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Self-thinning of leaf, wood and aboveground in overcrowded mangrove *Bruguiera gymnorrhiza* stands in Okinawa Island, Japan

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Abstract

The allometric relationships of mean tree height $\overline{H}\left(= g_\theta \cdot \overline{w}^\theta\right)$ and of organ mass density $\overline{d}\left(= \overline{w}/\overline{s} \cdot \overline{H} = g_\delta \cdot \overline{w}^\delta, \text{where } \overline{s}(= 1/\rho) \propto \overline{w}^\phi\right)$ to mean organ mass $\overline{w}$ were studied in *Bruguiera gymnorrhiza* stands. According to Weller's allometric model, the self-thinning exponent α was estimated to be 1.11 in leaf, 1.55 in wood and 1.47 in aboveground. The self-thinning exponent α in leaf was not significantly different from 1.0, which showed that the stand leaf biomass was constant regardless of the population density ρ. The α was not significantly different from 3/2 in wood and aboveground, which concluded that the 3/2 power law of self-thinning holds in overcrowded *B. gymnorrhiza* stands.

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1. Introduction

As trees in a stand grow they occupy an increasing amount of space, so that eventually the gaps between them are filled up and individuals begin to interfere with each other for access to resources like light, water and nutrients [1-2]. Such interference or competition within the stand induces size variation and also density-dependent mortality or self-thinning [3]. Thus density is reduced while mean

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plant mass and total biomass increase. The relationship between population density ρ and mean mass $\overline{w}$ of monospecific even-aged plant stands has been described by the 'self-thinning rule', '3/2 power law' or 'Yoda's law' after Yoda et al. [4] who first formulated it. The relationship can be expressed as,

$$\overline{w} = K \cdot \rho^{-\alpha} \tag{1}$$

where K is a multiplying factor which varies from species to species, and α is the self-thinning exponent which is close to 3/2 regardless of species, ages, or site conditions. Many workers have documented examples of this relationship [3], [5-9]. Many investigators have supported the claim that the 3/2 power law is applicable to a wide range of plant including grasses, commercial cultivars, weeds, grains, legumes and trees [2-4], [8], [10]. Many studies have confirmed the generality of the 3/2 power law of self-thinning for trees and shrubs growing in pure, as well as in mixed stands [2-3], [6-8], [11-15]. But some studies have shown that the slope of Eq. (1) has been found to be much more variable than -3/2 as the law states [9], [16-22]. Thus, the observed variability has led doubts on the generality of the 3/2 power law [9], [17], [20], [23].

Much interest on the self-thinning law has been focused on its theoretical significance [8], [12], [24-28] and demonstrated practical implications in forest management [29-35]. Several theories have been proposed [6], [12], [20], [23-25], [36-39]. The earliest geometric model [4] assumes plants do not change their properties as they grow larger and compete, so that the thinning exponent is always 3/2. However, the allometric model proposed by Weller [20] predicts that the thinning slope varies with the plant shape and biomass density (mass per unit occupied area), which can be derived from stand parameters, such as stem diameter and tree height. This model merits further investigation to test its applicability to diverse species because of its mathematical simplicity, which is important from a practical viewpoint.

Practical application of Weller's model in the analysis of stand density and plant mass has been demonstrated for some species [20]. In most studies on self-thinning, only aboveground mass has been measured [7], [40-41]. Little is known about the self-thinning relationship in Eq. (1) for leaf and wood (stem and branch) mass. The mechanisms of competition differ between different partial organs like leaf, stem and branch. Compared to annual stem increment, leaves and branches shed as new one grow. As a result, annual increment of leaves and branches are few. This might be expected to result in radically different thinning slopes in leaves and other organs. When total aboveground mass is related to the stand density, different thinning for various tree organs combines to form a compromise slope for the whole tree. Therefore, it is necessary to explore, separately, the thinning functions of tree organs to stand density.

The northernmost limit of *Bruguiera gymnorrhiza* (L.) Lamk. distribution is Amami Island in the northern part of the Ryukyu Archipelago, Japan [42]. Like many other mangrove species, *B. gymnorrhiza* also has some economic and ecological values and contributes to the sustainability of mangrove ecosystem. Much interest on self-thinning studies has been focused on terrestrial plant populations [1], [10], [43-45]. In contrast, little information is known about the self-thinning for mangroves [46], and there is no information of organs (leaf, stem and branch) self-thinning in *B. gymnorrhiza*. Therefore, such knowledge would be of fundamental importance for understanding the ecology and its management.

2. Methodology

2.1. Study site

This study was carried out in a mangrove *Bruguiera gymnorrhiza* (L.) Lamk. forest along the Okukubi River (26º27' N, 127º56' E) in Okinawa Island, Japan (Fig. 1). On the basis of the 2000–2009 data obtained from the Nago Meteorological Station, the mean monthly minimum and maximum, and mean annual temperatures were estimated to be $16.5 \pm 0.2°C$ in January and $28.9 \pm 0.2°C$ in July, and 22.8 ± 1.3 (SE) °C respectively. Mean monthly rainfall was more than 100 mm month^{-1} throughout the year, except for January (90.5 ± 12.3 (SE) mm month^{-1}) and February (80.9 ± 13.7 (SE) mm month^{-1}). The mean annual rainfall was 2017.3 ± 20.2 (SE) mm yr^{-1}. The warmth index was 213.3 ± 0.5 (SE) °C month, which is within the range of 180 to 240°C month of the subtropical region defined by Kira [47].
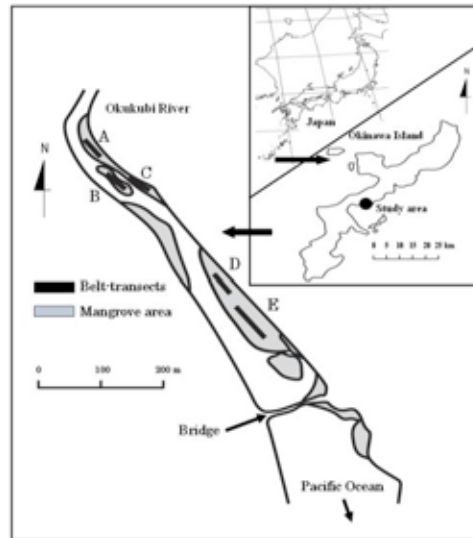

Fig. 1. Location map of the study area. Symbol A, plot 1 to plot 4; B, plot 5 to plot 8; C, plot 9 to plot 16; D, plot 17 to plot 23; E, plot 24 to plot 43

2.2. Tree census

A non-continuous 215 m long belt-transect (5 m wide) along the river was established in the pure *Bruguiera gymnorrhiza* forest (Fig. 1) and divided into 43 plots (5×5 m^2). Tree height, H (m), and stem diameter at $H/10$, $D_{0.1H}$ (cm), of all individuals in the plots were measured in March–April 2010. Means of H and $D_{0.1H}$ respectively ranged from 3.46 ± 0.06 to 8.48 ± 0.39 m and 4.09 ± 0.12 to 12.81 ± 1.11 (SE) cm.

2.3. Harvesting method

Eleven sample trees ranging from 0.72 to 9.88 m in H and from 1.82 to 59.5 cm in $D_{0.1H}$ were selected in the dense forest for harvesting. The total fresh mass of stem, branches and leaves of each tree were measured. Samples of stem, branches and leaves were taken for estimating the ratio of dry/fresh mass. All samples were dried in a ventilated oven at 80ºC for 48 to 168 hr depending on the size of samples and desiccated at a room temperature, and then weighed.

2.4. Weller's allometric model

Weller [20] proposed the allometric model based on the following three assumptions for overcrowded plant populations. Assumption 1: the mean occupied area per tree $\bar{s}$ is related with the mean aboveground mass $\bar{w}$ by the following allometric relationship,

$$\bar{s}\left(=\frac{1}{\rho}\right) = g_\phi \cdot \bar{w}^\phi \tag{2}$$

where ρ, g_ϕ and ϕ are the population density, the allometric coefficient and the allometric exponent, between $\bar{s}$ and $\bar{w}$, respectively. Assumption 2: the relationship between the mean tree height $\bar{H}$ and $\bar{w}$ can be expressed by the following allometric relationship,

$$\bar{H} = g_\theta \cdot \bar{w}^\theta \tag{3}$$

where g_θ and θ are the allometric coefficient and the allometric exponent between $\bar{H}$ and $\bar{w}$, respectively. Assumption 3: the relationship between the mean mass density $\bar{d}$ and $\bar{w}$ can also be expressed as follows,

$$\bar{d}\left(=\frac{\bar{w}}{\bar{s}\cdot\bar{H}}\right) = g_\delta \cdot \bar{w}^\delta \tag{4}$$

where g_δ and δ are the allometric coefficient and the allometric exponent between $\bar{d}$ and $\bar{w}$, respectively.

Combining Eqs. (2), (3) and (4) yields the following relation,

$$\bar{d} = \frac{\bar{w}}{\bar{s}\cdot\bar{H}} = \frac{1}{g_\phi \cdot g_\theta}\bar{w}^{1-(\phi+\theta)} = g_\delta \cdot \bar{w}^\delta \tag{5}$$

This relation stands for that the following equalities hold,

$$\delta = 1 - (\phi + \theta) \tag{6}$$

$$g_\delta = \frac{1}{g_\phi \cdot g_\theta} \tag{7}$$

As a result, the allometric constant ϕ in Eq. (2) can be given by the following equation,

$$\phi = 1 - (\delta + \theta) \tag{8}$$

Comparing Eqs. (1) and (2), the self-thinning exponent α in Eq. (1) is given by the following equation,

$$\alpha = \frac{1}{\phi} = \frac{1}{1-(\delta+\theta)} \tag{9}$$

Equation (9) allows the self-thinning exponent to be estimated from the allometric constants of θ in Eq. (3) and δ in Eq. (4).

On the other hand, Eq. (2) can be transformed as follows,

$$\overline{w} = \left(\frac{1}{g_\phi}\right)^{\frac{1}{\phi}} \cdot \rho^{-\frac{1}{\phi}} \qquad (10)$$

Considering Eq. (7), Eq. (10) can be rewritten in the form,

$$\overline{w} = \left(g_\delta \cdot g_\theta\right)^{\frac{1}{\phi}} \cdot \rho^{-\frac{1}{\phi}} \qquad (11)$$

Equation (11) is the same form as Eq. (1) proposed by Yoda et al. [4]. Thus, following equality holds,

$$K = \left(g_\delta \cdot g_\theta\right)^{\frac{1}{\phi}} \qquad (12)$$

Therefore, α and K values for plant organs (leaf and wood) and whole aboveground mass can be calculated on the basis of the allometric model as follows: the self-thinning exponent α can be estimated from Eq. (9) using the θ-value from Eq. (3) and the δ-value from Eq. (4). On the other hand, the multiplying factor K in Eq. (1) can also be estimated from Eq. (12) using the ϕ-value of Eq. (8), the g_θ-value of Eq. (3) and the g_δ-value of Eq. (4).

3. Results

3.1. Allometric relationship of $D_{0.1H}^2 H$ to organs mass and aboveground mass

Khan et al. [48] in mangrove *Kandelia obovata* Sheue, Liu and Yong plantation confirmed that the conventional allometric relationship where DBH is used was much lower in goodness of fit than the allometric relationship where $D_{0.1H}$ is used. The present study was the same as the result reported by them, i.e. coefficient of determination R^2 was 0.581 in the conventional method and 0.96 in the present method. Similar results were also reported by Ogawa and Kira [49] and Hagihara et al. [50].

Figures 2a, 2b and 2c show the allomteric relationships of w_L, w_W and w_T (kg) to $D_{0.1H}^2 H$ (cm^2 m) of 11 smaple trees, respectively. The allometric equations were established as follows,

$$w_L = 0.01185\left(D_{0.1H}^2 H\right)^{0.801} \qquad (13)$$

$$w_W = 0.01821\left(D_{0.1H}^2 H\right)^{1.119} \qquad (14)$$

$$w_T = 0.02804\left(D_{0.1H}^2 H\right)^{1.063} \qquad (15)$$

Equations (13), (14) and (15) were used for estimating w_L, w_W and w_T of individual trees of each plot, respectively. The value of allometric constant was close to unity for w_L ($t = 3.212$, df = 9, $p > 0.01$), w_W ($t = 3.162$, df = 9, $p > 0.01$) and w_T ($t = 1.536$, df = 9, $p > 0.01$), which indicates that w_L, w_W and w_T are nearly proportional to $D_{0.1H}^2 H$.
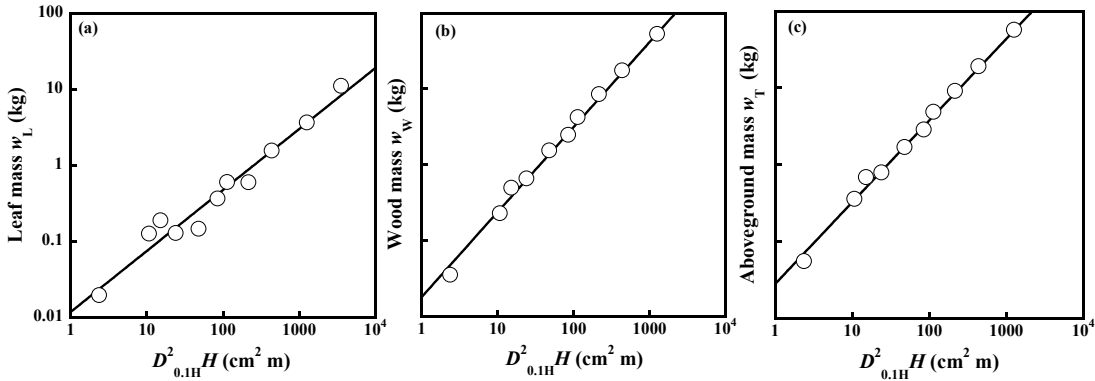
Fig. 2. Allometric relationships of leaf mass w_L (a), wood mass w_W (b) and aboveground mass w_T (c) and $D^2_{0.1H}H$ on log-log coordinates. The line is fitted using Eq. (13) for leaf mass ($R^2 = 0.94$), Eq. (14) for wood mass ($R^2 = 0.99$) and Eq. (15) for aboveground mass ($R^2 = 0.99$)

3.2. Allometric relationships of mean tree height to mean organ mass and mean aboveground mass
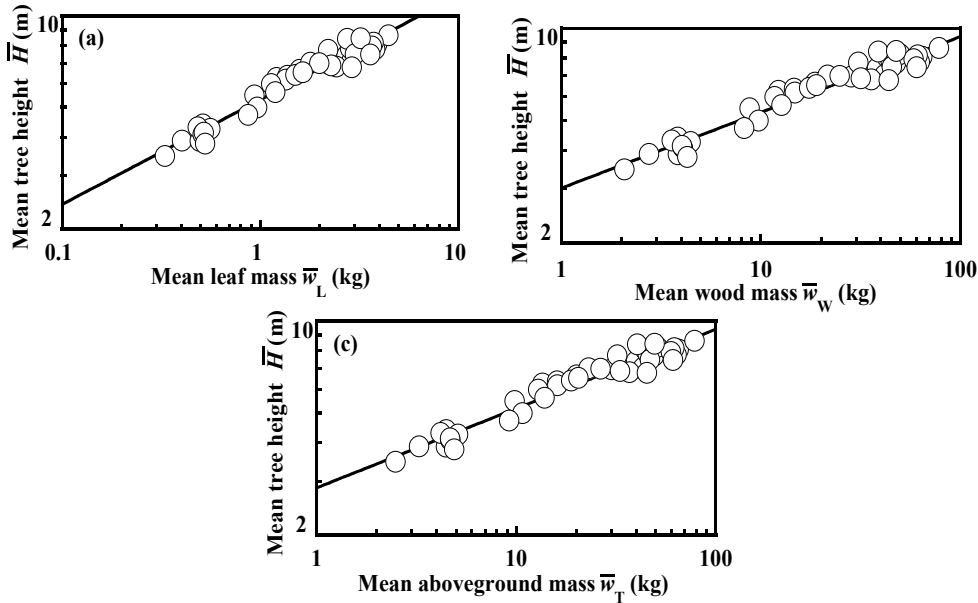

Fig. 3. Allometric relationships between mean tree height and mean leaf mass $\overline{w}_L$ (a), mean wood $\overline{w}_W$ (b) and mean aboveground mass $\overline{w}_T$ (c) on log-log coordinates. The straight line is fitted by Eq. (3) for leaf ($R^2 = 0.95$), for wood ($R^2 = 0.94$) and for aboveground ($R^2 = 0.95$).

The allometric relationships of mean tree height $\overline{H}$ to mean leaf mass, mean wood mass and mean aboveground mass are shown in Fig. 3. Mean tree height $\overline{H}$ increases with increasing mean organ mass and mean aboveground mass. The allometric relationship was formulated as shown in Eq. (3), where θ were estimated to be 0.34279, 0.24681 and 0.25947 in leaf, wood and aboveground mass,

respectively (Table 1). The value of g_θ was estimated to be 5.2926 m kg$^{-\theta}$, 3.0131 m kg$^{-\theta}$ and 2.8486 m kg$^{-\theta}$ in leaf, wood and aboveground mass, respectively.

3.3. Allometric relationships of mean organ mass density to mean organ mass and mean aboveground mass density to mean aboveground mass
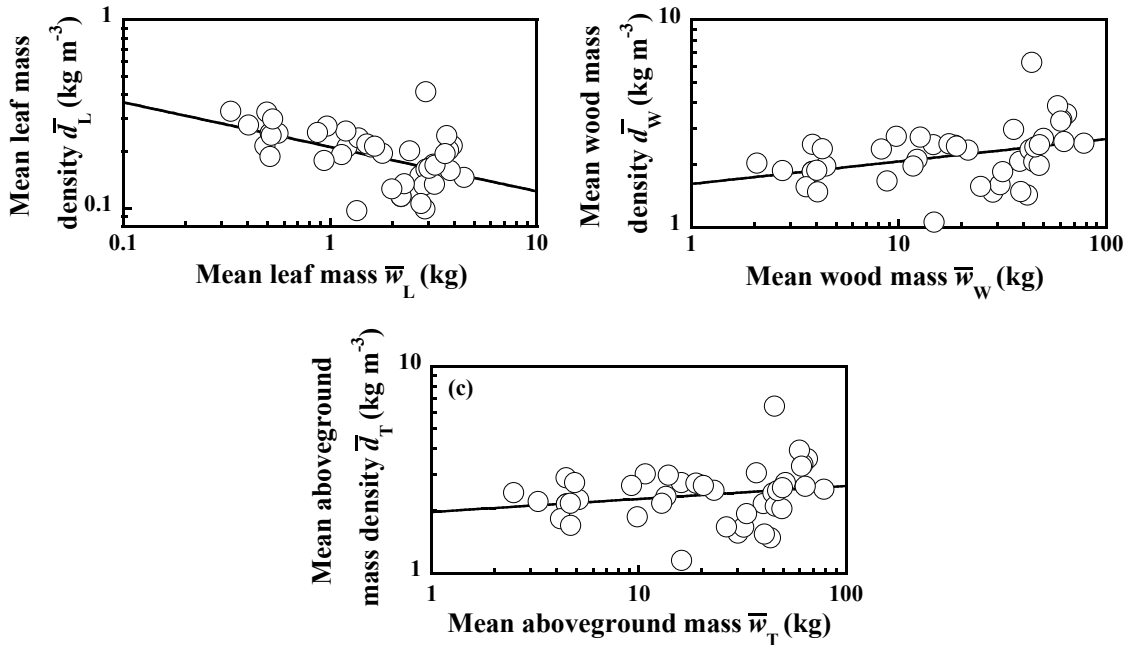

Fig. 4. Allometric relationships between mean leaf mass density $\bar{d}_L$ and mean leaf mass $\bar{w}_L$ (a), mean wood mass density $\bar{d}_W$ and mean wood $\bar{w}_W$ (b), mean aboveground mass density $\bar{d}_T$ and mean aboveground mass $\bar{w}_T$ (c). The straight line is fitted by Eq. (4): $\bar{d}_L = 0.2113 \cdot \bar{w}_L^{-0.2368}$ ($R^2 = 0.28$) for leaf, $\bar{d}_W = 1.6185 \cdot \bar{w}_W^{0.1083}$ ($R^2 = 0.14$) for wood and $\bar{d}_T = 1.9813 \cdot \bar{w}_T^{0.0628}$ ($R^2 = 0.05$) for aboveground

Table 1. Allometric exponents of tree height to mean organ mass and aboveground mass, θ, and of mean organ mass density and mean aboveground mass density to mean organ mass and aboveground mass, δ, and the self-thinning exponent, α

Organ	$\theta \pm$ SE	$\delta \pm$ SE	α
Leaf	0.3428 ± 0.0123	-0.2368 ± 0.0581	1.11
Wood	0.2468 ± 0.0094	0.1083 ± 0.0427	1.55
Aboveground	0.2595 ± 0.0098	0.0628 ± 0.0447	1.48

Figure 4 shows the allometric relationships of mean organ mass density and mean aboveground mass density to mean organ and mean aboveground mass. There was a significantly negative correlation between mean leaf mass density and mean leaf mass ($t = 4.0731$, df = 41, $p < 0.01$) while, mean wood mass density and mean wood mass showed positive correlation ($t = 2.5359$, df = 41, $p > 0.01$). However, the allometric constant δ between mean aboveground mass density and mean

aboveground mass was not significantly different from zero, i.e. $\delta = 0$ ($t = 1.4027$, df $= 41$, $p > 0.01$). The allometric relationship was formulated as shown in Eq. (4), where the allometric constant δ was -0.2368 $m^{-3} kg^{1-\delta}$, 0.1083 $m^{-3} kg^{1-\delta}$ and 0.0628 $m^{-3} kg^{1-\delta}$ in leaf, wood and aboveground, respectively.

The self-thinning exponent α in Eq. (1) was respectively estimated to be 1.11, 1.55 and 1.48 in leaf, wood and aboveground from Eq. (9) using the θ-value from Eq. (3) and δ-value from Eq. (4) (Table 1).
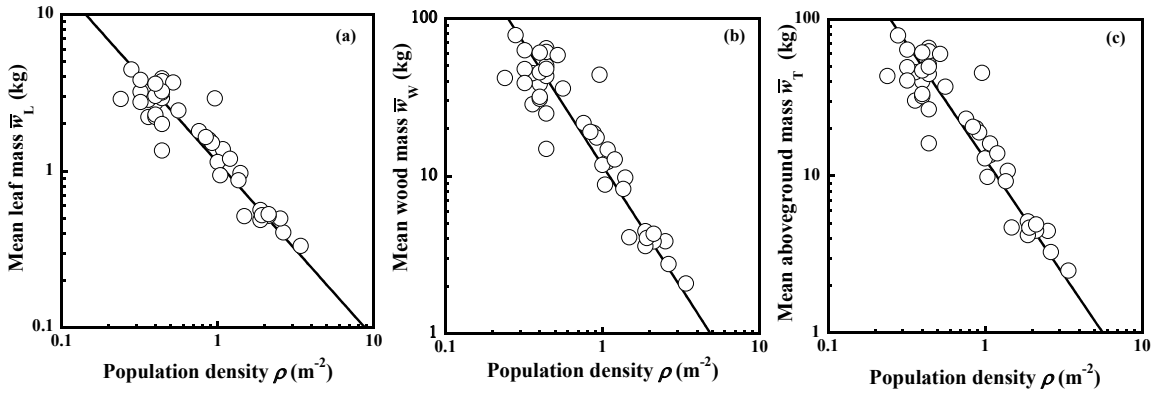
3.4. Self-thinning line

Fig. 5. Scatterplots of mean leaf mass $\overline{w}_L$ (a), wood mass $\overline{w}_W$ (b) and aboveground mass $\overline{w}_T$ (c) to population density ρ on log−log coordinates. The self-thinning line is given by Eq. (16) in $\overline{w}_L$ ($R^2 = 0.87$), Eq. (17) in $\overline{w}_W$ ($R^2 = 0.87$) and Eq. (18) in $\overline{w}_T$ ($R^2 = 0.87$)

Figure 5a shows the scatter plot of mean leaf mass $\overline{w}_L$ to population density ρ of each plot on logarithmic coordinates. The self-thinning line of leaf mass can be described by the following equation,

$$\overline{w}_L = 1.133 \cdot \rho^{-1.11} \tag{16}$$

where $\overline{w}_L$ is the mean leaf mass and K is the multiplying factor of leaf whose estimate was 1.133 kg $m^{-2/\o}$. As shown in Fig. 5a, the observed data are well fitted to Eq. (16). Equation (16) indicates that the α-value of leaf mass was not significantly different from 1.0 ($t = 1.968$, df $= 41$, $p > 0.05$), which showed that the stand leaf biomass is constant regardless of the population density ρ.

As shown in Figs. 5b and 5c, the self-thinning line of wood mass and aboveground mass can be described by the following equations,

$$\overline{w}_W = K \cdot \rho^{-1.55} \tag{17}$$

$$\overline{w}_T = K \cdot \rho^{-1.48} \tag{18}$$

where $\overline{w}_W$ and $\overline{w}_T$ is the mean wood mass and aboveground mass, and K is the multiplying factor whose estimate was 11.669 kg $m^{-2/\o}$ in wood and 12.850 kg $m^{-2/\o}$ in aboveground. The self-thinning

exponent α was 1.55 in wood (Eq. (17)) and 1.48 in aboveground (Eq. (18)), which was not significantly different from 3/2 in wood ($t = 0.556$, df = 41, $p > 0.05$) and aboveground ($t = 0.270$, df = 41, $p > 0.05$). These results can be regarded as evidence in favour of the 3/2 power law of self-thinning in wood and aboveground.

4. Discussion

The self-thinning exponent α concerning leaf mass calculated from Eq. (9) using different exponents θ and δ from Eq. (3) and Eq. (4) was 1.11 in leaf (Table 1), which was coincided with Eq. (16). On the other hand, the multiplying factor K in Eq. (12) calculated using the allometric coefficients g_θ and g_δ respectively from Eq. (3) and (4) in leaf was estimated to be 1.13 kg m$^{-2/\emptyset}$. The α-value was not significantly different from 1.0 ($t = 1.968$, df = 41, $p > 0.05$), which showed that the stand leaf biomass is constant regardless of the population density ρ. This study presented evidence for a constant amount of leaf biomass per ground area in self-thinning stands of *Bruguiera gymnorrhiza*. Similar results have been obtained for the self-thinning populations of *Trifolium pretense* and *Mercurialis perennis* [14], and *Pinus densiflora* and *Nothofagus solandri* [51]. Similarly, Moller [52] noted that the leaf biomass in *Fagus sylvatica* and *Picea abies* stands was comparatively constant regardless of the site, age, height and degree of thinning. Satoo et al. [53] also found that the leaf biomass was more or less constant irrespective of stand density in young plantations of *Pinus densiflora*. Therefore, it seems that the constant leaf biomass of stands experiencing self-thinning has been well established. On the other hand, it is commonly believed that the leaf biomass per ground area of developing population reaches a maximum value while the stand is relatively young, after which it decreases somewhat, then it assumes a nearly constant value at the older stand ages [54-55]. Thus, it can be postulated that the predictable size-density relations in self-thinning populations can be explained on the basis of regulation and redistribution of a fixed amount of foliage among a declining number individuals.

On the other hand, the self-thinning exponents α concerning wood mass using different exponents θ and δ respectively from Eq. (3) and Eq. (4) was 1.55 (Table 1), which was not significantly different from 3/2 ($t = 0.556$, df = 41, $p > 0.05$). But in case of leaves, the self-thinning exponent was not significantly different from 1.0. These results revealed that woody organs have a growth pattern different from leaves, i.e. the leaves are two-dimentional in shape, while woody organs are three-dimentional in shape [56]. The multiplying factor K in Eq. (12) calculated using the allometric coefficients g_θ and g_δ respectively from Eq. (3) and (4) in wood was estimated to be 11.669 kg m$^{-2/\emptyset}$. The α-value was not significantly different from 3/2, therefore, it is concluded that the 3/2 power law of self-thinning holds for wood mass in overcrowded *B. gymnorrhiza* stands.

The self-thinning exponent, based on the allometric relationships, concerning aboveground mass was 1.48 (Table 1) calculated from Eq. (9) using θ and δ respectively from Eq. (3) and Eq. (4). The δ-value in tree was not significantly different from zero ($t = 1.4027$, df = 41, $p > 0.05$). Weller [20] assumed that $\bar{d}$ is constant regardless of $\bar{w}$, i.e. δ is zero. Therefore, our study confirmed Weller's assumption. However, Xue et al. [57] reported in *Pinus tabulaeformis* Carr. and *Larix principis-rupprechtii* Mayr stands that the δ-values concerning mean stem volume were significantly larger than zero. The average of $\bar{d}$, i.e. biomass density (biomass/$\bar{H}$), was estimated to be 2.40 $\pm$ 0.12 (SE) kg m^{-3}, which was considerably higher than 1.3 to 1.5 kg m^{-3} of ordinary terrestrial forests except for dwarf pine (*Pinus pumila* Regel) forests having a quite high value of $\bar{d}$ [58]. This is because the height of *B. gymnorrhiza* growing near the northernmost limit of its distribution is low [59]. In fact, the mean height ranged from 3.5 to 8.6 m (Fig. 3); nevertheless the leaf mass might be large. The multiplying factor K in Eq. (12) calculated using the allometric coefficients g_θ and g_δ respectively from

Eq. (3) and (4) was estimated to be 12.850 kg m$^{-2/\text{ø}}$ in aboveground. The α-value was not significantly different from 3/2 ($t = 0.270$, df $= 41$, $p > 0.05$) in aboveground mass. This result is strongly in favour of the 3/2 power law based on the geometric model proposed by Yoda et al. [4], though there are debates that the self-thinning exponents is closer to 4/3 based on the metabolic model proposed by Enquist et al. [21-22].

5. Conclusion

It is concluded that the resultant self-thinning equations coincided with Eq. (16), (17) and (18). This means that the results based on the allometric model strengthens the justification of the simple geometric model proposed by Yoda et al. [4]. As far as the present overcrowded *B. gymnorrhiza* stands are concerned, the self-thinning can be explained by the simple geometric model, though there are debates that the self-thinning exponent is closer to 4/3 based on the metabolic model proposed by Enquist et al. [21-22].

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