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Temporal variation in litterfall production of *Bruguiera gymnorrhiza* stands on Okinawa Island, Japan

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**Abstract**

This study evaluated the litterfall dynamics of the mangrove *Bruguiera gymnorrhiza* along the Okukubi River, Okinawa Island, Japan. Leaf and stipule litterfalls occurred throughout the year, with respective distinct monthly patterns, and could be governed by monthly day length as well as monthly maximum wind speed and monthly mean air temperature, respectively. Branch litterfall depended on monthly maximum wind speed and increased exponentially with increasing monthly maximum wind speed. Flower and propagule litterfalls might be influenced by monthly mean air temperature and monthly day length, respectively. Leaves contributed the most to total litterfall and represented 71.0 and 68.7% of total litterfall in the first and second years, respectively. Annual leaf litterfall per plot was almost constant regardless of the tree density of the plot. *Bruguiera gymnorrhiza* showed a positive correlation between leaf production and reproductive organ production.

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**Keywords:** Monthly pattern; Environmental factors; Typhoon effect; Constant leaf biomass; Production load

**1. Introduction**

Mangroves are principal contributors of nutrients to coastal ecosystems. Litterfall is an important component of primary productivity, especially in light of its contribution to estuarine ecosystems [1]. Mangrove litterfall consists primarily of leaves, which become available to consumers and decomposers.

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Numerous studies have examined litterfall production in mangroves, particularly in tropical regions of Australia, Thailand, and Malaysia. However, data on species commonly found in subtropical regions are comparatively scarce [2-3]. Only a few studies have investigated litterfall production of *Bruguiera gymnorrhiza* (L.) Lam. stands [4-5] growing at the northern limit of their biogeographical distribution [6]. Therefore, the objectives of the present study were to (i) investigate monthly change in litterfall production of *B. gymnorrhiza* in relation to environmental factors, (ii) examine the relationship between leaf litterfall per tree and tree density, and (iii) evaluate the relationship between leaf and reproductive organ production.

2. Materials and Methods

2.1. Study Site

The study was conducted in a monospecific *Bruguiera gymnorrhiza* (L.) Lam. forest along the Okukubi River (26°27’ N, 127°56’ E) on Okinawa Island, Japan. During the study period, the average of mean annual air temperature was 23.2 ± 0.1°C (SE). The mean of annual day length was 4041.8 ± 3.9 h yr⁻¹, and the mean of annual rainfall was 2269.5 ± 183.5 mm yr⁻¹. The mean of monthly air relative humidity was 73.2 ± 0.4%. Monthly maximum wind speed varied from the lowest value of 9.4 m s⁻¹ in April 2011 to the highest of 36.2 m s⁻¹ in May 2011. We established a non-continuous (215 m × 5 m) belt-transect and divided it into 43 plots (5 m × 5 m each) in the *B. gymnorrhiza* forest. Tree height (*H*) and stem diameter at *H*/10 (*D₀.₁H*) were both measured in August 2010 and 2011. The means of tree density (*ρ*), *H*, and *D₀.₁H* were 0.93 ± 0.06 m⁻², 6.5 ± 0.1 m, and 8.7 ± 0.1 cm, respectively.

2.2. Litterfall Collection

Litterfall was collected using 1-mm mesh litter traps with a mouth area of 0.2 m². Two litter traps were placed in each plot at a height > 1 m from the ground to avoid tidal water. The litter traps were emptied monthly; the collected litterfall was kept in a cotton bag and transported to the laboratory where it was separated into leaves, stipules, branches, flower buds, flowers, and propagules. Individual litterfall components were dried at 80°C for 48 h, desiccated at room temperature, and then weighed using a digital balance (EK-600H, A & D Co., Ltd., Tokyo, Japan).

2.3. Statistical Analysis

Spearman’s rank correlation coefficient (*rₚ*) was used to evaluate the degree of harmony in monthly changes between years for each litterfall component. When *rₚ* = +1, the monthly changes in litterfall are completely harmonious between years; when *rₚ* = 0, the monthly changes are completely different between years; and when *rₚ* = -1, the monthly changes are completely opposite one another.

We performed a stepwise multiple regression analysis to determine the effects of five environmental factors (temperature, day length, rainfall, humidity, and maximum wind speed) on the litterfall of leaves, stipules, branches, flower buds, flowers, and propagules, using MA-MACRO/MRA software (ver. 3.0, Prac. Bus. Edu. Inst., Tokyo, Japan).

Mean annual leaf litterfall per tree was calculated by dividing annual leaf litterfall per plot by the number of trees in the plot. The relationship between mean annual leaf litterfall per tree (*l*, g yr⁻¹) and tree density (*ρ*, m⁻²) was described using the following power equation: *l* = *k* ⋅ *ρ*⁻*α*, where *k* and *α* are constants determined using KaleidaGraph (ver. 4.1, Synergy Software, USA).
3. Results and Discussion

Figure 1 shows the monthly patterns of litterfall components of *B. gymnorrhiza*. Leaf litterfall (Fig. 1a) and stipule litterfall (Fig. 1b) occurred continuously throughout the year, and each showed a clear monthly pattern; that is, leaf and stipule litterfalls were highest in summer and lowest in winter. These results are consistent with the observations of Hardiwinoto et al. [4], who recorded similar monthly patterns of leaf and stipule litterfalls in *B. gymnorrhiza* in Ohura Bay, Okinawa Island, Japan. Branch litterfall also showed a clear monthly pattern, with the highest peak in August (Fig. 1c). Flower bud litterfall was highest in summer and lowest in autumn and winter (Fig. 1d). Flower and propagule litterfalls were observed throughout the year but were highest in summer and lowest in winter (Fig. 1e and 1f). Spearman’s rank correlation coefficient ($r_s$) revealed that monthly trends of stipule ($r_s = 0.76, p = 0.005$), branch ($r_s = 0.63, p = 0.028$), and flower bud ($r_s = 0.68, p = 0.016$) litterfalls were harmonious, whereas leaf ($r_s = 0.57, p = 0.055$), flower ($r_s = 0.56, p = 0.060$), and propagule ($r_s = 0.51, p = 0.088$) litterfalls were different between years. Our monthly data suggest that monthly patterns of litterfall were consistent between years. Very high branch litterfall occurred in August and October 2010 and May and August 2011 because of typhoons with wind speeds exceeding 17.2 m s$^{-1}$. During the typhoons, green leaves were damaged and fell to the ground individually or while attached to living broken branches. These green leaves contributed to the excessive leaf litterfall (Fig 1a).

Figure 2 depicts the exponential relationship between branch litterfall and monthly maximum wind speed. Branch litterfall increased exponentially with increasing monthly maximum wind speed. Similar observations were recorded on Okinawa Island, Japan, by Hardiwinoto et al. [4] and Sharma et al. [3], who reported that typhoons had strong effects on branch litterfall of *B. gymnorrhiza* and *Kandelia obovata*, respectively. Branch litterfall of *Avicennia marina* (Forssk.) Vierh. was also correlated with storms on the Brisbane River, Queensland, Australia [7]. The frequent typhoons in Okinawa could be the main reason for the higher total branch litterfall rate of *B. gymnorrhiza* (Table 1).

Fig. 1. Monthly patterns of litterfall components of *B. gymnorrhiza*. Vertical bars represent one standard error of the mean.
The relationship between mean annual leaf litterfall per tree \((l, \text{ g yr}^{-1})\) and tree density \((\rho, \text{ m}^{-2})\) was described as \(l = 802.2 \cdot \rho^{-1.069}\) (Fig. 3). The exponent (-1.069) was very close to -1.0; thus, the following approximation holds: \(l = k \cdot \rho^{-1.0}\). According to this equation, the annual leaf litterfall per plot \((k = l \cdot \rho)\) was 749.1 ± 61.7 g m\(^{-2}\) yr\(^{-1}\), which was close to the mean annual leaf litterfall of 849.4 ± 104.0 g m\(^{-2}\) yr\(^{-1}\) (Table 1). This result indicates that annual leaf litterfall per plot was constant regardless of the number of trees in the plot. These data are generally consistent with the findings of Deshar et al. [8], who found that leaf biomass was constant in self-thinning stands of \textit{B. gymnorhiza} on Okinawa Island.

Figure 4 shows the correlation between stipule litterfall and reproductive organ litterfall. Stipule litterfall increased with increasing reproductive organ litterfall. In \textit{B. gymnorhiza}, flowering occurred throughout the year, and propagules were produced for more than half of the year. Flower buds and flowers of \textit{B. gymnorhiza} are reddish or yellow and contain carotenoids, which contribute less to the photosynthetic output of the plants [9]. Therefore, \textit{B. gymnorhiza} can be assumed to require more leaves to photosynthesize during reproductive organ production. High production of newly flushed leaves helps trees to produce more energy, which is used to produce more reproductive organs.

![Fig. 2. Exponential relationship between monthly branch litterfall and monthly maximum wind speed. ●: 1\(^{st}\) yr; ○: 2\(^{nd}\) yr.](image1)

![Fig. 3. Relationship between leaf litterfall per tree \((l)\) and tree density \((\rho)\) on log-log coordinates. The straight line is fit with \(l = 802.2 \cdot \rho^{-1.069} (R^2 = 0.82)\). ●: 1\(^{st}\) yr; ○: 2\(^{nd}\) yr.](image2)
Fig. 4. Correlation of stipule litterfall on reproductive litterfall ($r = 0.86, p < 0.001$).

Table 1. Annual amounts of litterfall components of $B. gymnorrhiza$ during the study period and significant values of t-test for comparisons of each litterfall component between 2010 and 2011

<table>
<thead>
<tr>
<th>Litterfall components</th>
<th>1st year</th>
<th>2nd year</th>
<th>t-statistic (P-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>953.44 ± 13.88 (71.0)</td>
<td>745.45 ± 20.28 (68.7)</td>
<td>10.15 (&lt;0.001)</td>
</tr>
<tr>
<td>Stipule</td>
<td>71.03 ± 1.24 (5.29)</td>
<td>45.2 ± 1.06 (4.16)</td>
<td>25.22 (&lt;0.001)</td>
</tr>
<tr>
<td>Branch</td>
<td>138.71 ± 8.96 (10.3)</td>
<td>266.69 ±14.48 (24.6)</td>
<td>8.72 (&lt;0.001)</td>
</tr>
<tr>
<td>Flower bud</td>
<td>2.13 ± 0.45 (0.16)</td>
<td>8.50 ± 0.75 (0.78)</td>
<td>8.41 (&lt;0.001)</td>
</tr>
<tr>
<td>Flower</td>
<td>139.47 ± 4.76 (10.4)</td>
<td>7.25 ± 0.74 (0.67)</td>
<td>64.84 (&lt;0.001)</td>
</tr>
<tr>
<td>Propagule</td>
<td>38.92 ± 5.37 (2.90)</td>
<td>12.42 ± 1.36 (1.14)</td>
<td>5.12 (&lt;0.001)</td>
</tr>
<tr>
<td>Total</td>
<td>1343.7 ± 25.15</td>
<td>1085.5 ± 30.55</td>
<td>7.33 (&lt;0.001)</td>
</tr>
</tbody>
</table>

Values are means (g m$^{-2}$ yr$^{-1}$) ± SE. Numerals in parentheses represent percentages of the total amounts.

Table 2. Adjusted $R^2$ values from the stepwise multiple regression analysis of litterfall components of $B. gymnorrhiza$ in relation to environmental factors. Significant probabilities are indicated by * ($P \leq 0.05$), ** ($P \leq 0.01$), or *** ($P \leq 0.001$)

<table>
<thead>
<tr>
<th>Component</th>
<th>Monthly mean temperature °C</th>
<th>Monthly day length h month$^{-1}$</th>
<th>Monthly rainfall mm month$^{-1}$</th>
<th>Monthly mean relative humidity %</th>
<th>Monthly maximum wind speed m$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>-</td>
<td>0.740**(0.836)</td>
<td>-</td>
<td>-</td>
<td>0.705**(0.836)</td>
</tr>
<tr>
<td>Stipule</td>
<td>0.480***(1.000)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.698***(1.000)</td>
</tr>
<tr>
<td>Branch</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.343**(1.000)</td>
</tr>
<tr>
<td>Flower bud</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Flower</td>
<td>0.174**(1.000)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Propagule</td>
<td>-</td>
<td>0.160**(1.000)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Numerals in parentheses are the tolerances of the coefficients of the multiple regression for a component.

As shown in Table 1, the mean amounts of each litterfall component significantly differed between years. Leaves contributed the most to total litterfall. Mean leaf litterfall was $953.44 \pm 13.88$ g m$^{-2}$ yr$^{-1}$ for the first year and $745.45 \pm 20.28$ g m$^{-2}$ yr$^{-1}$ for the second year, representing 71.0 and 68.7% for the first and second years, respectively (Table 1). Similar to other studies [10-11], leaves of $B. gymnorrhiza$ were the major contributors to total litterfall production.

Table 2 presents the results of the stepwise multiple regression analysis for litterfall components and environmental factors. Leaf litterfall was significantly affected by monthly maximum wind speed and...
monthly day length, whereas stipule litterfall was significantly correlated to monthly mean air temperature. Our results are supported by the findings of Nakagoshi and Nehira [12], who reported that cumulative temperature was directly proportional to the number of leaves and the rate of leaf production in mangrove seedlings. Branch and flower bud litterfalls depended on monthly maximum wind speed. In the Okukubi River, reproductive organs depended on monthly mean air temperature (flowers) or monthly day length (propagules), in agreement with Duke’s [13] findings that day length and air temperature strongly affected *A. marina* flowering in Australia, Papua New Guinea, and New Zealand.

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References