ORIGINAL ARTICLE

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Density effects on organs in self-thinning *Pinus densiflora* Sieb. et Zucc. stands

Abstract Although much research on the density effect in nonself-thinning populations has been conducted, there has been very little research on density effects in self-thinning populations. Furthermore, the density effect of plant organs in self-thinning populations is little reported. The present study analyzed the yield–density (Y–D) effects on organs, such as stem, branch and leaf, together with that on stands of self-thinning *Pinus densiflora* Sieb. et Zucc.. The stand yield- and organ Y–D effects were well described by reciprocal and parabolic equations, respectively, throughout the experiment. The value of coefficient B in the reciprocal equation decreased monotonically with increasing stand age and became significantly closer to zero at the end of experiment (33-year-old stand), indicating that the constant final stand yield was established regardless of the density realized. The value of the relative growth coefficient h in the allometric equation between mean organ weight and mean aboveground weight was significantly smaller than 1.0 for stem, indicating that stem yield increases monotonically with increasing realized density. The h-value was significantly larger than 1.0 for branch throughout the experiment, and for leaf except at 33 years old, indicating that optimum densities exist. The h-value for leaf was not significantly different from 1.0 at 33 years old, indicating that the leaf yield reached a constant level regardless of realized density. The constant final leaf yield was established at almost the same growth stage as the establishment of constant final stand yield.

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Introduction

As plants in a population develop, plant growth becomes limited by the rate of available resources, so that competition among plants occurs. During the early growth stage, such competition causes a decrease in mean plant weight with increasing density without mortality. However, as plants grow larger, density-dependent mortality begins, and an increase in mean plant weight is accompanied by a decrease in density. The phenomenon that mean plant weight decreases [competition–density (C–D) effect], whereas yield (mean plant weight times density) increases with increasing density [yield–density (Y–D) effect] is called the density effect (Kira et al. 1953).

Although some mathematical models have been proposed to describe the density effect (e.g. Shinozaki and Kira 1956; Bleasdale and Nelder 1960; Nelder 1962; Bleasdale 1967; Farazdaghi and Harris 1968; Watkinson 1980, 1984; Vandermeer 1984), the reciprocal equations of the C–D effect and Y–D effect proposed by Shinozaki and Kira (1956) are widely used. These reciprocal equations are based on the logistic theory of plant growth and explain the density effect fairly well over a wide range of density. Since the reciprocal equations were derived for nonself-thinning populations, Hagihara (1999) reconstructed a new model to describe the density effect in self-thinning populations in line with the Shinozaki–Kira theory. Hagihara's model was confirmed as being applicable to the density effect in self-thinning populations (Xue and Hagihara 1998, 1999, 2002; Stankova and Shibuya 2003).

The Y–D effect, especially the Y–D effects on organs, is more important than the C–D effect from both theoretical and practical viewpoints. For some herbaceous plants, the relationships between yields of plant organs and density have been reported (e.g. Bleasdale and Nelder 1960; Bleasdale 1967; Watkinson 1984).

Concerning woody species, little is known about the relationships between the yields of organs and density.

The present study employs data collected by Ando (1962) and Tadaki et al. (1979) in self-thinning *Pinus densiflora* Sieb. et Zucc. stands with different densities. The aims of this study were to examine (1) whether the Y–D effect of the stand can be explained by the reciprocal equation of the Y–D effect in self-thinning populations; (2) whether the Y–D effects on organs, such as stem, branch and leaf, can be explained by the parabolic equation derived from the reciprocal equation of the C–D effect in self-thinning populations and the allometric relationship of mean organ weight to mean aboveground weight; and (3) the difference in the Y–D effect among organs.
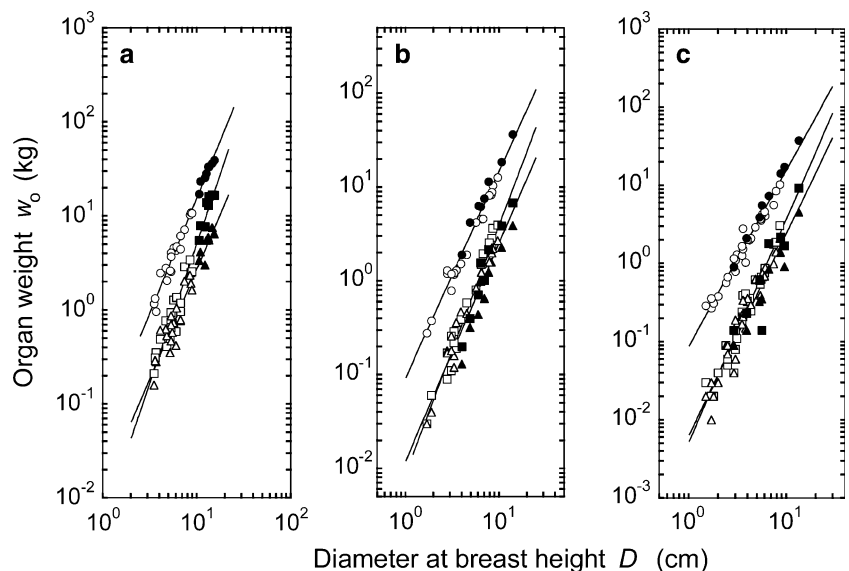
Materials and methods

Data source

Ando (1962) established three 0.01 ha plots with different densities in naturally regenerated 9-year-old stands of *Pinus densiflora* Sieb. et Zucc. When the stands were 14 years old, 20 sample trees for low- and middle-density stands, and 30 sample trees for a high-density stand were felled (Ando et al. 1962). When the stands were 33 years old, eight sample trees for each density stand were felled (Tadaki et al. 1979). The weight of organs, such as stem, branch and leaf, was measured for each sample tree.

Establishment of allometric relationships between organ weight and stem diameter at breast height

The following simple allometric equation for weight, w_o, of an organ, such as stem, branch or leaf, to stem diameter at breast height (DBH), D, was examined for each of the different density stands:

$$w_o = aD^b, \tag{1}$$

where a and b are coefficients specific to 14- or 33-year-old stands. First, it was confirmed that there were no significant differences (F-test) in error variance between the curvilinear regression lines of Eq. 1 for 14- and 33-year-old stands in each organ ($0.11 < P < 0.79$). Second, it was confirmed that the b-values of the respective curvilinear regression lines for 14- and 33-year-old stands were not significantly different (t-test) in each organ ($0.34 < P < 0.89$). Finally, it was confirmed that the a-values did not show significant differences (t-test) in each organ between 14- and 33-year-old stands ($0.12 < P < 0.94$) on the assumption that the b-value is the same between the two curvilinear regression lines. As a result, 14- and 33-year-old data could be lumped together for establishing the allometric relationship of Eq. 1 for each organ of each density, as shown in Fig. 1.

Estimate of mean organ weight

On the basis of the DBHs of all individuals recorded at 2-year intervals from 14 to 30 years old and at the age of 33 years (Tadaki et al. 1979), mean organ weight, w_x, was calculated using the allometric relationships established for different organs in different density stands (Fig. 1). Mean aboveground weight, w, was defined as the sum of the mean weights of organs.

Results

Allometric relationship between mean organ weight and mean aboveground weight

As shown in Fig. 2, the allometric relationship between mean organ weight, w_x, and mean aboveground weight, w, followed the equation (Kira et al. 1956):
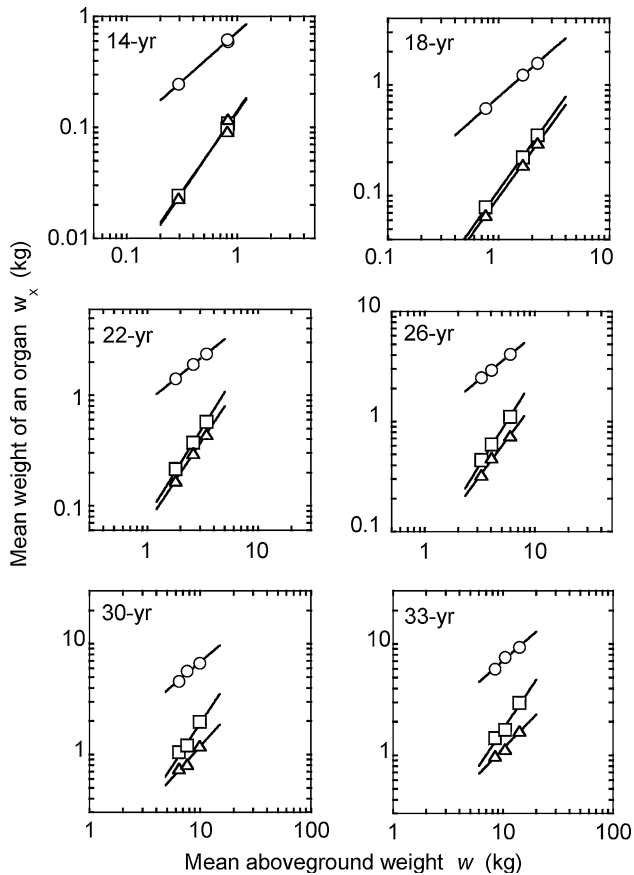

Fig. 1a–c Allometric relationships between organ weight, w_o, and diameter at breast height, D. The *straight lines* are based on Eq. 1. **a** Low-density stand ($R^2 = 0.98$ for stem, $R^2 = 0.95$ for branch, $R^2 = 0.94$ for leaf); **b** middle-density stand ($R^2 = 0.96$ for stem, $R^2 = 0.85$ for branch, $R^2 = 0.82$ for leaf); **c** high-density stand ($R^2 = 0.96$ for stem, $R^2 = 0.85$ for branch, $R^2 = 0.82$ for leaf). *Open circles* 14-year-old stem, *filled circles* 33-year-old stem, *open squares* 14-year-old branch, *filled squares* 33-year-old branch; *open triangles* 14-year-old leaf, *filled triangles* 33-year-old leaf

Fig. 2 Relationships of mean stem weight, w_S, branch weight, w_B, and leaf weight, w_L to mean aboveground weight, w. The *straight lines* were based on Eq. 2. *Circles* Stem ($R^2 > 0.97$); *squares* branch ($R^2 > 0.93$); *triangles* leaf ($R^2 > 0.94$)

$$w_x = gw^h, \tag{2}$$

where g and h are a coefficient and the relative growth coefficient specific to organs, respectively. As shown in Fig. 3, the value of h for stem was significantly less than 1.0 ($P < 0.031$), and showed an almost constant trend throughout the experiment ($P > 0.39$), ranging from 0.791 to 0.883. The h-value for branch was significantly larger than 1.0 ($P < 0.037$) and kept a more or less steady trend ($P > 0.16$) throughout the experiment between 1.41 and 1.66. The h-value for leaf was significantly larger than 1.0 ($P < 0.023$) except for 33-year-old stand, and the h-values ranged from 1.39 to 1.51 without showing a significant difference ($P > 0.93$) within the first half of the experiment and then decreased from 1.51 at the middle, reaching a significantly smaller value of 1.02 ($t = 3.44$, $P = 0.038$) at the end of experiment.

Density effect of self-thinning stands

Hagihara ([1999](#)) developed the reciprocal equation of the competition–density (C–D) effect in self-thinning stands on the basis of the logistic theory of the C–D
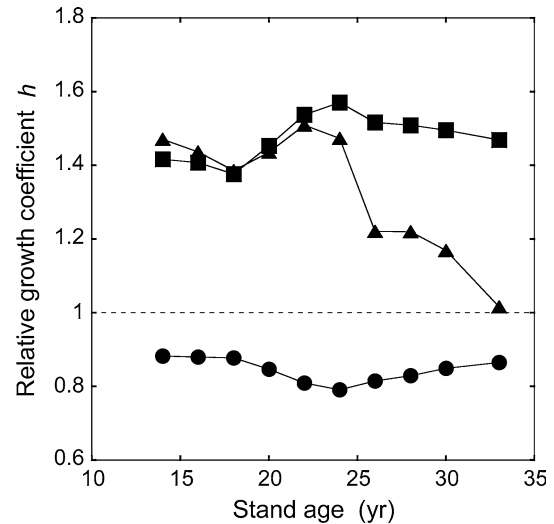

Fig. 3 Time trends of relative growth coefficient h in Eq. 2. *Circles* stem; *squares* branch; *triangles* leaf. The h-value for leaf at 33 years old was not significantly different from 1.0 ($t = 0.26$, $P = 0.42$)

effect in nonself-thinning populations (Shinozaki and Kira [1956](#)) as follows:

$$\frac{1}{w} = A_t\rho + B, \tag{3}$$

where w is the mean tree weight and ρ is the realized density, and A_t and B are coefficients specific to growth stages. It was confirmed that Eq. 3 well explained the C–D effect in stands of *Pinus densiflora* Sieb. et Zucc. (Xue and Hagihara [1998](#), [1999](#)), *Pinus massoniana* Lamb. (Xue and Hagihara [2002](#)), *Etula platyphylla* Sukatchev var. *japonica* Hara and *B. ermanii* Cham. (Stankova and Shibuya [2003](#)).

From Eq. 3, yield per area y, which is the product of w and realized density ρ, can be expressed as the reciprocal equation of the yield–density (Y–D) effect in self-thinning stands,

$$\frac{1}{y} = A_t + \frac{B}{\rho}. \tag{4}$$

The relationship between stand yield y and realized density ρ is shown in Fig. 4. Stand yield y (aboveground biomass) increased with increasing realized density ρ. The y–ρ relationships fitted well for all growth stages using the reciprocal equation of the Y–D effect given by Eq. 4. The stand Y–D curve on log–log coordinates shifted upward and leftward with increasing stand age. As shown in Fig. 5, the value of A_t decreased gradually from 0.0250 ha Mg^{-1} at 14 years old to 0.0119 ha Mg^{-1} at 33 years old, and the value of B decreased from 649 Mg^{-1} at 14 years old to 0.100 Mg^{-1} at 33 years old. When the stands were 14 years old, the number of trees in low-density stand was about 30% and 9%, respectively, of those of middle- and high-density stands, which resulted in low yield in low-density stand, though mean aboveground weight was greater in the low-den-
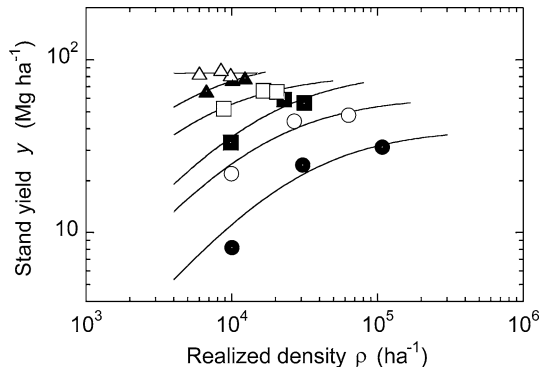
Fig. 4 Yield–density (Y–D) effect between stand yield y and realized density ρ. The data were fitted using Eq. 4. *Filled circles* 14-year-old ($R^2 = 0.94$), *open circles* 18-year-old ($R^2 = 0.92$), *filled squares* 22-year-old ($R^2 = 0.88$), *open squares* 26-year-old ($R^2 = 0.92$), *filled triangles* 30-year-old ($R^2 = 0.97$), *open triangles* 33-year-old
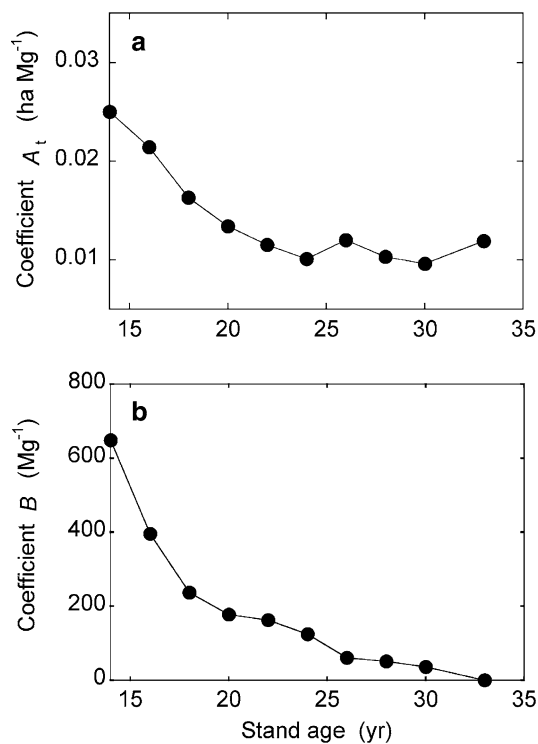

Fig. 5a,b Time trends of coefficients A_t and B in the reciprocal equation of the Y–D effect given by Eq. 4. **a** Coefficient A_t, **b** coefficient B. The value of B at 33 years old was not significantly different from zero ($t = 0.03$, $P = 0.98$)

sity stand than in middle- and high-density stands. Differences in stand yield among three different density stands decreased with increasing stand age, and the stand yield finally became constant irrespective of realized density at 33 years old.

The value of coefficient B in Eq. 4 decreased monotonically with increasing stand age (Fig. 5b) and became closer to zero at 33 years old ($t = 0.029$, $P = 0.98$). As the B-value approaches to zero, Eq. 4 can be written in the form:

$$Y = y|_{B \to 0} = \frac{1}{A_t}. \tag{5}$$

Therefore, final stand yield Y reaches a constant with a value of $1/A_t$ irrespective of realized density ρ. Figure 4 shows that the law of constant final yield (Kira et al. 1953; Hozumi et al. 1956) was established in *P. densiflora* stands.

Yield–density effect with respect to organs

Yield of an organ per area y_x, which is the product of mean organ weight w_x and realized density ρ, is derived as follows by considering Eqs. 2 and 3 (cf. Hozumi and Shinozaki 1960):

$$y_x = \frac{g\rho}{(A_t\rho + B)^h}. \tag{6}$$

When $h = 1$, Eq. 6 is synonymous with the reciprocal equation of Eq. 4. When $h < 1$, organ yield y_x increases monotonically with increasing realized density ρ, whereas when $h > 1$, y_x has its maximum at optimum realized density ρ_{opt} (Bleasdale and Thompson 1966; Hozumi 1973).

Figure 6a shows the relationship between stem yield, y_S, and realized density, ρ. The stem yield increased monotonically with increasing realized density, because the value of h was less than 1.0 (Fig. 3). The difference in stem yield among different density stands decreased with increasing stand age. The y_S–ρ relationships were well fitted by Eq. 6 throughout the experiment.

The parabolic relationship between branch yield, y_B, and realized density, ρ, is shown in Fig. 6b. This figure indicates that an optimum density exists at each growth stage except at 33 years old. The y_B–ρ curve given by Eq. 6, where the value of h was larger than 1.0 (Fig. 3), well explained the data, and the curve moved upwards and leftwards on log–log coordinates with the passage of time.

As shown in Fig. 6c, a parabolic relationship also exists between leaf yield, y_L, and realized density, ρ, where the h-value was larger than 1.0. The y_L–ρ relationship could be well described by Eq. 6. The time trend of the y_L–ρ relationship was almost the same as that of the y_B–ρ relationship (Fig. 6b).

Time trends of optimum density and maximum yield

By differentiating both sides of Eq. 6 with realized density, ρ, the optimum density, ρ_{opt}, of an organ in self-thinning stands can be obtained as follows (cf. Hozumi 1973):

$$\rho_{opt} = \frac{B}{A_t(h - 1)} \quad (h > 1). \tag{7}$$

The value of the relative growth coefficient h in Eq. 2 was less than 1.0 for mean stem weight, w_S, whereas the
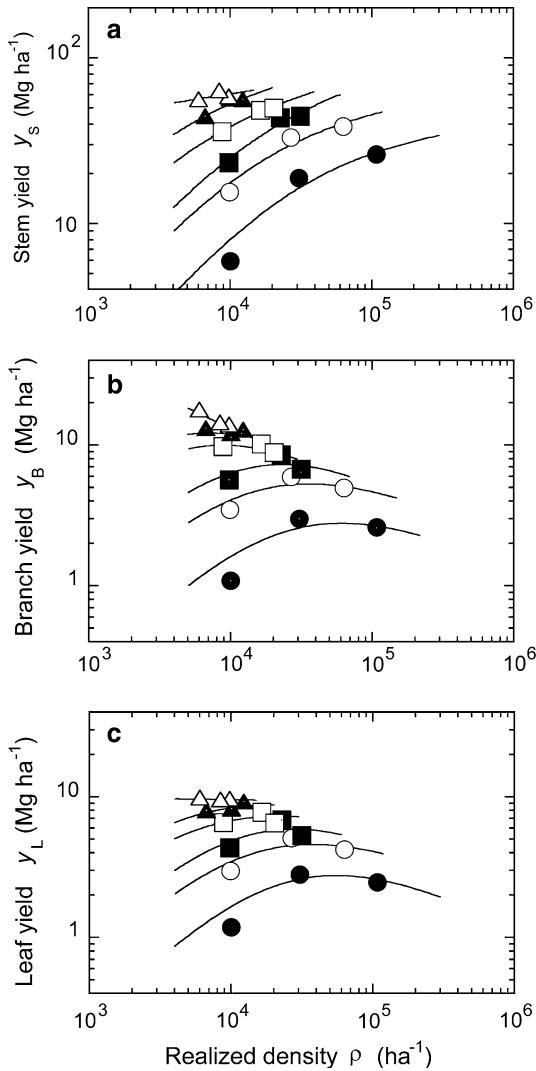
Fig. 6a–c Y–D effects between organ yield, y_x, and realized density ρ. **a** Stem, **b** branch, **c** leaf. The curves show Eq. 6, where the g- and h-value, and the A_t- and B-value are estimates, respectively, obtained in Eqs. 2 and 4. *Filled circles* 14-year-old ($R^2 = 0.98$ for stem, $R^2 = 0.86$ for branch, $R^2 = 0.90$ for leaf); *open circles*, 18-year-old ($R^2 = 0.98$ for stem, $R^2 = 0.85$ for branch, $R^2 = 0.88$ for leaf); *filled squares*, 22-year-old ($R^2 = 0.99$ for stem, $R^2 = 0.71$ for branch, $R^2 = 0.81$ for leaf); *open squares*, 26-year-old ($R^2 = 0.99$ for stem, $R^2 = 0.71$ for branch, $R^2 = 0.72$ for leaf); *filled triangles*, 30-year-old ($R^2 = 0.71$ for stem, $R^2 = 0.58$ for branch, $R^2 = 0.90$ for leaf); *open triangles*, 33-year-old ($R^2 = 0.98$ for stem, $R^2 = 0.93$ for branch)
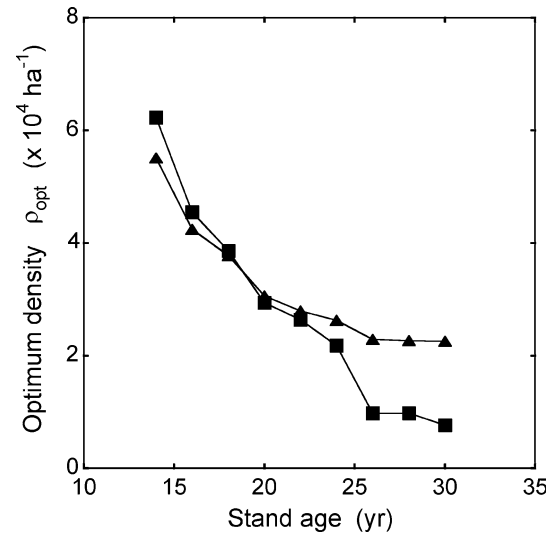

Fig. 7 Changes in optimum density, ρ_{opt}, for branch and leaf yields with stand development. *Squares* branch, *triangles* leaf. Optimum density, ρ_{opt}, was calculated from Eq. 7, using the h-value obtained from Eq. 2 and the A_t- and B-value obtained in Eq. 4
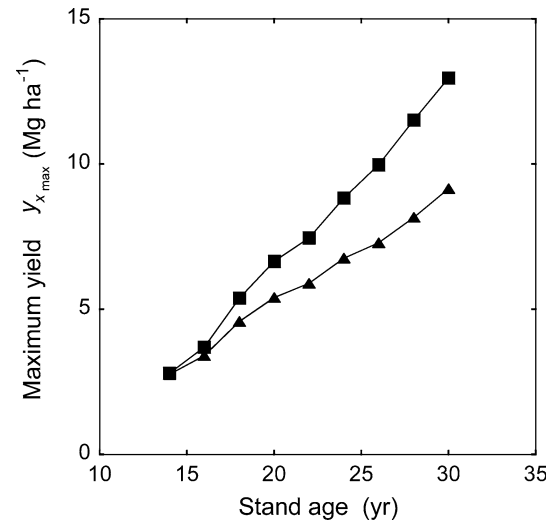

Fig. 8 Changes in maximum yield $y_{x_{max}}$ for branch and leaf with stand development. *Squares* branch, *triangles* leaf. Maximum yield $y_{x_{max}}$ was calculated from Eq. 8, using the values of g and h obtained in Eq. 2 and of A_t and B obtained from Eq. 4

value was larger than 1.0 for mean branch weight, w_B, and for mean leaf weight, w_L, except for the 33-year-old stand (Fig. 3). Therefore, from Eq. 7, optimum densities exist for branch and leaf yields.

Figure 7 depicts the time trends of optimum densities for branch and leaf yields calculated by Eq. 7. The optimum density was 60,607 ha^{-1} for branch and 55,111 ha^{-1} for leaf at 14 years old, and decreased gradually to 7,694 ha^{-1} for branch and 22,559 ha^{-1} for leaf at 30 years old. The optimum density for branch was greater than that for leaf from 14 to 18 years old,

with the former became smaller than the latter thereafter.

Inserting Eq. 7 into Eq. 6, maximum yield $y_{x_{max}}$ of an organ is given by the following equation (cf. Hozumi 1973):

$$ y_{x_{max}} = \frac{g}{A_t h}\left(\frac{h-1}{Bh}\right)^{h-1} \quad (h > 1). \tag{8} $$

As shown in Fig. 8, the maximum yield was 2.81 Mg ha^{-1} for branch and 2.76 Mg ha^{-1} for leaf at 14 years old and increased gradually to 13.0 Mg ha^{-1} for branch

and 9.16 Mg ha^{-1} for leaf at 30 years old. The difference between maximum yields of branch and leaf became larger with increasing stand age.

Discussion

Stand yield- and organ yield-realized density relationships were described well by Eqs. 4 and 6, respectively, at each growth stage (Figs. 3, 6), indicating that the analysis of the Y–D effect based on the two equations is useful.

The existence of optimum density for the leaf yield may be ascribed to leaf shading at the bottom of a canopy in high-density stands of *P. densiflora* having a shade-intolerant nature. As stands grow, however, the leaf yield reached a constant level regardless of realized density. Hozumi et al. (1962) pointed out that leaf yield is several times more strongly inhibited by increasing density than stand yield. As a result, the ceiling of leaf yield is observed to proceed towards that of stand yield. It seems that our results support their conclusion (cf. Figs. 4, 6c). However, our results make it clear that an optimum density for leaf yield before its actual ceiling exists.

The branch yield was also maximized at a certain density. However, the density that maximizes the branch yield appeared throughout the experiment—a different trend from the case of leaf yield. With increasing stand density, the number of lateral branches gradually decreases and their length becomes shorter. Weiner et al. (1990) and Weiner and Fishman (1994) pointed out that branches are fewer in highly crowded stands than in low-density stands. Therefore, an optimum density for the branch yield may exist.

In case of the stem yield, no particular density maximizing stem yield existed throughout the experiment. Begonia et al. (1988) and Jobidon (2000) suggested that competing vegetation induces a shift in carbon allocation from branch to stem, probably resulting from hormonal inhibition of lateral bud development. In a study on Scots pine trees, Nilsson and Albrektson (1993) found that the allocation of carbon to stem has high priority for trees under high competitive stress. Therefore, the stem yield probably increased monotonically with increasing realized density.

It is apparent from Fig. 5 that the value of coefficient B in Eq. 4 tended to be zero with the passage of time. As a result, Eq. 6 takes the form (cf. Hozumi 1973):

$$Y_x = y_x|_{B \to 0} = \frac{g}{A_t^h} \rho^{1-h}. \qquad (9)$$

When the value of relative growth coefficient h is smaller than 1.0, final organ yield Y_x increases with increasing realized density, ρ, which corresponds to the final stem yield (Fig. 6a). When the h-value is larger than 1.0, Y_x decreases with increasing realized density, which corresponds to final branch yield (Fig. 6b). When the h-value is equal to 1.0, Y_x reaches a constant with a value of g/A_t,

which corresponds to final leaf yield (Fig. 6c), where the h-value was not significantly different from 1.0 ($t = 0.102$, $P = 0.42$) (Fig. 3). Therefore, it is concluded that the density effect on organ yield differs among stem, branch and leaf.

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