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Density effects on the growth of self-thinning *Eucalyptus urophylla* stands

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Abstract Density effects on the growth of self-thinning *Eucalyptus urophylla* stands were examined for 7 years. Tree height and stem diameter at breast height were measured during the experimental period. Stems, branches, leaves, bark and roots of 45 *E. urophylla* trees were sampled in three different density stands in order to establish their biomass equations. Change trends of the biological time τ and density ρ were described used corresponding equations. The stem weight ratio increased and leaf weight ratio decreased, whereas those of branch, bark and root were relatively steady from 2 years after the planting. The competition-density (C-D) effect equation of mean organ weight w_o was derived by combining the allometric power relationship between mean tree weight w and w_o with the C-D effect equation of self-thinning stands. The equations of the C-D effect for w and ρ and for w_o and ρ were used to describe the C-D effects in tree and organs during course of self-thinning, respectively, and showed a good fit to the data. Leaf biomass of different density stands reached a more or less constant level with time elapse. High density produced the greatest biomass and stem biomass, so that it is the best choice in silvicultural practice.

Keywords Allometric relationship · C-D effect · *Eucalyptus urophylla* · Tree organ · Self-thinning

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Introduction

Competition among individual plants occurs as plants in a stand grow larger (Xue et al. 2010). Numerous studies have focused on plant competition (e.g. Fetene 2003; Hunt et al. 2006; Berger et al. 2008; Manning et al. 2009), because it is a key process affecting plant populations and communities (Berger et al. 2008). Competition-density (C-D) is an effect explaining the common finding that average plant size decreases when stand density increases. The relationship between plant weight and density is the reciprocal of the C-D effect (Shinozaki and Kira 1956), which can be examined by equations developed by authors such as Watkinson (1980, 1984) and Vandermeer (1984). This relationship is known as the logistic theory of the C-D effect and was initially developed for non-self-thinning stands (Stankova and Shibuya 2003).

Self-thinning or density-dependent mortality begins when competition becomes more severe. This can result in increases in mean plant size and a decrease in plant density. The logistic theory of the C-D effect can be applied to self-thinning stands, but there would be a theoretical limit in reconciling the C-D effect (Minowa 1982; Naito 1992). Hagihara (1999) constructed a model for describing the C-D effect in self-thinning stands in line with the logistic theory of the C-D effect, which predicts the C-D effect in stands of *Pinus densiflora* and *Pinus massoniana* (Xue and Hagihara 1998, 2002).

Quantifying the amount and distribution of biomass is important in understanding the structure and function of the ecosystem (Grove and Malajczuk 1985). Understanding the relationship between plant density and weight of particular tree organs (stem, branches, leaves, bark and roots) at all stages of tree growth would help to estimate biomass production and quantify stand development patterns over time. In most studies on C-D effect, only stem volume or tree weight has been measured (e.g. Xue and Hagihara 1998, 2002; Stankova and Shibuya 2003), little is known about the C-D effect on individual tree organs. Although Xue and Hagihara (2008) demonstrated the relationship between organ biomass and stand density in *P. densiflora* stands, their results were not related to root biomass. Since competition alters the biomass allocation patterns of tree organs (Xue et al. 2010), and the mechanisms of competition differ between the above- and below-ground parts of plants (Weiner 1990), it is important to examine the competitive effects on tree organs separately. Organ biomass can be estimated using standard forest inventory data and allometric relationships (e.g. Montagu et al. 2005; Xue and Hagihara 2008), although root weight is difficult and more expensive to obtain compared with above-ground components.

The increasing demand for wood has meant that plantations of fast-growing exotic trees have become an increasingly important source of wood products in China. *Eucalyptus urophylla* is a fast-growing species and good paper pulp as well as board species. This species originates in Indonesia and was introduced to China in the 1960s (Yang and Zhong 1997). It is one of the major silvicultural tree species planted for wood in South China. However, the C-D effect on *E. urophylla* tree organs has not been analyzed. Such information would help to estimate organ biomass production and quantify stand development patterns over time.

In this study, density effect on tree growth and organ biomass was examined in *E. urophylla* stands. The objectives of this study are (1) to examine growth characteristics of self-thinning *E. urophylla* stands; (2) to fit the C-D equation of organs to organ biomass; (3) to compare the difference in the C-D effect among organs; (4) to check whether the leaf biomass per unit land area remains constant in self-thinning stands with different densities.

Materials and methods

Study site

The experimental site is located in the central area of Leizhou Peninsula, Guangdong Province, China. This region has a tropical monsoon climate. Mean annual temperature, temperatures in the hottest month (July) and in the coldest month (January) are 22.9, 28.9 and 15.2°C, respectively. Mean annual rainfall and evaporation are 1,700 and 1,763 mm, respectively. The slope of experimental site is gentle having a slope of 5°. Soil is orthox resulting from shallow sea deposit, with a soil depth over 100 cm. Chemical characteristics of the soil at 0–40 cm depth were as follows: pH value was 5.1, contents of organic matter, total N, P and K were 11.44, 0.51, 0.18 and 2.03 g kg^{-1}, respectively, and available N, P and K contents were 38.06, 2.75 and 13.16 mg kg^{-1}, respectively. The main understory was *Eriachne pallescens* R. Br. with a cover of 60%.

Sampling methods

The *E. urophylla* S. T. Blake stands of 6.0 ha were established in 2000, which consisted of three-stand densities of 1,111 trees ha^{-1} (low density, 3 m × 3 m spacing), 1,667 trees ha^{-1} (middle density, 3 m × 2 m spacing) and 2,500 trees ha^{-1} (high density, 2 m × 2 m spacing). The investigated plot area was 30 m × 20 m. Three replicates of the plot were randomly located in each density stand. Tree height (h) and stem diameter at breast height of 1.3 m above the ground (d) (over bark diameter) for each tree were measured annually from age 1 to 7 years.

The h and d for all trees were measured at each plot, divided into five-diameter classes at 2-cm intervals, and then 15 sample trees proportionally distributed over the range of diameter in each density stand were selected for destructive harvesting in 2007. The root biomass (>0.2 cm in diameter) downwards to 1 m depth was estimated by excavating the soil around the roots according to the planting spacings (Fang et al. 2007). Roots were divided into root stock and three-diameter classes: 0.2–0.5, 0.5–2 and >2 cm. The stratified clipping method was followed at a 0.5-m interval (from the ground to the top) to estimate the weight of stem and bark of each sample tree at different strata, and fresh weight of leaves and branches contained in each 0.5 m thick horizontal layers was measured (Khan et al. 2005). Subsamples of stem, branches, leaves, bark and roots from each root class were taken for estimating the ratio of dry/fresh weight.

The following simple allometric equation for weight W_o of an organ, such as stem, branch, leaf, bark or root, to d and h was examined for each of different density stands:

$$W_o = a(d^2h)^b, \tag{1}$$

where a and b are coefficients. Separate equations for each plant organ and plant density were fitted using ordinary least-squares estimates (Table 1).

On the basis of the d and h of all individuals within each plot recorded at the annual measurements, it was possible to calculate mean organ weight, w_o, using these allometric relationships established for different organs in different density stands. Mean tree weight, w, was defined as the sum of mean weights of organs.

Table 1 Equations of organ dry weight of *Eucalyptus urophylla* at different densities

Density (tree ha^{-1})	Organs	Equation	R^2	P value	Samples
1,111	Stem	$w = 0.0062(d^2h)^{1.1787}$	0.998	<0.0001	15
	Branches	$w = 0.0047(d^2h)^{0.9857}$	0.999	<0.0001	15
	Leave	$w = 0.5150(d^2h)^{0.2834}$	0.994	<0.0001	15
	Bark	$w = 0.0029(d^2h)^{1.0910}$	0.999	<0.0001	15
	Root	$w = 0.0043(d^2h)^{1.0586}$	0.999	<0.0001	15
1,667	Stem	$w = 0.0050(d^2h)^{1.2106}$	0.957	<0.0001	15
	Branches	$w = 0.0027(d^2h)^{1.0394}$	0.975	<0.0001	15
	Leave	$w = 0.4182(d^2h)^{0.3204}$	0.977	<0.0001	15
	Bark	$w = 0.0019(d^2h)^{1.1512}$	0.979	<0.0001	15
	Root	$w = 0.0045(d^2h)^{1.1021}$	0.984	<0.0001	15
2,500	Stem	$w = 0.0082(d^2h)^{1.0971}$	0.997	<0.0001	15
	Branches	$w = 0.0036(d^2h)^{0.9457}$	0.994	<0.0001	15
	Leave	$w = 0.3786(d^2h)^{0.2954}$	0.999	<0.0001	10
	Bark	$w = 0.0021(d^2h)^{1.0910}$	0.999	<0.0001	15
	Root	$w = 0.0061(d^2h)^{0.9625}$	0.994	<0.0001	15

Model fitting

The equation

$$w_o = gw^k, \tag{2}$$

where w_o is mean organ weight, w is mean tree weight, and g the coefficient and k the allometric constant specific to growth stages (Kira et al. 1956; Xue and Hagihara 2008), was fitted to the data. The g and k were obtained by the method of least squares (Table 2).

Equation 2 was used to estimate relationship between mean tree weight w and mean organ weight w_o. Dividing both sides of Eq. 2 by w results in

$$\frac{w_o}{w} = gw^{k-1}, \tag{3}$$

where w_o/w stands for the dry weight ratio of each organ.

Hagihara (1999) developed the reciprocal equation of the C-D effect in self-thinning stands as follows:

$$\frac{1}{w} = A_t\rho + B, \tag{4}$$

where w is the mean tree weight and ρ is stand density, and A_t and B are coefficients specific to growth stages.

The mean organ weight w_o is derived by considering Eqs. 2 and 4 as follows:

$$w_o = \frac{g}{(A_t\rho + B)^k}. \tag{5}$$

The biological time τ is defined as the integral of the coefficient of growth $\lambda(t)$ with respect to physical time t (Shinozaki 1961):

$$\tau = \int_0^t \lambda(t)\,\mathrm{d}t \quad \text{or} \quad \mathrm{d}\tau = \lambda(t)\,\mathrm{d}t. \tag{6}$$

The τ can be derived by the following equation (Shinozaki and Kira 1956):

$$B = \frac{\mathrm{e}^{-\tau}}{w_0}, \tag{7}$$

where w_0 is initial mean plant weight.

The τ–t relationship can be expressed by a hyperbolic equation (Hozumi 1977) as

$$\frac{1}{\tau} = \frac{F}{t - L} + I, \tag{8}$$

where the reciprocal of F denotes the intrinsic growth rate at the initial growth stage, the reciprocal of I denotes the maximum value of τ as t tends to infinity and L denotes a lag time.

The relationship between stand density and biological time τ can be expressed by the following equation (Shinozaki 1961; Hozumi 1977):

$$\frac{1}{\rho} = \frac{1}{\rho_i} + q(\mathrm{e}^{\mu\tau} - 1). \tag{9}$$

where ρ_i is initial density, and q and μ are coefficients.

Relative growth rate (RGR), defined as the rate of size increase per unit of time per unit of size (i.e. RGR = (*d*size/*d*time)(1/size); Hunt 1990), is a sensitive measure of competitive ability, so that it and the above equations of the C-D effect in self-thinning stands were employed to examine various growth characteristics of *E. urophylla* stands.

Table 2 Coefficient $g^{(1-k)}$ and k in Eq. 2 and coefficients A_t and B in Eq. 3

Organs	Stand age (years)	g	k	R^2	A_t (ha kg^{-1})	B (kg^{-1})	R^2
Stem	1	0.2115	0.9218	0.999	0	0.4785	0.765
	2	0.3866	0.9987	0.907	0.0000260	0.1063	0.777
	3	0.6153	0.8845	0.994	0.0000170	0.0446	0.994
	4	0.9742	0.8058	0.987	0.0000091	0.0244	0.998
	5	0.9219	0.8586	0.992	0.0000062	0.0143	0.958
	6	0.5789	0.9970	0.995	0.0000076	0.0054	0.992
	7	0.6231	0.9855	0.998	0.0000044	0.0058	0.959
Branches	1	0.0320	1.8003	0.991			
	2	0.0841	1.0013	0.869			
	3	0.0306	1.4076	0.985			
	4	0.0168	1.5058	0.941			
	5	0.0096	1.5889	0.997			
	6	0.0380	1.1834	0.958			
	7	0.10817	1.0013	0.876			
Leaves	1	0.5002	1.2435	0.999			
	2	0.1813	1.2494	0.872			
	3	0.1109	1.1748	0.856			
	4	0.1117	1.0019	0.972			
	5	0.0794	1.0015	0.969			
	6	0.0511	1.0110	0.999			
	7	0.0463	1.0006	0.734			
Bark	1	0.0332	1.7861	0.974			
	2	0.0426	1.4190	0.872			
	3	0.0601	1.2639	0.971			
	4	0.0322	1.4179	0.998			
	5	0.0450	1.2916	0.932			
	6	0.1364	1.0021	0.880			
	7	0.1118	1.0240	0.991			
Root	1	0.0703	1.3401	0.921			
	2	0.1390	1.0031	0.999			
	3	0.1322	1.0672	0.998			
	4	0.1245	1.0683	0.995			
	5	0.1188	1.0677	0.983			
	6	0.1061	1.0842	0.999			
	7	0.0766	1.1566	0.989			

Results

The *E. urophylla* growth

Figure 1 shows the mean diameter at breast height D of *E. urophylla* in each density stand from 1 to 7 years after the planting. Stem diameter increased rapidly in the first 3 years and the RGRs of low-, middle- and high-density stand were above 0.36, 0.32 and 0.22 cm cm^{-1} year^{-1}, respectively, and then trees gradually decreased their growth rate. Increasing density led to a significant decrease in the diameter growth pattern of the *E. urophylla* trees from 3 years after the planting.

Height growth was less sensitive to the density effect than diameter growth. Although the mean tree height H was also affected by stand density, the trees in all density stands kept a relatively high RGR from 1 to 6 years after the planting (Fig. 2). In 6 years, the height growth of the high density stand became slow compared with other density stands.

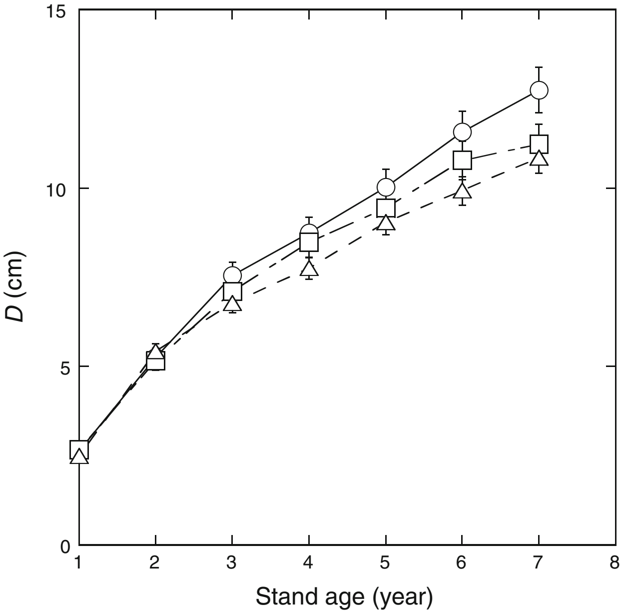

Fig. 1 Changes of mean diameter at breast height D of the *E. urophylla* stands with time. *Open circles* low-density stand, *open squares* middle-density stand, *open triangles* high-density stand

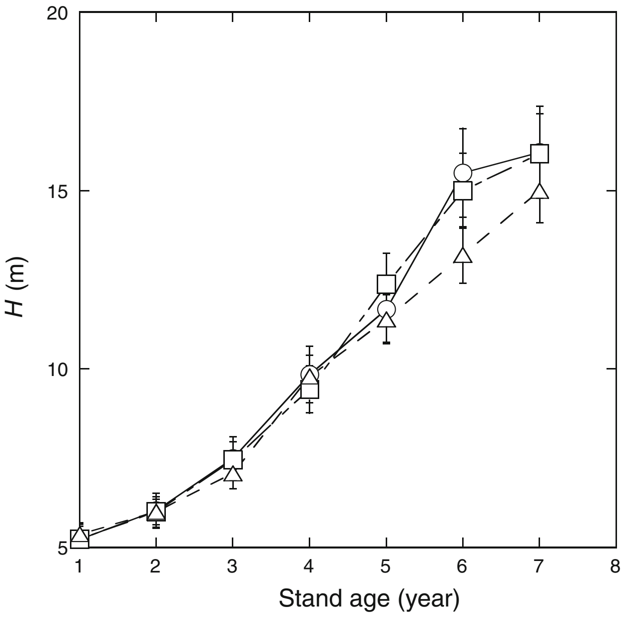

Fig. 2 Changes of mean tree height H of the *E. urophylla* stands with time. *Open circles* low-density stand, *open squares* middle-density stand, *open triangles* high-density stand

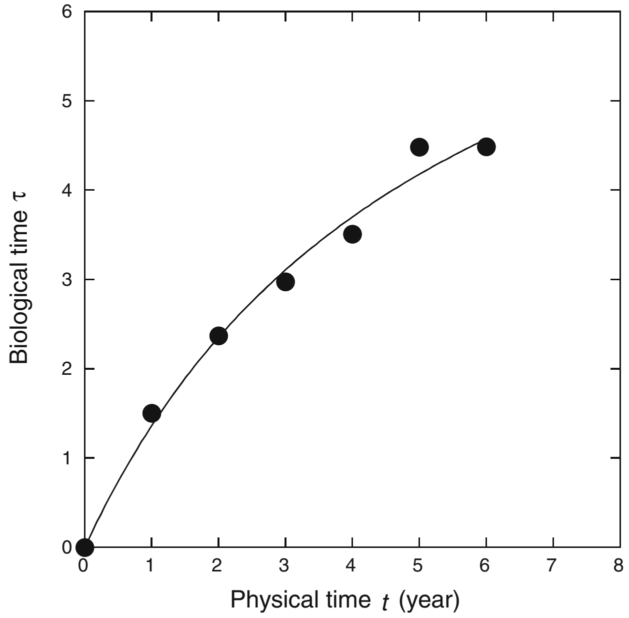

Fig. 3 Relationship between biological time τ and physical time t. The regression was given by Eq. 8 ($R^2 = 0.990$)

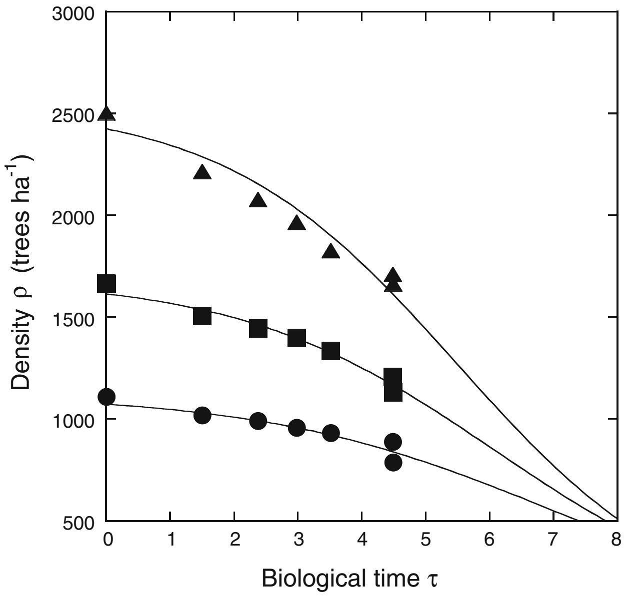

Fig. 4 Change trend of density ρ with biological time τ. *Filled circles* low-density stand, *filled squares* middle-density stand, *filled triangles* high-density stand. The data were fitted using Eq. 9 ($R^2 = 0.895$ for low-density stand stem, $R^2 = 0.966$ for middle-density, $R^2 = 0.925$ for high-density stand)

Biological time τ

With increasing physical time t, the biological time τ increased rapidly during early growth stages and became slow gradually during later growth stages (Fig. 3). The τ–t curve given by Eq. 8 was steep from 1 to 5 years and became less steep from 6 to 7 years. The constants F, I and L were calculated to be 0.6182 year, 0.1155 and 0.001 year, respectively.

Tree density

Figure 4 shows changes in tree density in each stand during the stand development from 1 to 7 years. The mortality was caused by a crowding effect, competition in the high-density stand was more intense than the low-density stand, so that the mortality was increased with increasing density. The relationships were well fitted with Eq. 9 ($R^2 > 0.895$), and different stand densities tend to converge to the same density level after a sufficient lapse of time.

Allometric relationships between the weights of tree organs and the tree weight

The w_o/w stands for the dry weight ratio of each organ, which is shown in Fig. 5a–c. The stem weight ratio increased after the planting, which changed from 0.18 to 0.58, from 0.19 to 0.58 and from 0.21 to 0.59, in the low-, middle- and high-density stands, respectively. However, leaf weight ratio decreased from 0.61 to 0.05, from 0.60 to 0.05 and from 0.58 to 0.05 in the corresponding stands. The weight ratios of branch, bark and root remained relatively steady from 2 years after the planting.

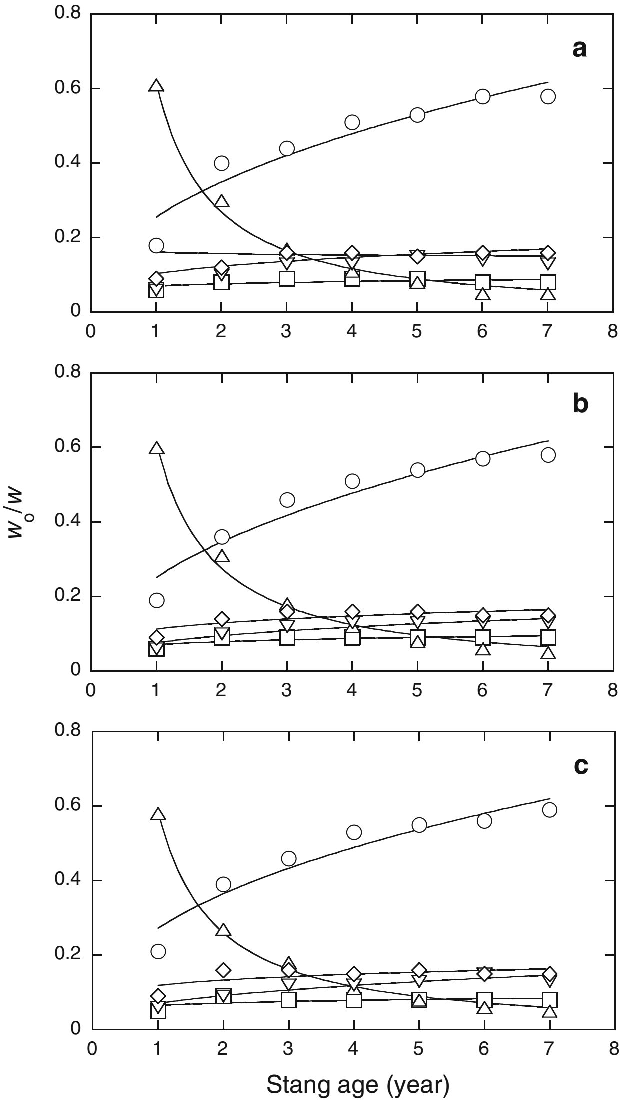

Fig. 5 Relationships between dry weight ratios w_o/w of stems (*open circles*), branches (*open squares*), leaves (*open triangles*), bark (*open inverted triangles*) and root (*open diamonds*) to mean dry weight w of trees. The curves are fitted by Eq. 8. **a** The low-density stand ($R^2 > 0.908$ for each organ), **b** the medium-density stand ($R^2 > 0.826$ for each organ), **c** the high-density stand ($R^2 > 0.868$ for each organ)

The C-D effect of self-thinning stands

Figure 6 shows the relationship of mean tree w to density ρ in the *E. urophylla* stands. The C-D effect was evident from 3 years after planting and was well described with the reciprocal equation given by Eq. 4 at a given time ($R^2 > 0.776$ for each growth stage). Difference among densities in mean tree weight was evident from 2 years after the planting, when trees in the low-density stand were already 20 and 21% larger in mean weight than those in the middle- and high-density stand (Fig. 6). The relative growth advantage of the former had increased to 23 and 39% by the 7th year. The C-D curve shifted upward with the progress of time. The changes of the coefficients A_t and B in Eq. 4 were shown in Table 2. Initially, the coefficient A_t increased abruptly up to a maximum value, and thereafter decreased gradually with increasing stand age, whereas the coefficient B decreased and tended to close to zero.

The C-D effect strongly affected mean stem weight w_S from 3 to 7 years (Fig. 7a). The mean stem weight of the low-density stand increased by 60.9 kg from 2 to 7 years, which was 24 and 39% more than the middle- and high-density stands, indicating that competition in the middle- and high-density stands had become more intense with

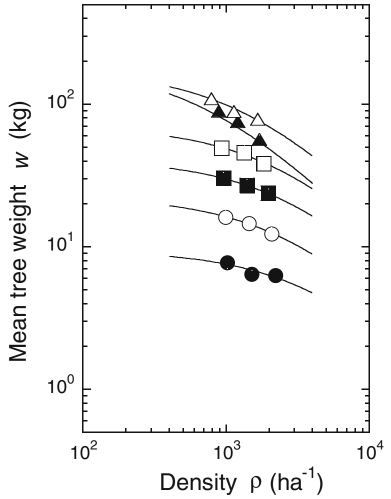

Fig. 6 The C-D effect between mean tree weight w and density ρ at a given time in the *E. urophylla* stands. The curves were fitted using Eq. 4. *Filled circles* 2-year-old ($R^2 = 0.776$), *open circles* 3-year-old ($R^2 = 0.992$), *filled squares* 4-year-old ($R^2 = 0.998$), *open squares* 5-year-old ($R^2 = 0.958$), *filled triangles* 6-year-old ($R^2 = 0.808$), *open triangles* 7-year-old ($R^2 = 0.955$)

time relative to the low-density stand. The $w_{\rm S}$–ρ data was well fitted by Eq. 5 at each growth stage and the change trend of the $w_{\rm S}$–ρ curve was the same as the w–ρ curve.

During the 5 years between ages 3 and 7 increment in mean branch weight in the low-density stand was 7.2 kg, 11% and 37% more than the middle- and high- density stands. The $w_{\rm Br}$–ρ data points were well described by $w_{\rm Br}$–ρ curve given by Eq. 5 (Fig. 7b). The time trend of the $w_{\rm Br}$–ρ relationship was almost the same as that of the $w_{\rm S}$–ρ relationship.

The increment in mean leaf weight in the low-, middle- and high-density stands were 2.5, 2.4 and 2.1 kg from 2 to 7 years, respectively, which were less than those of mean stem or mean branches, so that scale of the $w_{\rm L}$–ρ curve was smaller than the two latters (Fig. 7c). The $w_{\rm L}$–ρ curve given by Eq. 5 moved up on log–log coordinates during the whole experimental period.

The relationships between mean bark weight $w_{\rm Ba}$ and density ρ as well as between mean root weight $w_{\rm R}$ and density ρ are shown in Fig. 7d and e, respectively. The two figures indicate that $w_{\rm Ba}$–ρ and $w_{\rm R}$–ρ relationships could be well described by Eq. 5. The $w_{\rm Ba}$–ρ and $w_{\rm R}$–ρ curves moved upwards on log–log coordinates from 3 to 7 years in the *E. urophylla* stands.

Discussion

The *E. urophylla* growth

The reduction in stem diameter with increasing density from 1,111 to 2,500 tree ha^{-1} in the *E. urophylla* stands is consistent with other density experiments in *E. nitens* (Pinkard and Neilsen 2003), *E. grandis* (Kearney 1999),

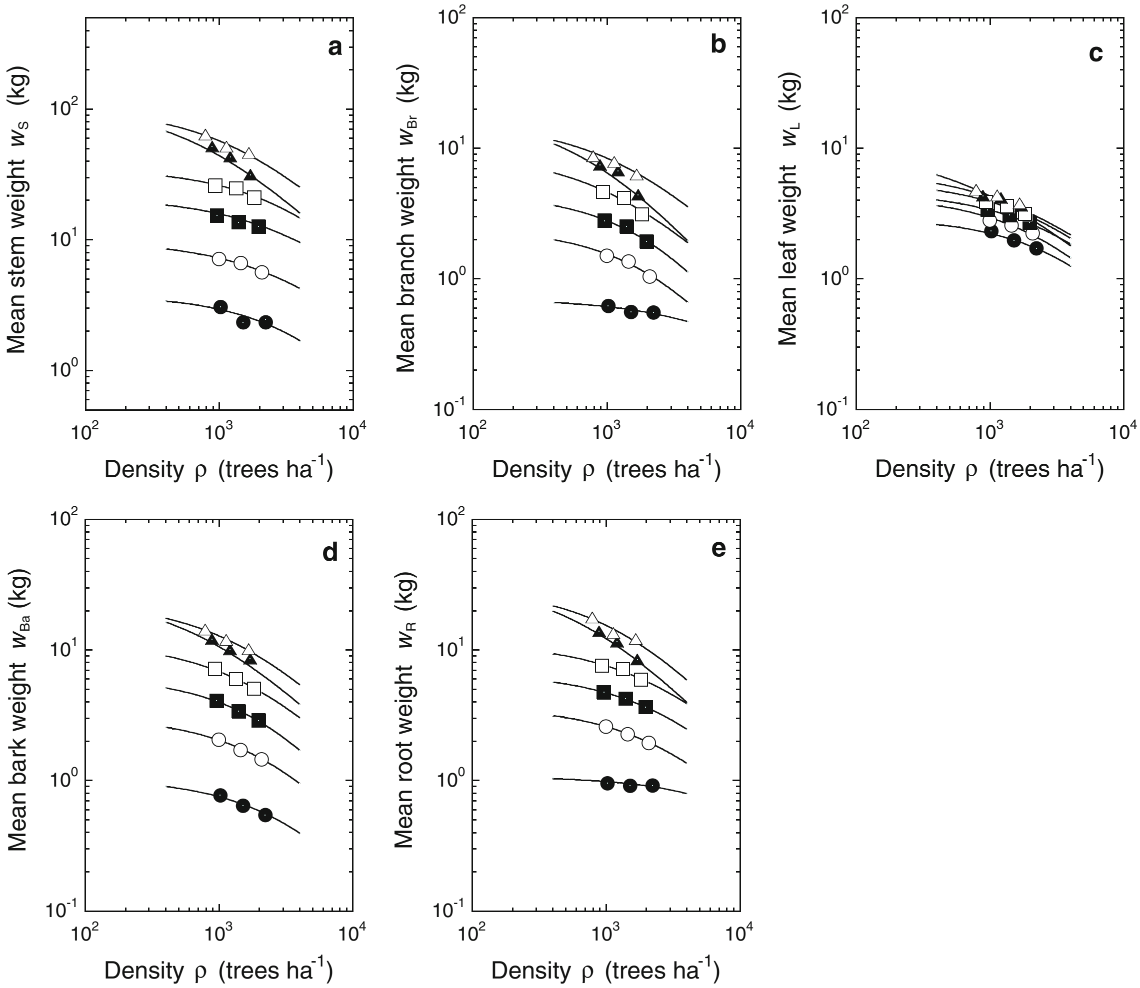

Fig. 7 The C-D effects between organ yield $w_{\rm o}$ and density ρ. **a** Stem, **b** branch, **c** leaf, **d** bark, and **e** root. The curves show Eq. 5, where the g and k values, and the $A_{\rm t}$ and B values are obtained from Eqs. 2 and 4, respectively. *Filled circles* 2-year-old ($R^2 > 0.753$ for each organ), *open circles* 3-year-old ($R^2 > 0.845$ for each organ), *filled squares* 4-year-old ($R^2 > 0.803$ for each organ), *open squares* 5-year-old ($R^2 > 0.922$ for each organ), *filled triangles* 6-year-old ($R^2 > 0.803$ for each organ), *open triangles* 7-year-old ($R^2 > 0.884$ for each organ)

E. urophylla, *E. pellita*, *E. camaldulensis* (Bernardo et al. 1998), *E. pilularis* and *E. cloeziana* (Alcorn et al. 2007). The increased competition for environmental resources (light, water and nutrients) with increased stand density can reduce average stem diameter within the stand (e.g. Kearney 1999; Neilsen and Gerrand 1999; Alcorn et al. 2007). Compared with the low-density stand, lateral growth of the crown in the high-density stand is impeded early, resulting in a small crown width. Meanwhile, natural pruning in the high-density stand occurs earlier and stronger than in the low-density stand, so that the crown length of the former is smaller than the latter. Therefore, crown size decreases with increasing density, whereas a small crown contains fewer leaves, which is unfavorable for photosynthesis and weakens the growth of tree diameter, as a result, diameter growth decreased with increasing density.

The effect of planting density on height growth was not as pronounced as the effects on diameter in this study, which is consistent with other studies (e.g. Deans and Milne 1999; Neilsen and Gerrand 1999). The relationship between height growth and density varies with tree species, site and the stage of stand growth. Some studies indicate that height growth is insensitive to density (e.g. Seidel 1984; Lanner 1985). However, a few studies show that height growth increases with increasing density in young plantations (Gilbert et al. 1995; Knowe and Hibbs 1996; Ritchie 1997). In addition, some researchers reported that height growth in intermediate densities was greater than in the high and the low densities (e.g. Cole and Newton 1987; Giordano and Hibbs 1993; Pienaar and Shiver 1993). In contrast with the above results, our study shows that height growth of the *E. urophylla* increases with decreasing density, which is consistent with studies in eucalypts (Opie et al. 1984; Alcorn et al. 2007) and other broadleaf (e.g. Niemistö 1995) and conifer species (e.g. Malimbwi et al. 1992). As individual trees in a stand grow, individual competition for resources in the high-density stand is more intense than in the low-density stand. Compared to the low-density stand, the leaves within and among individual trees in the high-density stand overlap with each other, and the growth of leaves located the lower crown is repressed, which reduces individual photosynthesis and affects tree growth, so that height growth in the high-density stand is slightly smaller than that in the low-density stand.

In the stands with complete crown closure, density is inversely related to the square of average crown diameter. A close relationship exists between average stem diameter and crown width, whereas the correlation between height and crown dimensions is negative when diameter is equal (Zeide 2010), and therefore the latter is a better predictor of density than average height. Stem volume is a function of tree height or diameter and a good proxy of tree biomass. Therefore, tree height or diameter is good indicators of tree biomass.

The C-D effect

Shinozaki and Kira (1956) developed the reciprocal equation of the C-D effect in populations as follows:

$$\frac{1}{w} = A\rho + B. \tag{10}$$

Here, A and B are coefficients at a given growth stage, and the coefficients A and B are, respectively, defined as

$$A = \mathrm{e}^{-\tau} \int_0^\tau \frac{\mathrm{e}^\tau}{Y(t)}\, \mathrm{d}\tau, \tag{11}$$

and

$$B = \frac{\mathrm{e}^{-\tau}}{w_0}, \tag{12}$$

where $Y(t)$ is the final yield, τ is called biological time, and initial mean plant weight w_0 is independent of density ρ (Shinozaki 1961). The population density in Eq. 10 does not decrease with plant growth, i.e. the population grows without self-thinning.

Hagihara (1999) constructed a model for describing the C-D effect in self-thinning stands in line with the logistic theory of the C-D effect as Eq. 4, and a new assumption about the relationship between the actual density ρ and initial density ρ_i is newly incorporated into the logistic theory of the density effect in self-thinning populations. The coefficient A_t and B in Eq. 4 is, respectively, defined as

$$A_t = \mathrm{e}^{-\tau} \int_0^\tau \frac{\mathrm{e}^\tau}{Y(t)}\, \mathrm{d}\tau - \varepsilon \frac{\mathrm{e}^{-\tau}}{w_0}, \tag{13}$$

and

$$B = \frac{\mathrm{e}^{-\tau}}{w_0}. \tag{12}$$

where ε is a coefficient independent of both ρ and ρ_i, but is a function of time. The coefficient A_t in Eq. 4 is quite different from the coefficient A in Eq. 10. The difference between Eqs. 4 and 10 results from the difference in mathematics interpretation between coefficient A_t in Eq. 4 and coefficient A in Eq. 10. Considering Eqs. 11, 12 and 13, it follows that A_t is equal to the sum of A and $-\varepsilon B$.

Equation 4 used simple variables (w and ρ) and well fit the observed data as shown in this study, and its validity is also supported by the data of *P. densiflora* (Xue and Hagihara 1998), *P. massoniana* (Xue and Hagihara 2002) and *Betula platyphylla* var. *japonica* and *Betula ermanii* (Stankova and Shibuya 2003). This suggests that Eq. 4 can be applied to analyze the growth characteristics and dynamics of stands with different densities under self-thinning. The analysis of the plant growth during the course of self-thinning using Hagihara's model would contribute towards solving the problems because of its wide applicability. The results show that Eq. 5 derived from allometric equation and the C-D theories is validated on 7-year-old *E. urophylla* data, and the observed w_o value was highly correlated with simulated w_o value (Fig. 7a–e). Equation 5 provides a high degree of accuracy in predicting organ biomass allocation patterns for different density stands, and it can be applied to stands where previous information of organ biomass and density is available. Moreover, this equation can predict organ biomass over a wider density range (Fig. 7a–e), which is comprehensive and convenient for the growth analysis of self-thinning stands. Equation 9 can be well fitted using simple variables (ρ, ρ_i, τ) and shows the relationship between density of the *E. urophylla* stands and biological time τ during the self-thinning process, which is important for understanding the growth behavior of the plant population. Although there are many tree species being used for reforestation in China, their C-D effect during the course of self-thinning has been poorly reported. Therefore, Eqs. 5 and 9 will be a useful tool in comparing the C-D effect among different species and densities.

Equation 5 can be used to analyze the organ growth of 7-year-old *E. urophylla* stands with different densities under self-thinning. However, the model application should be age-dependent, since the theory of density effect is based on the logistic growth of plant. As trees grow older and taller, they spend more energy to supply leaves with the same amount of water than do younger and shorter trees. Taller stems entail greater expenditures for their construction and maintenance (Zeide 1995). As a result, trees have to allocate a decreasing portion of their resources to leaves, and their closure decreases (Zeide 1991). Since growth of tree organs may not obey a logistic growth law in older stands, Eq. 5 should be applied only to the self-thinning young stands.

In the evaluation of stand growth stage, the physical time is not a good indicator of stand growth, because it does not reflect physiological condition and the site quality on which the stand growth is dependent (Stankova and Shibuya 2003), whereas value of biological time τ relates to physiological and environmental conditions of stand growth (Shinozaki 1961). Therefore, coefficients A_t and B in Eq. 5 and density ρ in Eq. 9 are expressed as functions of biological time. Although biological time τ cannot be estimated from the stand data directly, it can be derived based on coefficient B and initial mean plant weight (Xue and Hagihara 2002). In this study, the C-D effect equation of organ (Eq. 5) and density-biological time equation (Eq. 9) are successfully used to the *E. urophylla* stands, indicating that biological time is a applicable and practical indicator of stand development stage.

Organ biomass change

There is a slight increment in mean leaf weight w_L from 6 to 7 years in *E. urophylla* stands, and their values are 0.11, 0.05 and 0.05 kg kg^{-1} year^{-1} in the low-, middle- and high-density stands, respectively, and corresponding leaf biomass decreases by 1 and 2% and increases by 2% due to decreasing density, which indicates that leaf biomass reaches a more or less constant level. Ogawa (2008) also demonstrated constant leaf biomass in mature forest stands after canopy closure. As self-thinning occurs, unoccupied space is produced. Therefore, the survivors can extend more branches and develop more leaves, and result in increment in the mean leaf mass per tree, which may cause that the leaf biomass per unit land area will remain more-or-less constant in self-thinning stands (Ogawa et al. 2010). Therefore, constant leaf biomass might be a common feature of forest stands.

The *E. urophylla* biomass distribution by organs shows a significant increase over time for stems and a significant decrease for leaves. The stem weight proportion increased from 36–38% at 2 years to 57–59% at 7 years, whereas the leaf weight proportion decreased from 29–31 to 4–5% in all stands. Stem weight proportions at 7 years in the present results are in close proximity with estimates obtained from *Eucalyptus* stands in Australia (Cromer 1996; Zewdie et al. 2009), but which are higher than *E. urophylla* stands in Leizhou Peninsula, China (Xue 2009) and lower than *E. urophylla* stands in Fujian Province and Guangxi Province, China (Lin et al. 2003; Ye et al. 2010). Leaf weight proportions are lower than the data of Cromer (1996) and Zewdie et al. (2009), but they are the same as estimates obtained from *E. urophylla* stands by Xue (2009) and higher than data coming from Lin et al. (2003) and Ye et al. (2010). Therefore, *E. urophylla* is characterized by growth having an high stem biomass proportion and a low leaf biomass proportion. Beadle and Mummery (1989) reported a similar decrease to that reported here in the ratio of leaf area to sapwood area in two provenances of *E. nitens* between ages 1 and 4 years. This decrease is matched with a change in carbon allocation from leaf mass to stem. Zeide (1985) and Zewdie et al. (2009) also concluded that the percent contribution of stem increased whereas that of leaves decreased with increasing stand age. The period of time leading up to canopy closure is characterized by changes in the relative partitioning of biomass between leaves and stem (Beadle and Inions 1990). After canopy closure, the proportion of the stem continues to increases, whereas the proportion of leaves decreases as trees grow older and taller. The reason is that older and taller trees entail greater expenditures for their construction and maintenance, and spend more energy to supply leaves with the same amount of water than do younger and shorter trees (Zeide 1995). Competing vegetation induces a shift in carbon allocation from the leaves to the stem, probably the result of a hormonal inhibition in lateral bud development (Xue and Hagihara 2008). Moreover, the rapidly changing light conditions experienced by individual crowns within the stand may cause this change (Medhurst et al. 1999).

Stand density determines the timing and intensity of resource competition among trees (Harrington et al. 2009) and influences forest productivity and diameter (Zeide 2005). It allows a forester to estimate the patterns of stand development (Sprintsin et al. 2009). Results of this research indicate that biomass of individual trees is maximized when stands are grown at the low density that promote crown development and thereby accelerate individual tree growth. However, total biomass is maximized at the high density, which was 51 and 29% greater than those of low- and middle-density stands when the *E. urophylla* stands were 7 years old. Since the main objective for *E. urophylla* stands is the production of pulpwood, high density produces the greatest biomass, especially the greatest stem biomass, which is 52 and 32% greater than those of low- and middle-density stands 7 years after planting, so that it is the best choice in silvicultural practice. Stand density has an important effect on total stem volume of stands. High density leads to a relatively long period of intense competition among trees, and therefore release treatments from the competition should be carried out early in the stands. Light thinning is recommended, which can produce the most desirable stand-level volume growth.

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