mass (w_{Li}) of individual trees. *Circles* this study, *squares* Hagihara et al. (1993). The regression line is given by Eq. 2 ($R^2 = 0.92$, $P < 0.001$)

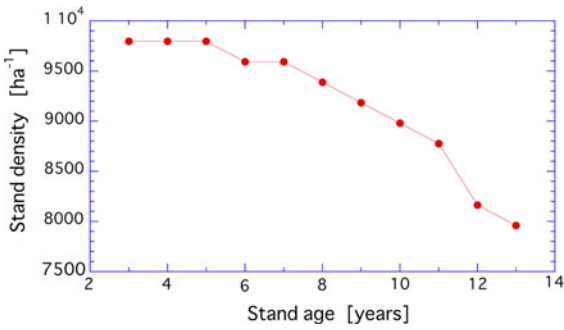


Fig. 3 Trend in stand density with stand age

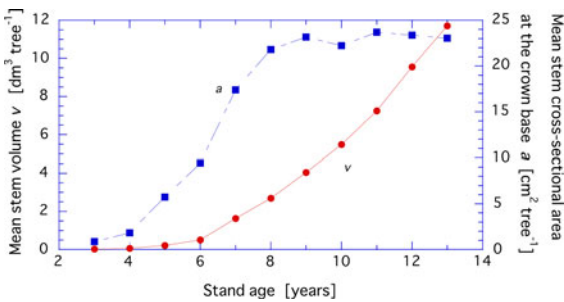


Fig. 4 Trend in mean stem volume (v ; squares) and mean stem cross-sectional area at the crown base (a ; circles) with stand age

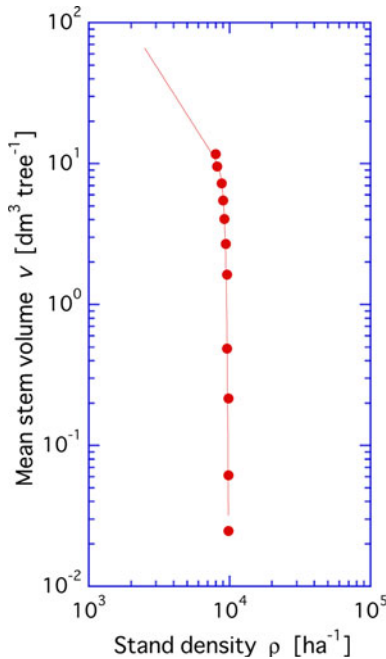


Fig. 5 Relationship between mean stem volume (v) and stand density (ρ). The time trajectory of v and ρ is given by Eq. 3 ($R^2 = 0.98$)

and the average stem volume increases with no corresponding reduction in stand density. At this stage, the time trajectory parallels the y-axis (stage 1). Eventually, the stand becomes sufficiently crowded that an increase in the average stem volume cannot occur unless some trees die. At this stage, the time trajectory begins to curve left, indicating a reduction in stand density (stage 2). Following its initial curve to the left, the time trajectory asymptotically approaches a straight line and then closely follows this line, which means that a given increase in the average stem volume is matched by a given reduction in stand density (stage 3). The v - ρ trajectory given by Eq. 3 indicates that the trajectory gradually approaches and eventually moves along the self-thinning line, described below, in the final stage of stand development:

$$v = K\rho^{-\alpha}, \tag{4}$$

where $-\alpha$ represents the slope of the self-thinning line on a $\log v$ - $\log \rho$ graph. The value of α was computed to be 1.505 in the present analysis.

Changes in stand stem cross-sectional area at the crown base

The stand stem cross-sectional area at the crown base (A) is defined as the product of the mean stem cross-sectional area at the crown base (a) and the stand density (ρ), as follows:

$$A \equiv a\rho. \tag{5}$$

Figure 6 shows seasonal changes in the stand stem cross-sectional area at the crown base over the whole experimental period. During the period up to 1990, the seasonal changes consisted of a series of asymptotic growth curves, whereas during the period after 1991, the seasonal changes showed an oscillatory trend.

As shown in Fig. 7, the stand stem cross-sectional area at the crown base was related to age. From 3 to 5 years of age, the stem cross-sectional area at the crown base increased slightly; it then increased rapidly until 8 years of age before increasing slightly to a peak at 9 years of age; thereafter, it decreased slightly. As a is constant after the age of 9 years (Fig. 4), A peaked at the age of 9 years because of the continuous reduction in the stand density (ρ) (Fig. 3). Based on changes in the stand stem cross-sectional

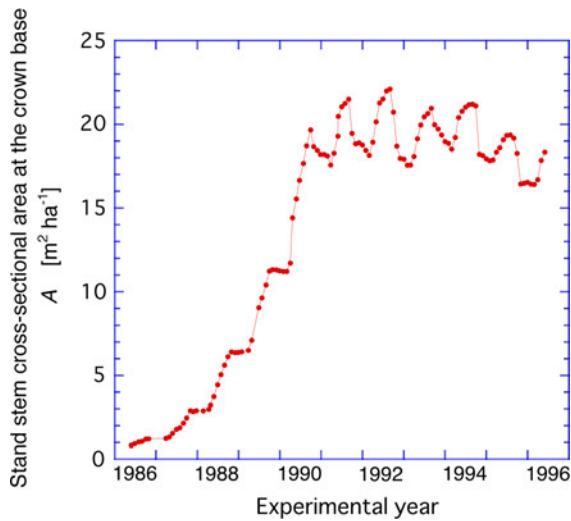


Fig. 6 Seasonal changes in the stand stem cross-sectional area at the crown base (A) over the whole experimental period of 1986–1996

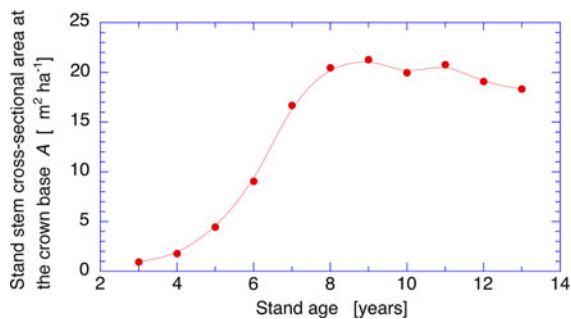


Fig. 7 Trend in stand stem cross-sectional area at the crown base (A) with stand age

area at the crown base with stand age, the leaf biomass per unit land area is considered to peak at the age of 9 years.

Relationship between stand stem cross-sectional area at the crown base and stand density

As the stand density changes with stand age (Fig. 3), the relationship between stand stem cross-sectional area at the crown base and stand density showed an optimum curve in which the optimum density was around 9200 ha^{-1} (Fig. 8). Before the optimum density is reached, the gradient of the relationship is steep because there is little mortality and rapid leaf growth. In contrast, after the optimum density is

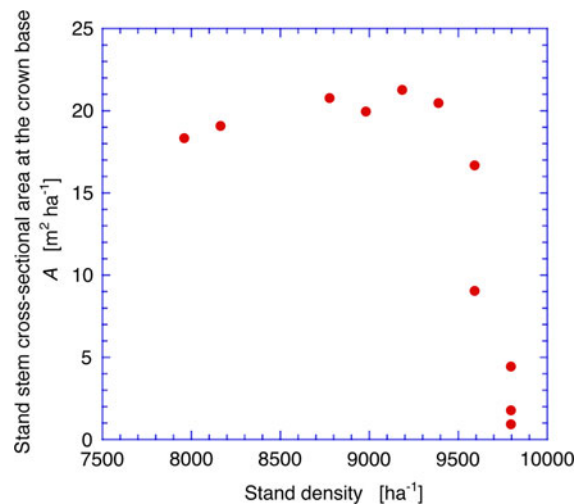


Fig. 8 Relationship between stand stem cross-sectional area at the crown base (A) and stand density

reached, the gradient is gentle. Hozumi and Shinozaki (1960) reported a gradual reduction in leaf biomass with decreasing stand density in young Japanese red pine (*Pinus densiflora*; data provided by Satoo et al. 1955).

Maximum leaf biomass and leaf area index

Based on the allometric relationships described in Eqs. 1 and 2, the maximum leaf biomass and leaf area index at the age of 9 years were estimated to be 12.93 Mg ha^{-1} and 5.73 ha ha^{-1} , respectively. According to Tadaki (1977), the leaf biomass and leaf area index of 26 hinoki cypress plantations were approximately 14 ± 2.5 (mean \pm SD) Mg ha^{-1} and $5\text{--}7 \text{ ha ha}^{-1}$, respectively. Therefore, the present estimates of leaf biomass and leaf area index are within the approximate ranges of published results for hinoki cypress plantations.

Discussion

Seasonal patterns of stand stem cross-sectional area at the crown base

We recognized two patterns of seasonal fluctuations in the stand stem cross-sectional area at the crown base (Fig. 6). The first pattern is related solely to stem growth in the forest gaps before canopy closure,

whereas the second pattern is related to both stem growth and branch pruning when there are no gaps after full canopy closure. In the second pattern, the stand stem cross-sectional area at the crown base decreases with branch pruning during autumn and winter every year, although it increases with stem growth during spring and summer. Considering the two different growth patterns, we deduce that growth conditions (e.g., the light environment) are different before and after canopy closure.

Reasonability of estimates of leaf biomass and leaf area index

Möller (1946) first reported that the leaf area index in closed forest canopies of the same species is only slightly influenced by factors such as site quality, stand age, tree height, stand density, and degree of thinning. Tadaki (1977) summarized the extensive available data on leaf biomass and the leaf area index for Japanese forests, and noted that leaf biomass tends to have similar values not only in forests composed of related species but also within a group of forests dominated by the same life form species. Therefore, the leaf biomass and leaf area index of the dense stand of hinoki cypress investigated in our study, which reached maximum values in the early stage of stand development, are equivalent to the estimates previously reported for other hinoki cypress stands (see Tadaki 1977).

Hypothetical trends in leaf biomass, surface area, and primary productivity

To date, two different trends have been reported for leaf biomass and leaf area index with stand development: in one trend, the biomass increases and is then maintained at a more-or-less constant level (Kira and Shidei 1967; Tadaki 1977), whereas in the other trend, the leaf area index increases and then decreases with stand development (Rauner 1976; Ryan et al. 1997). In the present study, we predicted that the stand density would continue to decrease after the study period because of self-thinning (Fig. 9a). As self-thinning occurs, unoccupied space is produced. Therefore, the survivors can extend more branches and develop more leaves, meaning that the mean leaf mass per tree increases with stand development after it has started to maintain a constant level (Fig. 9b).

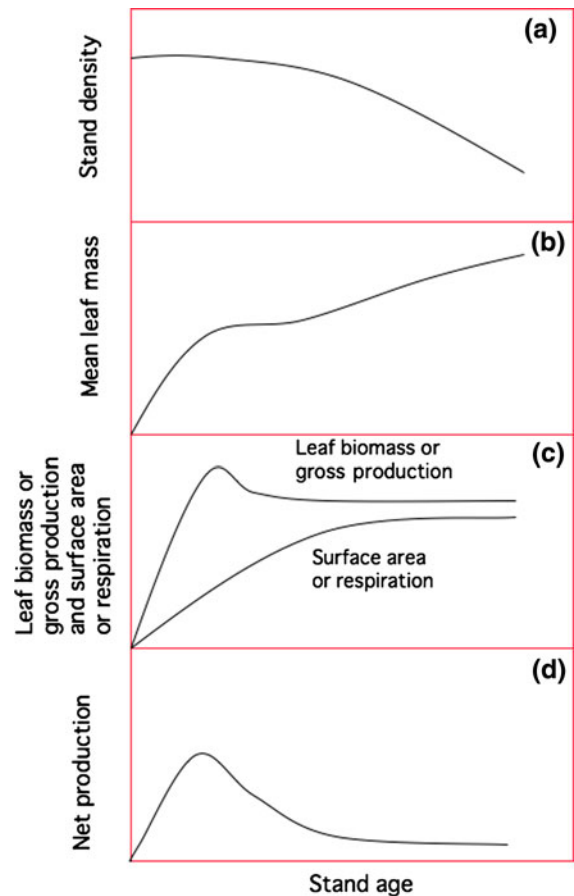


Fig. 9 Hypothetical trends in stand density (a), mean leaf mass of individual trees (b), and leaf biomass or gross production rate and surface area or respiration rate (c), and net production rate (d) with stand age

Considering this increase in the mean leaf mass per tree, it is reasonable to hypothesize that the leaf biomass per unit land area will remain more-or-less constant in the present stand (Fig. 9c).

Since plant weight (w) and volume (v) are isometrically related as $w \propto v$ (White 1981), w may be substituted in Eq. 4; i.e., $w \propto \rho^{-\alpha}$. As the self-thinning exponent α is close to $3/2$ in the present study, the tree surface area (s) is given as $s \propto w^{2/3} \propto \rho^{-1}$, suggesting that the stand surface area of trees ($= s\rho$) is constant under the $3/2$ power law of self-thinning. Therefore, the stand surface area increases with stand development and then remains more-or-less constant after canopy closure (Fig. 9c). Reich et al. (2006) also reported that the individual respiration rate (r) is related to plant weight as $r \propto w^{3/4}$, and Enquist and

colleagues (West et al. 1997, 1999, 2001; Enquist et al. 1998) argued that the self-thinning slope (α) is 4/3 rather than 3/2. Therefore, the individual respiration rate can be expressed as $r = \psi K \rho^{-1}$, and the stand respiration rate becomes constant ($= \psi K$). In fact, Oohata and Shidei (1974) and Ogawa et al. (1985) provided experimental evidence that the stand respiration rate is more-or-less constant after canopy closure (Fig. 9c).

If we assume that photosynthetic activity is constant, irrespective of the stage of stand development, the temporal trend in the gross production rate of the stand is the same as the trend in leaf biomass during stand development (Fig. 9c). Kira and Shidei (1967) proposed a hypothetical trend in which the leaf biomass and gross production rate tend to culminate with closure of the canopy. Culmination of the leaf biomass and the gross production rate may be characteristic of the pole stage of stand development. The relationship between the stand stem cross-sectional area at the crown base and stand density (Fig. 8) indicates that the leaf biomass and gross production rate have an optimum density, which is around 9200 ha⁻¹, in the present stand. Based on their first approximation model of canopy photosynthesis, Monsi and Saeki (1953) showed that pure stands of a plant species, which have specific values for the light extinction coefficient and the efficiency of light interception by their leaves, have an optimum leaf area index that assures the maximum rate of surplus photosynthesis in the canopy. Therefore, it is not unreasonable to consider the existence of an upper limit of leaf biomass for forests of a given species or a group of ecologically similar species (Tadaki 1977, Satoo and Madgwick 1982).

Conversely, the temporal trend in the stand respiration rate with stand age is the same as that for the stand surface area (Fig. 9c), because the respiration rates of trees are proportional to their surface areas (Ninomiya and Hozumi 1981). Oohata and Shidei (1974) and Ogawa et al. (1985) reported that the stand respiration rate remains constant after closure of the forest canopy, based on the assumption that the surface area of woody organs reaches a constant level. The net production rate, which is defined as the difference between the gross production rate and the stand respiration rate, is constant in the later stages of stand development,

when the 3/2 power law of self-thinning is realized (Fig. 9d).

The 3/2 power law of self-thinning and biomass density

As the self-thinning exponent α in Eq. 3 or 4 was close to 3/2, the present study provides experimental evidence supporting the 3/2 power law of self-thinning (Yoda et al. 1963). However, judging from the v - ρ trajectory shown in Fig. 5, the 3/2 power law of self-thinning would be realized after a certain period of time after canopy closure in the present stand. Xue et al. (1997) reported a similar tendency for the 3/2 power law of self-thinning in a stand of *Larix principis-rupprechtii* Mayr.

According to Lonsdale and Watkinson (1983) and Weller (1987), the biomass density (mass per unit occupied space) has an important influence on the slope of the self-thinning line. However, few reports of biomass density are based on experimental data (e.g., Lonsdale and Watkinson 1983; Weller 1989; Xue et al. 1998). During the present study period, a hypothetical trend in biomass density with stand development could be determined based on the results for stand density (Fig. 3) and stem cross-sectional area at the crown base (Figs. 4, 7). After planting, the biomass density increases with shoot expansion and then decreases with a reduction in stand density and a constant mean cross-sectional area at the crown base near the pole stage of stand development. The decrease in leaf biomass density is considered to reduce the self-shading of leaves, which is closely related to the high gross production of the stand near the pole stage.

In conclusion, the leaf stand biomass of the present material showed a peak and was assumed to be constant at the later stage of stand development, where 3/2 power laws of self-thinning held. When 3/2 or 4/3 power law of self-thinning held, stand respiration was considered to be constant. The present study inferred the time trend of the primary production from the leaf biomass change and self-thinning law.

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