**Original Article**

**Title: Carrying capacity for tree biomass of a subtropical mangrove along a river in Japan inferred from forest structural features.**

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**Abstract:**

A subtropical mangrove along the Miyara River in Ishigaki Island, Japan was studied for evaluating the carrying capacity for biomass of the monospecific stands. *Rhizophora stylosa* and *Bruguiera gymnorrhiza* were dominant in the downstream area whereas *B. gymnorrhiza* in the upstream. The stem diameter *D,* stem height *H*, fine roots mass were measured and, aboveground biomass *AGB*, belowground coarse root biomass *BGB*coarse were estimated. The *AGB*, *BGB*coarse and fine root mass were estimated as 128.46 Mg ha-1, 31.01 Mg ha-1 and 12.75 Mg ha-1 in the *R. stylosa*; 269.82 Mg ha-1, 93.68 Mg ha-1 and 11.13 Mg ha-1 in the downstream *B. gymnorrhiza*; and, 227.94 Mg ha-1, 81.05 Mg ha-1 and 6.35 Mg ha-1 in the upstream *B. gymnorrhiza* plots, respectively. The *AGB* did not differ among theplots, meanwhile *BGB*coarse was significantly lower and fine root mass was significantly higher in the *R. stylosa* plots than in the downstream *B. gymnorrhiza* plots. Significantly lower mean individual phytomass *w*t specific to tree density *ρ* of *R. stylosa* plots than *B. gymnorrhiza* plots in the *ρ* **–** *w*t relationship was found, which denoted the lower carrying capacity for *AGB* of *R. stylosa* than that of *B. gymnorrhiza*. The results rejected our hypothesis that the stressful edaphic conditions, such as high soil salinity and low pH at the downstream, limit biomass and potential canopy height *H*max of mangrove along a river gradient but partly supported another hypothesis that biomass and *H*max differs between different mangrove species at the same edaphic environment.

**Key words**: Aboveground biomass, belowground biomass, fine root mass, core sampling method, carrying capacity.

**Introduction**

The spatial patterns of species composition and stand structure in mangroves are affected by the degree of tidal inundation, salinity or other measurable gradients (Gleason and Ewel, 2002; Satyanarayana et al., 2002). Two major environmental gradients; from the river mouth to upstream and from riverside to inland are generally observed in riverine mangroves (Bunt, 1996). However, there are few studies on the structure of monospecific stands and interspecific variation along rivers (Enoki et al., 2014; Khan et al., 2013) focusing on salinity and nutrient gradients (Sofawi, 2017; Suwa et al., 2009).

The variation of the stem diameter - height (*D* ˗ *H*) relationship is an important element for describing forest stands (Mugasha et al., 2013) which provide clues on how trees acclimate to their environment or compete for resources (Canham et al., 2006), and the potential tree height indicates a site index in forestry (Thomas, 1996). It has been proposed that variability in the *D* ˗ *H* relationships within and among different habitats is adaptive and a passive response to an environmental gradient; of factors such as light, elevation, slope, aspect or proximity to the coast (Schmidt et al., 2011). Strong empirical associations have been noted between the *D* ˗ *H* relationship and tree density *ρ* (Temesgen et al., 2007). Crowding reduces the growth rates of individuals but is dependent on their size (Vandermeer and Goldberg, 2003), and thus the mean *ρ* **–** mean individual phytomass *w*t relationship provides information about the stand-carrying capacity which varies by locations.

The studies on belowground roots (Wang et al., 2018), especially fine roots are scarce (Smithwick et al., 2014; Warren et al., 2015) but fine root biomass is one of the major components of forest ecosystem (Van Do et al., 2015) because it represents a large carbon cost to trees and is an important carbon source to the soil (Zhou et al., 2014).

Mangrove tree biomass is sensitive to soil nitrogen (*N*) availability (Feller et al., 2003; McKee et al., 2007), salinity and pH (Koch, 1997; Feller et al., 2003). The leaf mass area (*LMA*) of a species is a good indicator of resources acquisition (Wright et al., 2004) which is linked to photosynthesis activities ([Hassiotou](https://pubmed.ncbi.nlm.nih.gov/?term=Hassiotou%20F%5BAuthor%5D) et al., 2010); therefore, a higher *LMA* represents higher resource acquisition. High soil salinity and low pH increase stress conditions for growth whereas higher available *N* and *LMA* indicate the higher biomass growth. Suwa et al. (2009) showed that tree height and size decrease with the increasing stress conditions, including an increase in pore water salinity and a decrease in soil *N*.

In the present study, we analyzed the stand structure and biomass components including above- and belowground biomass in the monospecific mangrove stands along the Miyara River of Ishigaki Island, Japan, for evaluating the carrying capacity of biomass along a river gradient through testing the following hypothesis: The stressful edaphic conditions, such as high pore salinity and low pH at the downstream areas, limit biomass and potential canopy height of mangrove along a river gradient. Also, we tested the following hypothesis that biomass and potential height differs between different mangrove species even at the same edaphic environment.

**2. Materials and methods**

**2.1 Study site**

We conducted this study along the Miyara River (24°21′N, 124°12′E), on Ishigaki Island, Japan (Fig. 1). Mean monthly temperature from January, 2001 to October, 2022 ranged between 18.9° C during January and 29.8° C during July resulting in an average of 24.6° C. Mean monthly rainfall varied between 127.3 mm during March and 278 mm during September with an average rainfall of 177.1 mm.

Three true mangrove species were observed along the river: *Bruguiera gymnorrhiza* (L.) Lamk., *Rhizophora stylosa* Griff., and *Kandelia obovata* (S., L.) Yong. *K. obovata* was observed only in small patches scattered along the bank of river. In this study, we focused on downstream *R. stylosa* and *B. gymnorrhiza* plots for comparisons among different species, and *B. gymnorrhiza* plots in the upstream and downstream for comparisons among different locations along the river.

**2.2 Study plot and topographic measurement**

A total, of 12 plots were established; each plot had a 7 m radius and 153.9 m2 area, of which four *B. gymnorrhiza* plots in the upstream area; and four *B. gymnorrhiza* and four *R. stylosa* plots were established in the downstream area along the Miyara River of Ishigaki in 2021. A minimum distance of 25 m from the center of one plot to another was maintained. The comparative elevation of each plot was measured near the center of the plot. To measure the comparative elevation of each plot, we used 2 m long PVC pipes. Initially, PVC pipes were rubbed with white powder. The water level was continuously monitored over a week by observing the clear marks of the water on the pipes. We assumed the lowest mark of the water level among the plots as “0” m and then calculated the comparative elevation of all other plots respective to that plot. In the present study, the elevation of plot 3 of upstream *B. gymnorrhiza* was found to be the lowest and considered as “0” m (actual value of 47 cm).

**2.3 Tree census and estimation of biomass**

The stem diameter at 1.3 m (*D)* of the trees with *D* > 5 cm within a 7 m radius plot was recorded with a measuring tape, and trees with *D* < 5 cm were recorded within a 2 m radius from the center of the plot (Kaufmann and Donato, 2012). Tree height (*H*) was measured using a 15 m-height fiberglass pole (AT-15, Myzox Co., Ltd., Aichi) or a laser range finder (TruPulse360, Laser Technology, Inc., Colorado). *D* of *R. stylosa* trees was measured 0.1 m above the highest prop root (Clough et al., 1997). We used the equations provided by Chave et al. (2005) and Clough and Scott (1989) to estimate above-ground biomass (*AGB*) and above-ground roots biomass (*AGB*roots) of *R. stylosa,* respectively. The equations of Tamai et al. (1986) were used to estimate *AGB*, and belowground biomass of coarse roots (*BGB*coarse) of *B. gymnorrhiza* and *R. stylosa,* respectively, which included only coarse roots (>2 mm in diameter).

For *R. stylosa*,

*AGB* = 0.0509 × *WD* × *D2 H*………..….(1)

*AGB* *(Roots)=*  0.0068× *D*3.1353……………………(2)

*BGB* = 0.00974×(*D2 H*)1.05……………………..(3)

For *B. gymnorrhiza*,

*AGB* = 0.033141×(*D2 H*)1.0338………………….(4)

*BGB* = 0.0188×(*D*2 *H*0.909)……………….…..(5)

where, *WD* is wood density, for which data were collected from the global wood density database (Zanne et al., 2009). The calculated mean values for the Asian region were used in this study. Here, the mean values of *WD* for *R. stylosa* and *B. gymnorrhiza* were 0.83 and 0.86, respectively.

**2.4 Soil and leaf properties analysis**

Total soil *N* was analyzed from oven-dried soil samples by CN˗analyzer (JM Macro Corder-1000, J-Science Co, Ltd., Kyoto, Japan). Pore water was collected from three different positions in each plot by digging holes. A 15 ml cylinder syringe with a filter was used for pore water extraction to remove soil from the water. A standard pH meter (LAQUAtwin, HORIBA Advanced Techno Co., Ltd., Japan) was calibrated using buffer solutions (pH 4 and 7) to measure the pH of soil pore water. Soil pore water salinity was measured using a salinity meter (Atago ES-421, Tokyo, Japan).

A scanner (Epson ES-G11000, Japan) and GIMP 2.10.22 software (free online software for image processing and area calculation) were used to scan and measure the leaf area of eight fully expanded leaves in the sun in each plot of the two species. In total, leaf areas of 96 leaves, 32 from each of the downstream *R. stylosa*, the downstream *B. gymnorrhiza* and the upstream *B. gymnorrhiza* plots were measured, respectively. Then, weights were taken after oven drying at a constant temperature of 65oC for 72 hours to calculate *LMA* (kg m-2).

**2.5 Measurement of fine root biomass**

The core sampling method was applied to measure fine root (< 2 mm in root diameter) mass to a soil depth of 30 cm soil depth from the ground surface. In total, 96 soil cores were measured from March 2022 to September 2022; eight core samples from every survey plot were obtained. The soil core was prepared using a stainless-steel cylinder with an inner diameter of 5 cm and a length of 40 cm (Zibo Baishun Stainless Steel, Zhoucun, China). The sampled soil cores were mixed with water and passed through a 2 mm sieve to remove leaves, and branches along with other debris from the soil. Furthermore, after washing away the mud particles, the remaining were collected and packed in a bag, brought back to the laboratory, and stored in a freezer at -20° C. Finally, samples were placed in an oven at 65° C for 72 hours and then the dry masses were measured.

* 1. **Statistical analysis and applied models**

One-way analysis of variance (ANOVA) was performed using KaleidaGraph version 4.0 software (Hulinks Co., Ltd., Tokyo, Japan) to evaluate the effect of difference of threegroup of *R. stylosa*, downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots (defined as *plots*)on the focal biometrics such as *D*, *H*, *AGB*, *BGB*, fine root mass, soil salinity, soil pH, soil *N* and comparative elevation, and post-hoc Bonferroni test was performed to examine the difference of the focal biometrics among the plots.

The relationship between mean individual phytomass *w*t (kg) and tree density *ρ* (ha-1) were modeled with the following power equation (Yoda et al., 1963; White and Harper, 1970; Hutchings and Budd, 1981; Zeide, 1987; Weller, 1989):

*w*t = *k* *ρ*-α ………………………..(6)

where, *k* and *α* arecoefficients, respectively. Log-transformed values of *w*t and *ρ* were used to determine the value of *k* and *α* considering additive error structures (Kerkhoff and Enquist, 2009).

To test the variation of the *ρ* ˗ *w*trelationshipsamong the three sites, ANCOVA (analysis of covariance) was performed after the log transformation of Eq. 6. The Bonferroni post-hoc test was performed to examine pair-wise differences among the three sites whenever the ANCOVA detected a significant effect of site on the response variable.

A hyperbolic function was used to evaluate the tree *D*˗*H* relationships.

*H* = ………………………..(7)

where, *H*max is the asymptotic maximal tree height; and ‘*a*’ is a coefficient. Eq. 7 corresponds to a special case of a generalized allometric function when the value of the exponent for *D* is assumed as one (Ogawa et al., 1965; Kira and Ogawa, 1971). We performed *F*-test to examine differences in the *D* ˗ *H* relationships among sites within a species as well as between two species within a site. In each case, the pooled data as well as the data of each site position (downstream or upstream) were regressed separately. The resulting residual sums of squares (RSS) values were used for the *F*-test (Aiba and Kohyama, 1997; Suwa et al., 2009).

**3. Results**

**3.1 Tree census and measurement of above-ground biomass**

*Bruguiera gymnorrhiza* (L.) Lamk. was dominant across the entire mangrove area along the Miyara River, whereas *R. stylosa* Griff. was observed only in the downstream area. *K. obovata* (S., L.) Yong grew only along the edges of the river in the downstream area. The *H* of *R. stylosa*, downstream and upstream *B. gymnorrhiza* plots were observed 5.80 ± 0.09 m, 8.15 ± 0.86 m and 6.70 ± 0.85 m respectively (Table 1). The one-way ANOVA suggested that the effect of *plots* on the mean values of *H* was significant (*p* < 0.01) and the post-hoc test suggested that mean values of *H* of the downstream *B. gymnorrhiza* plots were significantly higher than those of *R. stylosa* plots (*p* < 0.01) and than those of upstream *B. gymnorrhiza* plots (*p* < 0.05).

The *D* of *R. stylosa*, downstream and upstream *B. gymnorrhiza* plots were observed 7.86 ± 1.37 cm, 16.77 ± 4.75 cm and 12.94 ± 0.86 cm, respectively (Table 1). The effect of *plots* on the mean *D* was significant (*p* < 0.05) in the one-way ANOVA (Table 1) and the post-hoc test showed that the *D* of the *R. stylosa* plots was significantly lower than that of downstream *B. gymnorrhiza* plots (*p* < 0.01) although an insignificant variation was observed between downstream *B. gymnorrhiza* plots with those of the upstream *B. gymnorrhiza* plots (*p* > 0.05). The *D* classes in Fig 2 shows that 52% of the trees of *R. stylosa* were within 9 cm of diameter class, which is 20% and 41% for the downstream and the upstream *B. gymnorrhiza* plots, respectively. Maximum *D* for *R. stylosa* was 17 cm which extended more than 21 cm for downstream and upstream *B. gymnorrhiza* plots.

The mean *AGB*, for *R. stylosa*, downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* trees, were observed 128.5 ± 44.5 Mg ha-1; 269.8 ± 72.8 and 227.9 ± 30.8 Mg ha-1, respectively (Table 1). An insignificant variation of the effect of *plots* on *AGB* among plots was found in one-way ANOVA (*p* > 0.05, Fig. 3).

The *ρ* were 11306 ± 9603 ha-1 in the *R. stylosa* plots, 2864 ± 1778 ha-1 in the downstream *B. gymnorrhiza* plots and 4531 ± 1799 ha-1 inthe upstream *B. gymnorrhiza* plots,respectively (Table 1). The one-way ANOVA suggested an insignificant effect of *plots* on tree density *ρ* among plots (*p* > 0.05, Table 1).

The cumulative basal area were observed 32.41 ± 14.09 m2 ha-1, 53.36 ± 14.68 m2 ha-1 and 50.58 ± 4.99 m2 ha-1 for the *R. stylosa*, the downstream *B. gymnorrhiza* and the upstream *B. gymnorrhiza* plots, respectively (Table 1). An insignificant variation was suggested in the one-way ANOVA of basal area among plots (*p* > 0.05).

**3.2 Belowground coarse root and fine root estimation**

Themean coarse root biomass *BGB*coarse were observed 31.01 ± 11.42 Mg ha-1 for the *R. stylosa* plots, 93.68 ± 23.40 Mg ha-1 for the downstream *B. gymnorrhiza* plots, and 81.05 ± 9.70 Mg ha-1 fortheupstream *B. gymnorrhiza* plots, respectively (Table 1). The one-way ANOVA result suggested that the effect of *plots* on *BGB*coarse was significant (*p* < 0.01) and the post-hoc test suggested that the *BGB*coarse of the *R. stylosa* plots were significantly lower than that of the downstream *B. gymnorrhiza* plots (*p* < 0.01, Fig. 3); and that of the upstream *B. gymnorrhiza* plots (*p* < 0.01, Fig. 3).

The fine root biomass was observed as 12.75 ± 1.05 Mg ha-1, 11.13 ± 1.23 Mg ha-1 and 6.35 ± 3.34 Mg ha-1 for the *R. stylosa* plots, the downstream *B. gymnorrhiza* plots and the upstream *B. gymnorrhiza* plots, respectively (Table 1). The effect of the *plots* on fine root biomass was found significant (*p* < 0.01) in one-way ANOVA and the post-hoc test suggested that the fine root biomass of *R. stylosa* plots was significantly higher than those of the upstream *B. gymnorrhiza* plots (*p* < 0.01, Fig. 3); and the downstream *B. gymnorrhiza* plots was significantly higher than that of the upstream *B. gymnorrhiza* plots (*p* < 0.05, Fig. 3).

Thetotal belowground biomass *BGB*total of the *R. stylosa*, downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots were measured 43.76 ± 10.49 Mg ha-1, 104.81 ± 24.17 Mg ha-1 and 87.40 ± 12.91 Mg ha-1, respectively (Table 1). The one–way ANOVA suggested that the effect of *plots* on *BGB*total was significant and the post-hoc test suggested that the estimated *BGB*total for the *R. stylosa* plots was significantly higher than that of the downstream *B. gymnorrhiza* plots (*p* < 0.01), and that of the upstream *B. gymnorrhiza* plots (*p* < 0.05).

**3.3 Soil and leaf properties**

Mean soil pore water salinity (%) of *R. stylosa*,downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots,were 0.91 ± 0.2, 0.76 ± 0.22 and 0.16 ± 0.05, respectively (Table 2). The one-way ANOVA suggested that the effect of *plots* on salinity was significant (p <0.01) and the post-hoc test suggested that the soil salinity of upstream *B. gymnorrhiza* plots were significantly lower than that of downstream *B. gymnorrhiza* plots (*p* < 0.01), and *R. stylosa* plots (*p* < 0.01).

Mean pH were measured as 7.28 ± 0.12, 7.05 ± 0.12 and 7.54 ± 0.11, respectively for *R. stylosa*,downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots (Table 2). The effect of *plots* on pH was significant (*p* < 0.01) in resulted one-way ANOVA and the post-hoc test suggested that the pH of upstream *B. gymnorrhiza* plots were significantly higher than that of downstream *B. gymnorrhiza* plots (*p* < 0.01), and *R. stylosa* plots (*p* < 0.05).

Mean soil *N* were 0.16 ± 0.02, 0.17 ± 0.02 and 0.12 ± 0.02 for the *R. stylosa*,downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots, respectively (Table 2). The one-way ANOVA showed that the effect of plots on soil *N* (%) was significant (*p* < 0.05) and the post-hoc test showed higher soil *N* at the downstream *B. gymnorrhiza* plots than those at the upstream *B. gymnorrhiza* plots (*p* < 0.05).

*LMA* (g cm-2) were 0.032 ± 0.003, 0.029 ± 0.002 and 0.025 ± 0.003 for the *R. stylosa*, downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots, respectively (Table 2). One-way ANOVA suggested that the variation of *LMA* among *plots* was significant (*p* < 0.01) and the post-hoc test suggested that *LMA* at the *R. stylosa* plots was significantly higher than that at the upstream *B. gymnorrhiza* plots (*p* < 0.01).

The comparative elevations were 51.75 ± 18.93 cm (S.D), 23.25 ± 17.39 cm and 4.25 ± 4.63 cm for *R. stylosa*, downstream *B. gymnorrhiza* and upstream *B. gymnorrhiza* plots, respectively (Table 2). A significant effect of *plots* on comparative elevation was suggested by one-way ANOVA ((*p* < 0.01) and the post-hoc test suggested that the comparative elevation was higher at *R. stylosa* plots than those at the upstream *B. gymnorrhiza* plots (*p* < 0.01).

**3.4 Analysis of the *D* ˗ *H*** **relationships**

According to the analysis of the *D* ˗ *H* relationship (Fig. 4) based on Eq.1, it did not differ between the downstream and upstream *B. gymnorrhiza* plots (*F*(2, 331) =1.05, *p* = 0.32); and between the downstream *B. gymnorrhiza* and *R. stylosa* plots (*F*(2, 527) =1.06, *p* = 0.24). The *a* and *H*maxin Eq. 7 were estimated as 2.20 m cm-1  and 9.30 m for *R. stylosa* plots, 1.78 m cm-1 and 12.26 m for the downstream *B. gymnorrhiza* plots, and 1.25 m cm-1  and 13.07 m for the upstream *B. gymnorrhiza* plots, respectively (Table 3) (see Fig. S6 for details).

**3.5 Analysis of the *ρ* ˗ wt** **relationships**

The *ρ* ˗ *w*trelationships were regressed with Eq. 2 (Fig. 5; *R*2 = 0.99, 0.97 and 0.96 for *R. stylosa* plots, the downstream *B. gymnorrhiza* plots and the upstream *B. gymnorrhiza* plots, respectively).

As summarized in table 3, the estimated values of *α* were -0.65 ± 0.04 (SE), -1.37 ± 0.21 and -1.32 ± 0.15 for the *R. stylosa* plots, the downstream *B. gymnorrhiza* plots and the upstream *B. gymnorrhiza* plots, respectively. The values of intercept (ln*k* in Eq. 2) were estimated as 9.97 ± 0.37 (SE), 15.84 ± 1.64, 15.01 ± 1.24 for the *R. stylosa* plots, the downstream *B. gymnorrhiza* plots and the upstream *B. gymnorrhiza* plots, respectively.

ANCOVA suggested that the *α* did not show differ significant difference between the upstream and the downstream *B. gymnorrhiza* plots (*p* > 0.05). On the other hand, the estimated *α* wassignificantly higher in the downstream *R. stylosa* plots than that in the *B. gymnorrhiza* plots (*p* = 0.006).

**4. Discussion**

**4.1 Forest structural feature and above-ground biomass distribution**

Dominant mangrove species in the present study site was *Bruguiera gymnorrhiza* around the upstream area, while the downstream area was occupied mostly by *R. stylosa* and *B. gymnorrhiza* with some *K. obovata* trees scattered along the banks of the river which is a typical species zonation pattern for mangroves around the Ryukyu archipelago as reported in Enoki et al. (2009) and Suwa et al. (2009). In the present study, the mean *H* of *B. gymnorrhiza* was significantly higher in the downstream plots than that in the upstream plots (*p* < 0.05), whereas the maximum potential tree height (*H*max in Eq. 7) did not differ significantly between the upstream and downstream plots (Table 3). The *D* and *H* of the downstream *B. gymnorrhiza* plots were significantly higher than those of the upstream plots (*p* < 0.05), resulting in a higher cumulative basal area in the downstream plots than those in the upstream plots. *Bruguiera gymnorrhiza* has more shade-tolerant characteristics when grown in almost the same habitat with *Rhizophora* species (Putz and Chan, 1986). The relatively high canopy height (*H*) and shade-tolerant characteristics of *B. gymnorrhiza* imply a greater potential for them to be dominant than *R. stylosa* at our present study site, similar reported by Enoki et al. (2009) for mangroves in Iriomote Island near the present study site.

Here, insignificant variation among the study plots were observed and estimated *AGB* as 128.5˗269.8 Mg ha-1 for mangroves along the Miyara river which was much higher than 97.6˗108.1 Mg ha-1 reported for mangroves in Ishigaki Island by Suzuki and Tagawa (1983) that have a mean *H* of6 m as opposed to 5.8˗8.15 m for the trees in the present study. The *AGB* and mean *H* decreased gradually with increasing latitude (Saenger et al., 1993; Khan et al., 2009). The present study site located in a subtropical zone at a high latitude, and the *AGB* was relatively high compared to other mangroves in high latitude areas as previously reported in the Ryukyu Islands of Japan (Table 4), but similar to some mangroves in low latitude areas. On the contrary, mean *H* remained consistent with that of the other high latitude mangroves. Although, mean *H* is causally responsible for biomass accumulation (Saenger et al., 1993), other factors, such as basal area and *ρ* also affect *AGB*. We suspect that the relatively higher cumulative basal area for *R. stylosa* and *B. gymnorrhiza* of the present study (32.88 m2 ha-1 in *R. stylosa* and 51˗53.4 m2 ha-1 in *B. gymnorrhiza*) than those in the other high latitude mangroves could contribute to their higher *AGB* estimation (Table 4).

The mean individual phytomass *w*t and tree density *ρ* showeda linear negative correlation to each other (Fig. 5) on logarithmic scale (Weller, 1987 and 1989), which indicated the balance between individual growth and mortality at the stand level (Analuddin et al., 2009). As showing in Fig. 5, the difference of *ρ* ˗ *w*t relationships between the upstream and downstream *B. gymnorrhiza* plots was insignificant (*p* > 0.05, ANCOVA). The *α* value in Eq. 6 was estimated as -1.33 ± 0.19 (95% confidence interval CI) for *B. gymnorrhiza* stands including both the upstream and downstream plots, was significantly lower than -1.0 considering its range of 95% confidence intervals (Table 3), which implies that *AGB* increases with decreasing tree density as *B*. *gymnorrhiza* stands grow similar to other *B*. *gymnorrhiza* stands in Okinawa island, Japan (Deshar et al. 2012, Kamara et al. 2014). The previous studies on *B*. *gymnorrhiza* stands reported that the *α* value was close to -3/2 (Deshar et al. 2012, Kamara et al. 2014), which is namely the 2/3 law of self-thinning phenomenon (Yoda et al. 1963). In general, *ρ* decreases successively owing to the death of smaller trees caused by one side competition under crowded conditions (Weiner and Whigham 1988), and surviving trees continued to grow, i.e. *ρ* decreases and *w*t increases as a forest grows. The present study also confirmed that the estimated *α* values for *B. gymnorrhiza* stands were insignificantly different from -3/2 taking into account its 95% confidence interval (Table 3).

However, the *ρ* ˗ *w*t relationships differed significantly between the *B. gymnorrhiza* and *R. stylosa* plots at the downstream site (*p* < 0.01, ANCOVA). For a lower range of *ρ* < 104 ha-1, the *R. stylosa* plots showed apparently lower *w*t than the *B. gymnorrhiza* plots (Fig. 5). In the *R. stylosa* plots, the *α* value was estimated as -0.65 ± 0.08 (95% CI) which was significantly higher than -1.0 (Table3). Here, we report the *ρ* ˗ *w*t relationship for *R. stylosa* stands for the first time, which has not been fully studied yet, in alliance with the 2/3 law of self-thinning phenomenon reported for *Rhizophora* spp. plantations in Thailand by Kongsanchai (1988). Interestingly, the estimated *α* value (> -1.0) implies that *AGB* decreases with decreasing tree density as the *R. stylosa* stand grows. This may be because *R. stylosa* growth was limited at the edge of the river in the present study site and old growth *R. stylosa* trees were severely damaged which might be due to frequent flooding or wind disturbance near the edge of the river (see Fig. S7). Thus, there was an apparent interspecific difference in the *ρ* ˗ *w*t relationship between the *B. gymnorrhiza* and the *R. stylosa* plots which indicated a higher carrying capacity for *w*t or*AGB* of the *B. gymnorrhiza* trees than for the *R. stylosa* trees in the present study. Also, *Bruguiera gymnorrhiza* has been reported as one of the most shade-tolerant species in mangrove environment and exhibits enhanced shade tolerance when grown along with *Rhizophora* species (Putz and Chan, 1986), these shade-tolerant characteristics may prove to be beneficial over *R. stylosa* for light resource competition in the present study.

**4.2 Belowground coarse and fine root distribution**

Lower *w*t might be one of the reasons for allocating lower *BGB* in the upstream *B. gymnorrhiza* plots than that of the downstream because belowground tree biomass allocation is positively correlated with that of aboveground parts because these are controlled by the same edaphic factors. Generally, stress condition like high salinity reduces belowground root biomass production (Sherman et al., 2003) but in our case, the salinity in the downstream (0.76˗0.91%) was quite lower compared to the salinity of the downstream sites of Okukubi river (2.58˗2.63%; Suwa et al., 2009) and the Fukido river (2.97˗3.30%; Yoshikai et al., 2022) which implies that the salinity level in the present study plots might not be enough to limit *BGB*. The higher *BGB* in the downstream plots than in the upstream plots; where salinity in the downstream was higher than upstream was supported as higher *BGB* with increasing salinity was observed for *Avicennia marina* and *Aegiceras corniculatum* dominated mangrove forests (Ball et al., 1997). In addition, linear trend of increasing *BGB* with increasing soil pore water salinity was observed *Rhizophora mangle* and *Laguncularia racemosa* dominated mangrove forest at Samana bay, Dominican Republic (Sherman et al., 2003). Moreover, the higher *BGB* in the downstream plots might be a consequence of the higher soil *N* in this area than in the upstream plots. The *BGB* of mangroves in the present study has similarity with that of some high latitude mangroves (Table 5), where it has been reported that high latitude areas tend to show high *BGB* in terrestrial forests (Vogel et al., 2008). The root shoot ratio (RSR) also has implications for *BGB* allocation, which generally correlates negatively with *H* (Wang et al., 2008). In the present study, the RSR increased with decrease in *H* in the upstream *B. gymnorrhiza* plots than those of downstream plots. Furthermore, RSR decreased with decreasing of *H* in *R. stylosa* plots compared to *B. gymnorrhiza* plots. The RSR of *R. stylosa* was smaller than that of *B. gymnorrhiza* because a significant part of the root mass was allocated to *AGB*root in *R. stylosa* whereas most of the root mass was allocated to *BGB* in *B. gymnorrhiza* (Kamruzzaman et al., 2019).

Komiyama et al., (1987) observed the higher root biomass within a denser *Rhizophora* spp. forest compared to that of less dense *Bruguiera* spp. and *Sonneratia* spp. forests. In the present study,we also found higher *BGB* in dense *R. stylosa* stands (11306 ha-1) than less dense *B. gymnorrhiza* stand (2572˗4109 ha-1) although the variation in tree density was not significant (Table 1).

The mean *BGB* of *B. gymnorrhiza* plots (80˗93.1 Mg ha−1) in the present study was lower than that of *B. gymnorrhiza* dominated stand (106.6˗173.3 Mg ha−1) in southern Thailand (Komiyama et al., 1987). The mean *BGB* of the present study was consistent with *BGB* found in the Sundarban mangrove forest (82 Mg ha−1) in Bangladesh (Kamruzzaman et al., 2018). Belowground coarse root biomass of the present study plots (66˗93 Mg ha-1) lies in the range of *BGB* of Hawkesbury river, Australia (35˗166 Mg ha-1, Saintilan, 1997), Rookery bay and naples bay, Florida, USA (61.85˗153.95 Mg ha-1, Giraldo, 2005), Mayaguez, Puerto Rico (64.4 Mg ha-1, Golley et al., 1962), Samana bay, Dominican Republic (67.8 Mg ha-1 , Sherman et al., 2003), Manko wetland, Japan (71.8 and 71.5 Mg ha-1, Khan et al., 2009; and Khan and Kabir, 2017, respectively), higher than that of mangroves in Western Australia (17.90˗50.30 Mg ha-1,Alongi et al., 2000), Thailand (25.48˗45.77 Mg ha-1, Poungpan, 2016), and lower than that of mangroves in Indonesia (164.44˗178.45 Mg ha-1, Komiyama et al., 1988), Brisbane River, Australia (109˗127 Mg ha-1, Mackey, 1993), Thailand (84.80˗509.50 Mg ha-1, Komiyama et al., 1987 and Komiyama et al., 2000), Pacific coast, Panama (306 Mg ha-1, Golley et al., 1969).

The significantly lower fine root mass in the downstream *B. gymnorrhiza* plots than in the *R. stylosa* plots in the present study was consistent with a fine root study on Iriomote Island, Japan near the present study site (Fujimoto et al., 2021). The fine root contribution to the total belowground biomass in the present study (7.27˗29.13%) was consistent with that of mangroves in the Dominical Republic (11.96%, Sherman et al., 2003), Taylor River (13.79%, Moya et al., 2011) and Shark River (18.18%, Moya et al., 2011) in the USA; and Micronesia (12.98˗21.85%, Cormier et al., 2015); and lower than that in Thailand (46.32˗56.82%, Chalermchatwilai et al., 2011, Komiyama et al., 1987) (Table 5). Lower fine root mass were observed in the low latitudes (Table 5) with some exceptions as high fine root mass was observed in low latitude in southern Thailand (137.5˗236.4 Mg ha-1, Komiyama et al., 1987) where they used trench method, and low fine root biomass was observed in high latitude in Mexico (1.8 Mg ha-1, Adame et al., 2014) where they applied ingrowth core method. These previous studies (Komiyama et al., 1987, Adame et al., 2014) are completely different sampling methods from the method used in the present study.

**4.3 Growth conditions at upstream and downstream sites**

The relatively high soil pore water salinity observed in the downstream plots (0.17% ± 0.02 in Table 2) compared to that in the upstream plots (0.12% ± 0.02), which was similar to the results of previous studies on mangroves in Japan (Suwa et al., 2009; Enoki et al., 2009; Yoshikai et al., 2022). These studies reported lower canopy heights (Suwa et al., 2009; Enoki et al., 2009) and lower *AGB* (Yoshikai et al., 2022) at downstream sites than that at the upstream. In contrast, the present study found that *H* and *D* of *B. gymnorrhiza* were significantly higher at the downstream plots than at the upstream plots, even though the downstream plots had higher soil salinity and pH than the upstream plots. Furthermore, insignificant variation of *AGB* was observed in the downstream *B. gymnorrhiza* plots with that of upstream plots. This may be partly because of the difference in soil salinity between the present study site and other mangroves reported by the previous studies, that is, the soil salinity in the downstream plots in the present study site ranged from 0.76˗0.91% which was apparently lower than 2.58˗2.63% at the downstream site in the Okukubi River (Suwa et al., 2009) and 2.97˗3.30% at the downstream site in the Fukido River (Yoshikai et al., 2022). Therefore, we concluded that the salinity conditions at the downstream site in the present study may not be sufficient to limit the growth of mangrove trees. On the other hand, soil *N* was significantly higher at the downstream plots than at upstream plots in the present study site, which can partly explain the reason why the downstream *B. gymnorrhiza* plots showed higher mean values in *D*, *H*, *AGB*, *BGB* and fine roots mass than the upstream *B. gymnorrhiza* plots (Table 2). Furthermore, the *LMA* of *B. gymnorrhiza* treeswas significantly higher in the downstream plots than in the upstream plots, that is, the *LMA* is highly correlated with the maximum photosynthetic rate (Wright et al., 2004). Thus, the results of the *LMA* also implies that the environmental conditions was more suitable for growth of *B. gymnorrhiza* trees at the downstream plots than at the upstream plots in the present study site, even though the downstream site showed significantly higher pore water salinity at the downstream site.

**5. Conclusion**

We tested a hypothesis that the stressful edaphic conditions, such as high pore salinity and low pH at the downstream areas, limit biomass and potential canopy height of mangrove along a river gradient. The present results showed that the downstream areas are characterized by higher salinity and lower pH than the upstream area but the estimated mean *AGB, BGB*, fine roots mass and *H* were not significantly higher in the upstream *B. gymnorrhiza* plots than those in the downstream *B. gymnorrhiza* plots. In addition, the *D* ˗ *H* and the *ρ - w*t relationships also did not differ between the upstream and downstream *B. gymnorrhiza* plots. Thus the present study clearly rejected our hypothesis though some previous studies reported the decreasing of *AGB* and *H* with increasing soil salinity from upstream to downstream areas in subtropical mangroves (Enoki et al., 2009; Suwa et al., 2009). It was concluded that the soil salinity at downstream areas was not enough high to limit biomass and canopy height of the *B. gymnorrhiza* plots in the present study site where the salinity ranged from 0.16% at the upstream area to 0.76% at the downstream area. Instead of salinity and pH conditions, significantly high soil *N* and *LMA* at the downstream *B. gymnorrhiza* plots partly explained the high mean *H* and fine roots mass, compared with that at upstream *B. gymnorrhiza* plots. In the comparison between the *B. gymnorrhiza* and the *R. stylosa* plots, we found that mean *D*, mean *H* and *BGB*coarse were lower in the *R. stylosa* plots than that in the *B. gymnorrhiza* plots at downstream area. Also, the *ρ - w*t relationships differed significantly between the *B. gymnorrhiza* and the *R. stylosa* plots. The difference of the *ρ - w*t relationships suggested that *w*t specific to *ρ* waslower in the  *R. stylosa* plots than that in the *B. gymnorrhiza* plots. Furthermore, the analysis of the *ρ - w*t relationships using the power function model in Eq. 6 suggested that *AGB* of the *R. stylosa* plots decreases as stand grow to be older, that is, the exponent α in Eq. 6 was significantly higher than unity, which implied that the carrying capacity for *AGB* was lower at the *R. stylosa* plots than at the *B. gymnorrhiza* plots in the present study.

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