Regeneration failure and seedling growth of *Dipterocarpus gracilis*, a vulnerable dipterocarp in a tropical monsoon forest in Central Java, Indonesia

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Abstract. Romadini NP, Indrioko S, Widiyatno, Faridah E. 2022. Regeneration failure and seedling growth of *Dipterocarpus gracilis*, a vulnerable dipterocarp in a tropical monsoon forest in Central Java, Indonesia. Biodiversitas 23: 4928-4939. *Dipterocarpus gracilis* Blume is a vulnerable native dipterocarp species on Java Island, Indonesia. Yet, limited understanding regarding its regeneration capacity in its natural habitat is available to support a sustainable population. The research aimed to investigate the survival and growth of *D. gracilis* seedlings across canopy openness (CO) in Kecubung Uloelanang Nature Reserve, Central Java, Indonesia. After 10 months of observation, the highest survival rate was found in CO >20%–25% (44%), and the lowest survival rate was observed in CO <15%–20% (20%). The highest relative growth rate of height (RGR H) and the relative growth rate of diameter (RGR D) were found in CO >20%–25% (1.03 ± 0.03 cm and 1.87 ± 0.03 mm). CO <15% showed the lowest RGR H and RGR D (0.6 ± 0.02 cm and 1.39 ± 0.02 mm). The RGR H and D showed a significant CO >20%–25% increase compared with other canopy classes. Pearson’s correlation between RGR D and CO was 0.466 (p >0.05). Our observation indicated that dry months were a critical period for seedling survival. This study showed poor regeneration capacity of *D. gracilis*, implying that failure in a seedling establishment over time would alter the tree demographics of *D. gracilis*.

**Keywords**: Nature Conservation Reserve, relative growth rate, shade-tolerant, survival, vulnerable

INTRODUCTION

Forest conservation and restoration planning require an understanding of the dynamics of vegetation at community and species levels. In ensuring forest sustainability and dynamics, natural regeneration is a prominent factor that could be affected by both biotic and abiotic factors (Borja 2014; Bose et al. 2016). The dynamics at the species level play an important role in the composition, structure, and diversity of vegetation at the community level (Liu et al. 2020). In this regard, seedling dynamics at the species level and seedling regeneration are critical in determining the trajectory of vegetation succession, starting from the young stage to a more mature level. The transition from seedling to sapling is considered a bottleneck in tree establishment (Yan et al. 2015). This is particularly eminent in highly diverse tropical forest ecosystems where a high diversity of species coexist, which has a consequence on the intraspecies and interspecies competition for resources such as light, water, and nutrients. However, ecologists do not clearly understand the relative contributions of ecological processes that promote seedling regeneration which affects species coexistence (Liu et al. 2020). Principally, knowledge of seedling ecology and demography is important in the context of conservation areas and regarding species with conservation concerns. Such understanding has been necessary to support biodiversity conservation over the last 20 years and has been insufficient to protect biodiversity (Clark et al. 2013; Bridgewater et al. 2016; Heywood 2016, 2017, 2019).

The seedling establishment of the family Dipterocarpaceae, which is a typical plant group commonly found in South Asia and Southeast Asia tropical forests, is particularly vulnerable to the infrequent rainfall caused by specific seed characteristics, namely recalcitrant (O’Brien et al. 2013), where the seed cannot survive during the dry period. Furthermore, gap size affects tree species regeneration, leading to important changes in factors such as light intensity, soil moisture, and soil biological properties, which are different for different-sized gaps (Muscolo et al. 2014). The effect of precipitation fluctuations on plant growth is becoming increasingly important as the global precipitation cycle is expected to intensify with climate change. Nevertheless, with limited dispersal capacity, narrow environmental niches, and dispersed populations of species in fragmented landscapes, the expected climate change promotes extinction despite protecting all populations.

*Dipterocarpus gracilis* Blume is a dipterocarp species native to the Andaman Islands, Bangladesh, Brunei, Indonesia, Myanmar, Peninsular, Singapore, Sabah, Sarawak, and Thailand (Ly et al. 2017). In Indonesia, this
species is naturally distributed in Java, Sumatra, and Kalimantan islands. The *D. gracilis* is a large emergent tree that grows to 100-150 cm in diameter and is found in lowland evergreen, semi-evergreen forests and seasonally dry tropical rain forests, well-drained soils, valleys, hill slopes, or ridges (Chua et al. 2010). A tree with a height of 40-50 m (Ashton 1982), a straight cylindrical trunk, and a high branch-free trunk is often a dominant part of the canopy. The *D. gracilis* produces commercial timber and has a high economic value of non-timber forest products, namely oleoresin (Aslam et al. 2015, Dymose et al. 2017; Fernandes and Maharani 2019; Suiuay et al. 2019).

The International Union for Conservation of Nature (IUCN) Red List assigns this species as Vulnerable (Ly et al. 2017). The remaining population of *D. gracilis* on Java Island is found in Kecubung Ulolanalang Nature Reserve, with a total area of only 69.7 ha surrounded by extensive teak plantations. The local population of *D. gracilis* in Kecubung Ulolanang is threatened by its small population and habitat size in which their genetic diversity is reduced due to a decrease in heterozygosity, which is indicated by drift and the increased tendency of inbreeding (Romadini et al. 2021). Previous studies report that *D. gracilis* is threatened by habitat loss and declining habitat quality (Ly et al. 2017). Moreover, deforestation and exploitation of timber were the major drivers of vulnerability. Although this species is an ecologically important climax species that fill the remaining natural forests on this island, there have been few studies on it, particularly on the population on Java Island.

The *D. gracilis* are typically late-succession canopy species, and their regeneration is important for the future of intact tropical forests and for accelerating the success of the recovery of degraded forests. In an uneven-aged forest of the Kecubung Ulolanang Nature Reserve, failure to regenerate from the germination to seedling establishment stages is a crucial problem. However, the characteristics and factors affecting the natural regeneration of *D. gracilis* seedlings remain unclear. This research aimed to investigate the survival and growth patterns of *D. gracilis* seedlings in the Kecubung Ulolanang Nature Reserve. We focus on the seedling demographic dynamics in response to canopy during rainy and dry seasons. The survival and initial growth of *D. gracilis* seedlings in the understory were evaluated following the flowering and fruiting seasons in Kecubung Ulolanang Nature Reserve from December 2018 to February 2019.

**MATERIALS AND METHODS**

**Study area**

The study was conducted in Kecubung Ulolanang Nature Reserve in Subah District, Batang Regency, Central Java, Indonesia (06°51’46” to 007°11’43” South latitude and 109°40’19” to 110°03’06” East longitude) (Figure 1). The reserve covers an area of 67.9 ha and is classified as Schmidt and Ferguson climate type B. The Kecubung Ulolanang Nature Reserve has an average altitude of about 165 m asl, bordering with Prigi Rivers, High Conservation Value (HCV), and teak plantation of Perhutani. Natural Resources Conservation Agency of Central Java (Indonesian: Balai Konservasi Sumber Daya Alam Jawa Tengah) (NRCA 2014) reported that the forest topography is rolling hills, with slopes widening to the south.

![Figure 1. Map of the study area in Kecubung Ulolanang Nature Reserve in Batang Regency, Central Java, Indonesia (NRCA 2022)](image-url)
Sampling design

**Design of permanent sample plots**

Plots were designed to identify the differences in the survival and growth of *D. gracilis* across canopy openness (CO) levels. Parameters measured included: (i) survival rate, (ii) seedling height and diameter increment, and (iii) relative growth rate (RGR) of the seedling in terms of height and diameter during the observation period. We established ten 0.40 ha (20 m x 20 m) plots to monitor the seedlings in 2019. The plot location was determined using the purposive sampling method based on the presence or absence of natural regeneration at the seedling level. The criteria for the seedlings measured were <10 cm in diameter at breast height, <1.5 m in height, and 3-4 young leaves. After the plots were determined, the percentage of CO was measured in each plot.

**Site and canopy condition of permanent sample plots**

The percentage of CO was calculated as the percentage of open sky observed beneath a forest canopy. We captured three photos of the hemispherical canopy at each plot with a height of 30 cm from the ground using a fish-eye camera. The hemispherical photo was obtained at the end of the rainy season in May 2019. The CO was calculated using the image analysis of the Gap Light Analyzer software. The percentage of CO in all plots ranged from 12 ± 1% to 25 ± 4.3%. Based on the percentage of CO obtained (Table 1), canopy opening was divided into three categories, namely, classes I (<15%), II (15%-20%), and III (>20%-25%).

Soil samples were collected from two soil depths: 0-10 and 10-20 cm. At each plot, a soil sample was obtained from five points and then composited into one. The soil texture in the measurement plots at a depth of 0-10 cm had a higher clay percentage than sand and silt, except for the CO >20%-25% measurement plot, and at a depth of 10-20 cm, clay had the highest proportion in all classes. Soil acidity conditions at a depth of 0-10 cm indicated slightly acidic (CO >20%-25%) to acidic (CO <15% and CO of 15%-20%) soil conditions, and at a soil depth of 10-20 cm, all classes indicated moderate soil conditions. The macronutrient contents (organic C, N, P, Ca, K, and Mg) in all classes at these two depths had the same level. The percentage of organic C was high (3.21-3.60), and the total N was moderate. For P, the highest content was observed at a depth of 0-10 cm in the CO class of >20%. However, two cations, namely Ca and Mg, showed very low values in all classes at both depths. Cation exchange capacity (CEC), a parameter that estimates the soil’s capability to attract, retain, and exchange cation elements, ranged from 12.54 to 14.54 at 0-10 cm depth. In addition, at the depth of 10-20 cm, the CEC values ranged from 13.90 to 15.16. Regardless, the CEC values across canopy classes at both depths were categorized in the same range, indicating a loam soil texture. The observed soil properties and the method used are presented in Table 2.

### Table 1. Distribution of plots and number of samples of *D. gracilis* seedlings in Kecubung Ulolanang Nature Reserve, Batang Regency, Central Java, Indonesia, based on canopy openness

<table>
<thead>
<tr>
<th>Class</th>
<th>Range of CO canopy openness (%)</th>
<th>Number of plots</th>
<th>Number of samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO I(&lt;15%)</td>
<td>12-13</td>
<td>4</td>
<td>614</td>
</tr>
<tr>
<td>CO II (15%-20%)</td>
<td>15-17</td>
<td>3</td>
<td>129</td>
</tr>
<tr>
<td>CO III (&gt;20%-25%)</td>
<td>21-25</td>
<td>3</td>
<td>139</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>10</td>
<td>910</td>
</tr>
</tbody>
</table>

### Table 2. Soil physical and chemical properties across varying soil depths and canopy openness classes in Kecubung Ulolanang Nature Reserve, Batang Regency, Central Java, Indonesia

<table>
<thead>
<tr>
<th>Soil properties</th>
<th>Measurement method</th>
<th>Depth of 0-10 cm</th>
<th>Depth of 10-20 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>CO &lt;15%</td>
<td>CO 15%-20%</td>
</tr>
<tr>
<td>Texture</td>
<td>Hydrometer</td>
<td>22.25</td>
<td>29.67</td>
</tr>
<tr>
<td>Sand (%)</td>
<td></td>
<td>35.25</td>
<td>34.67</td>
</tr>
<tr>
<td>Silt (%)</td>
<td></td>
<td>42.50</td>
<td>35.67</td>
</tr>
<tr>
<td>Clay (%)</td>
<td></td>
<td>5.20</td>
<td>5.57</td>
</tr>
<tr>
<td>pH (H₂O)</td>
<td></td>
<td>3.58</td>
<td>3.60</td>
</tr>
<tr>
<td>C Organic (%)</td>
<td>pH meter 1:5</td>
<td>(High)</td>
<td>(High)</td>
</tr>
<tr>
<td>N (tot %)</td>
<td>Walkley &amp; Black</td>
<td>0.31</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>(Moderate)</td>
<td>(Moderate)</td>
<td>(Moderate)</td>
</tr>
<tr>
<td>P (ppm)</td>
<td>Kjeldahl</td>
<td>36.75</td>
<td>35.67</td>
</tr>
<tr>
<td>Ca (tot %)</td>
<td>Morgan Wolf</td>
<td>0.09</td>
<td>0.06</td>
</tr>
<tr>
<td>Mg (tot %)</td>
<td>Atomic Absorption</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Spectroscopy (AAS)</td>
<td>(Very low)</td>
<td>(Very low)</td>
</tr>
<tr>
<td>K (ppm)</td>
<td>Atomic Absorption</td>
<td>178.5</td>
<td>83.67</td>
</tr>
<tr>
<td></td>
<td>Spectroscopy</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Soil properties Measurement method Dept of 0-10 cm Depth of 10-20 cm

<table>
<thead>
<tr>
<th>CO</th>
<th>CEC (cmol (+) kg⁻¹)</th>
<th>CO &lt;15%</th>
<th>CO 15%-20%</th>
<th>CO &gt;20%-25%</th>
<th>CO &lt;15%</th>
<th>CO 15%-20%</th>
<th>CO 15%-20%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Morgan Wolf Distillation</td>
<td>14.54</td>
<td>12.54</td>
<td>13.36</td>
<td>15.16</td>
<td>14.51</td>
<td>13.90</td>
</tr>
</tbody>
</table>

Note: C organic; N = nitrogen; P = total phosphorus; Ca = total calcium; Mg = available magnesium; K = available potassium; CEC = cation exchange capacity

Climate variables (i.e., rainfall (mm), air humidity (%), air temperature (°C), sunlight intensity, and soil moisture (%) at depths of 0-10 and 10-20 cm) were measured during the dry and rainy seasons from May 2019 to January 2020. A data logger located at the center of the study area was used to measure each variable. In addition, secondary data on historical rainfall were obtained from the 134 Subah District weather stations showing that the annual rainfall (2017 and 2018) fluctuated between 2,000 and 2,100 mm (Figure 2).

Data collection

At each plot, we measured the height (from root collar to apex) and diameter at the ground level (basal diameter) of all D. gracilis seedlings. The seedlings were counted per plot and tagged at the initial census in May 2019, approximately 3-5 months after the flowering and fruiting events. The seedling censuses were continued every two months until January 2020. The tagged seedlings were measured for percentage of survival, stem diameter (nearest 0.1 mm), and stem height (nearest 0.1 cm). The percentage of survival of the tagged seedlings was assessed by counting the survived and dead individuals on each plot. Height and diameter increments (I) were calculated as follows:

\[ I_i = (S_{t_2} - S_{t_1}) \]

where \( S_1 \) and \( S_1 \) are the height or diameter of \( i \)th seedling at the start and end measurements, respectively.

The RGRs of stem height (RGR H) and stem basal diameter (RGR D) of the seedling over the ten-month observation period were calculated as follows:

\[ \text{RGR} = \ln (H_2) - \ln (H_1) / (t_2 - t_1) \]

\[ \text{RGR} = \ln (D_2) - \ln (D_1) / (t_2 - t_1) \]

where \( H_2 \) and \( H_1 \) are stem height; \( D_2 \) and \( D_1 \) are stem diameter, and \( t_2 - t_1 \) is 10 months (observation period from April 2019 to January 2020)

Data analysis

We used a one-way analysis of variance to examine the different effects of the CO class on seedling height, diameter, height increment, diameter increment, and RGR H and RGR D among CO classes. Then, Tukey’s honestly significant difference tests were used for multiple comparisons among class means. The differences with \( P \leq 0.05 \) were considered as significant. The coefficient correlation between RGR (D and H) and CO was determined using Pearson’s correlation analysis. Data were analyzed using SAS OnDemand for the University version and Microsoft Excel of Microsoft 365®.

RESULTS AND DISCUSSION

Survival rate

The survival rate of D. gracilis at 10 months after germination differed among the classes of CO. Class III (CO >20%-25%) had the highest survival rate of seedlings with 44% (Table 3). Across all CO classes, the survival rate slightly decreased from June until September 2019. At the end of the observation, the survival rates in all classes were under 50%.

Where there were five rainy months with the highest rainfall occurring in January 2020 (Figure 3). There was no rain in June and from August to October 2019, then increased from November 2019 to January 2020. In 2019, the total annual rainfall decreased
(1,572 mm/year), affecting soil moisture in general. Figure 3 shows that the soil moisture at two depths (0-10 and 0-20 cm) decreased when the rainfall decreased. The soil moisture at a depth of 0-10 cm was <5% from May 2019 to November 2019, and it increased dramatically to the maximum value (27%). Meanwhile, at a depth of 0-20 cm, the soil moisture was higher than that at a depth of 0-10 cm. From June to November, the soil moisture at a depth of 0-20 cm was in the range of 25%-31%. Meanwhile, from December 2019 to January 2020, the soil moisture reached 70%. This finding was probably a result of the differences in the proportion of soil texture at both depths (Table 2).

Table 3. The survival of D. gracilis seedlings in Kecubung Ulolanang Nature Reserve, Batang Regency, Central Java, Indonesia, during the observation periods

<table>
<thead>
<tr>
<th>Canopy openness class</th>
<th>Observation period</th>
</tr>
</thead>
<tbody>
<tr>
<td>I (CO &lt;15%)</td>
<td>100% (614)</td>
</tr>
<tr>
<td>II (15%–20%)</td>
<td>100% (129)</td>
</tr>
<tr>
<td>III (&gt;20%–25%)</td>
<td>100% (167)</td>
</tr>
</tbody>
</table>

Note: The number of seedlings of each plot is in parentheses

Figure 3. Monthly rainfall and average soil moisture in Kecubung Ulolanang Nature Reserve, Batang Regency, Central Java Province, Indonesia, from May 2019 to January 2020

Figure 4. Average monthly flux and air temperature in Kecubung Ulolanang Nature Reserve, Batang Regency, Central Java Province, Indonesia, during the observation period
Table 4. Growth parameters of *D. gracilis* seedlings across canopy openness classes from April 2019 to January 2020 in Kecubung Ulolanang Nature Reserve, Batang Regency, Central Java Province, Indonesia, (mean ± standard error). Different letters indicate significant differences among the classes using Tukey’s method at P = 0.05.

<table>
<thead>
<tr>
<th>Canopy openness class</th>
<th>Seedling height (cm)</th>
<th>Seedling diameter (mm)</th>
<th>Height increment (cm)</th>
<th>Diameter increment (mm)</th>
<th>RGR H (cm)</th>
<th>RGR D (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I (CO &lt;15%)</td>
<td>18.53 ± 0.21**</td>
<td>2.52 ± 0.03**</td>
<td>1.63 ± 0.04b</td>
<td>0.60 ± 0.02b</td>
<td>0.6 ± 0.02b</td>
<td>1.39 ± 0.02b</td>
</tr>
<tr>
<td>II (15%-20%)</td>
<td>19.72 ± 0.52b*</td>
<td>2.59 ± 0.09b</td>
<td>2.02 ± 0.01b</td>
<td>0.66 ± 0.04b</td>
<td>0.76 ± 0.05b</td>
<td>1.47 ± 0.05b</td>
</tr>
<tr>
<td>III (&gt;20%-25%)</td>
<td>20.88 ± 0.36***</td>
<td>2.77 ± 0.06**</td>
<td>4.25 ± 0.06a</td>
<td>1.01 ± 0.03a</td>
<td>1.03 ± 0.03a</td>
<td>1.87 ± 0.03a</td>
</tr>
</tbody>
</table>

Fig. 5. Pearson’s correlations between canopy openness and Relative Growth Rate of height (RGR H) and diameter (RGR D) of *D. gracilis* seedlings after the 10-month observation period.

The average monthly air temperature was between 30 to 33°C, which slightly increased from April to November (Figure 4) and then slightly decreased in December 2019. Meanwhile, the monthly flux drastically increased from June 2019 to September 2019. Air humidity from April 2019 until January 2020 was constantly between 94% and 95%.

Increment and RGR of the seedling

The highest height and diameter increments were found in CO >20%-25% (CO III; 4.25 ± 0.06 cm and 1.01 ± 0.03 mm, respectively; Table 4). Meanwhile, the lowest height and diameter increments were observed in CO <15% (CO I; 1.63 ± 0.0 cm and 0.60 ± 0.02 mm, respectively).

In this study, the RGR H of *D. gracilis* seedlings experienced a significant increase in class III of CO (>20%-25%) compared with other canopy classes. However, no significant difference was observed between CO classes I (<15%) and II (15%-20%). In addition, the RGR D of *D. gracilis* seedlings showed no significant difference between CO classes I (<15%) and II (15%-20%). However, a significant difference was detected between CO classes III compared with other canopy classes. The RGR H and RGR D among CO classes ranged from 0.60 ± 0.02 mm to 1.01 ± 0.03 mm and from 1.39 ± 0.02 mm to 1.87 ± 0.03 mm, respectively (Table 4). The Pearson’s correlation between RGR D and CO was 0.466 (p >0.05). RGR H was not significantly correlated with CO, and the Pearson’s correlation between them was 0.817 (p <0.01; Figure 5).

Discussion

Plants require water, nutrients, and light to grow and survive (Do et al. 2020). Previous research by Queenborough et al. (2009) showed that the natural regeneration of plant community is influenced by a variety of environmental factors. In tropical and subtropical primary forests, seedlings and saplings are more vulnerable than adults because of the abiotic. By contrast, this study showed that nutrients were not the principal factor affecting the difference among plots. The seedlings of *D. gracilis* have specific characteristics of canopy openness establishment to allow their growth. Moreover, they grew better in the rainy months than in the dry months. Nevertheless, environmental variable measurements in these study sites suggested that seedling survival decreased in the undergrowth/canopy gap, coupled with a periodic decrease in the soil moisture during the dry season, and this condition may be associated with low light levels. *D. gracilis*, as a species with a declining population, should be studied in terms of climate change, which affects natural resources and ecosystem services (Hansen and Phillips 2015).
The amount of light received in the forest floor is an important factor affecting the distribution pattern of *D. gracilis* species. Several factors support a possible explanation for the distribution pattern of *D. gracilis* across the plots in Kecubung Ulolanang Nature Reserve. Seedlings were more likely to be found in darker areas. This finding can be due to the limited range of light levels available in our research sites (<15%-25%). Many shade-tolerant dipterocarps require light levels in this range. The *D. gracilis* is also a large-seeded tropical climax species with recalcitrant seeds, indicating that it is shade-tolerant. Furthermore, our finding also supported a previous study that concluded that the *Dipterocarpus* with late-successional tropical seedlings is the most shade-tolerant genus in Dipterocarpaceae family (Do et al. 2020).

A previous study on 12 dipterocarp species in an old-growth Bornean tropical rain forest following their mast fruiting event reported that 32.9% ± 22.4% (12.2%-59.5%) of all dipterocarp seedlings survived 1.5 years after mast fruiting (Oshima et al. 2015) but showed a decreasing survival trend. Similarly, our result revealed that seedling survival in all canopy openness classes showed a decreasing trend over time (Figure 6). However, differences in survival rates were observed across CO classes. In this study, the seedlings of *D. gracilis* were more likely to survive at sites with high CO (Table 3). At the end of the observation, CO class III (>20%-25%) had a higher survival rate than the other classes (CO classes I and II: 15%-20% and >20%, respectively). For all CO classes, high mortality rates were observed during 2-6 months after the seedling was established. Nevertheless, the percentage of seedling survival decreased along with the decrease in rainfall. In the dry season, the percentage of seedling mortality in all CO classes increased drastically. This research showed a reduction in the percentage of seedling mortality after the eighth month of the ripening period. In this study, the period of June 2019 to September 2019 was a critical period for seedling survival (Table 3) because of the lack of rainfall and very low soil moisture. The decreased rainfall caused seedling water stress, and the mortality rate increased. This result agrees with a study by Widiyatno et al. (2020), which showed that the survival rate of some light-demanding and shade-tolerant species dipterocarp species declined in earlier growth stage and stabilized when the site microclimate became favorable. In another study, Wongprom (2020) reported the higher mortality of *D. gracilis* may have been caused by stronger light intensity. Our result strengthens previous studies, which showed that dipterocarp survival rate correlated with sunlight and water availability (Sakai et al. 2013; Ghazoul 2016).

The continued availability of water is needed by *D. gracilis*, especially in the seedling growth phase. Other dipterocarp species showed a similar tendency to thrive when rainfall is more or less evenly throughout the year (Indrioko et al. 2021). Although the site received a sufficient total annual rainfall, dry months were still observed, especially during the dry season, which caused stress on plants due to the lack of water and reduced capacity of physiological processes, resulting in tree death (Indrioko et al. 2021). The low precipitation (<100 mm rainfall per month) caused significant mortality of seedlings in the wild habitat. In addition, the sand proportion of the soil texture at a depth of 0-10 cm was higher compared with that at a depth of 0-20 cm. As a result, the soil infiltration at a depth of 0-10 cm was faster, and the ability to hold water was lower. Thus, in addition to being affected by canopy openness, the survival rate was also influenced by the availability of water and soil moisture. Our study was similar to that of Surayothee et al. (2021), who reported that the availability of water during the dry season or the transition from the dry season to the rainy season is the most important limiting factor for trees. In a previous study by Surayothee et al. (2021), the growth trend of *Choerospondias axillaris* (Roxb.) B.L.Burtt & A.W.Hill declined. This result may be related to rising temperatures and/or lowering trends of precipitation at the study site. Vlam et al. (2014) also

![Figure 6. Survival rate of *D. gracilis* seedlings under various canopy openness classes and monthly rainfalls during the observation periods.](image-url)
reported that the annual growth fluctuations of tropical trees are determined by a combination of temperature and precipitation variations. As the temperature rises due to global warming, the predominantly negative relationship between temperature and growth may indicate that the growth rate of tropical trees is declining, increasing tree mortality (Trenberth et al. 2014; Allen et al. 2015). Therefore, climatic factors are important for the survival of D. gracilis seedlings.

The D. gracilis flowering and fruiting seasons occur twice a year, indicating a sub-annual pattern (Hartiningtias et al. 2019). Flowering occurs between February-March and August-September. The fruiting season is between June-July and January-February. In the study site, D. gracilis mature trees bore more fruiting in January-February and then germinated in March-April (Romadini et al. 2021 data not shown). However, the seedlings will only obtain water from rain until May. The seedlings must survive the dry season until the next rainy season. This period is critical for survival and seedling growth. Conditions that are repeated every year result in a very low number of seedlings that can grow into the sapling stage.

A low seedling increment was observed during the observation period of ten months (Figure 7), ranging from 0.60 mm to 1.01 mm for diameter and from 1.63 cm to 4.25 cm for height. The final observation resulted in a larger diameter and height of CO class III (20%-25%) than CO class I (CO <15%) and II (15%-20%). Another trend showed the increased seedling height for CO class I and a fluctuating trend for CO classes II and III (Figure 8). However, the increase in height was low, ranging from 0.60 mm to 1.01 mm for ten months. Meanwhile, seedling height growth ranged from 1.63 cm to 4.25 cm for ten months. At the end of the observation, CO class III (20%-25%) had a larger diameter and height than CO classes I (CO <15%) and II (15%-20%). In general, the increment in the height and diameter of seedlings differed in each season. The results showed that D. gracilis needed evenly distributed monthly rainfall to sustain water availability. Moreover, a relatively large canopy openness was essential in the early stages of seedling growth.

![Figure 7. Height increment of D. gracilis seedlings under various canopy openness classes and monthly rainfalls during the observation periods.](image)

![Figure 8. Diameter increment of D. gracilis seedlings under various canopy openness classes and monthly rainfalls during the observation periods.](image)
Our results suggest that *D. gracilis* showed different diameter and height growth rates due to different sunlight requirements during early development (Table 4). This study showed that the canopy condition correlated with the relative growth in height and diameter (Figure 5), suggesting that *D. gracilis* requires a very low light intensity at the germination stage, which is characterized by the number of seedlings in CO class I. In closed-canopy forests, the availability of undergrowth light is usually low. Still, the shading trees occasionally die, creating canopy gaps and providing high irradiance to the lower layers of the forest (Jin et al. 2018). However, the need for light intensity increases as the seedlings grow, and it must be supported by water availability (Figures 8, 9, 10). A previous study reported the differential responses of large and small-seeded species to watering frequency and temporal distribution of rainless periods (Oshima et al. 2015), which altered the timing of rainless periods (before or after germination) and the competitive advantage between seed sizes. The short-term rainless periods delayed the germination of small-seeded species, which gave a temporal advantage to large-seeded species. However, at the seedling stage, large seedlings that emerged from large seeds were susceptible to growth-inhibiting water fluctuations.

The *D. gracilis* is a large, shade-tolerant, and slow-growing dipterocarp species (Phillips et al. 2002). Unlike the fast-growing dipterocarp species, which are more resistant to drought and transplant stress (Appanah and Weinland 1996; Sasaki 2006), *D. gracilis*, alike the shade-tolerant ones, requires light at least after the sapling stage and early development. On the contrary, light-demanding dipterocarp species (e.g., *Shorea balangeran* (Korth.) Burck (Lestari et al. 2019), *S. macrophylla* (De Vriese) P.S. Ashton, *S. leprosula* Miq., *S. johorensis* Foxw., *S. parvifolia* Dyer, *S. ovalis* (Korth.) Blume, *S.
scaberrima Burck, and S. dasypylla Foxw.) require full sunlight at the early stage of growth (Appanah and Weinland 1996; King et al. 2005). Widiyatno et al. (2020), in a study on dipterocarp species for enrichment planting in a secondary tropical rainforest, reported that many shade-tolerant dipterocarp species require mild environmental conditions for early growth. Moreover, Schönbeck et al. (2015) reported that late successional species showed higher mortality in dry years than pioneer species.

The existence of the D. gracilis remnant natural population in Kecubung Ulolanang Nature Reserve has an important conservation value in the context of its distribution on Java Island. According to Deb et al. (2017), 34 species of Dipterocarpus are listed as critically endangered species. However, determining the sustainability of this species can be particularly challenging. In this study site, D. gracilis showed poor regeneration, which was indicated by the failure in a seedling establishment over time. The failure in a seedling establishment over time would alter the tree demographics of D. gracilis populations. This condition will potentially cause negative growth trends in the future. In addition, in this small population, D. gracilis seedlings showed a low-level genetic diversity due to genetic drift and inbreeding (Romadini et al. 2021). Inbreeding depression can occur in Dipterocarpaceae at all stages of development, including seed formation and germination, seedling development, and sapling establishment (Tsumura 2011). On the other hand, the dry soil, high temperature, and increased water loss through extensive leaf areas of the seedling of particular species are likely to be disadvantageous in wide canopy gaps (O’Brien et al. 2013; Do et al. 2020), as also indicated in this study. Furthermore, being intolerant to water stress, Dipterocarpus spp., a C3 plant (Raes et al. 2014), has low photosynthetic efficiency. This condition affects the survival rate of D. gracilis seedlings and their growth. Although the populations are protected for this species, the anticipated climate changes can drive them to extinction.

Based on the population size and the number of mature individuals in India, D. gracilis is categorized as Critically Endangered according to the Red List of the International Union for Conservation of Nature (IUCN) (Barik et al. 2018). This assignment might also be applied to the Indonesian population because the passive conservation approach to conserving biodiversity is insufficient to guarantee long-term species survival. Volis (2019) recommended a new conservation approach for protected areas by conducting restoration through population enrichment to conserve biodiversity. This approach can be an optional solution for various challenges in conservation strategies. Population enrichment might be needed to increase the sapling and pole density of D. gracilis to provide a better vegetation structure and composition in the study site. Such a strategy is implemented for the conservation of Eusideroxylon zwageri Teijsm. & Binn. (Bornean ironwood; Vulnerable under IUCN Red List) at Malaiu Basin Conservation Area Sabah, Malaysia, by conducting active conservation intervention that focuses on the vulnerable seedling stage (i.e., ex-situ cultivation and reintroduction after reaching the sapling stage) (Qie et al. 2019). The D. gracilis population in this study site, which is shade-tolerant, has a high chance of survival in a shaded understory, and adapting after the site’s microclimate may be favorable for their growth. Thus, a strategy to keep soil moisture and sustain water availability, especially during critical times in the dry season, should be developed to increase the survival rate of D. gracilis seedlings.

Another strategy is the application of organic mulch using plant litter. Organic mulching effectively modifies the structure of soil ecosystems. This step is necessary to ensure that ecosystems function properly (Rafi and Kazemi 2021). Jordán et al. (2011) stated that mulch protects the soil surface, plays an important role in soil and water conservation, and improves soil quality. Mulch also creates a favorable environment through the decomposition of mulch substrates. Previous studies showed that mulch addition significantly improved the growth of Dryobalanops aromatica C.F.Gaertn. and S. parvifolia when grown in degraded secondary forests (Vincent and Davies 2003). In addition, under dry conditions (e.g., dry grasslands or dry periods) or depending on the litter amount (low to medium litter amount), litter presence has a positive effect on the seedling establishment (Lloyd et al. 2013). Moreover, Brearley et al. (2003) reported that the plant litter collected from the nearby mother trees increased the association between dipterocarp seedling growth and dipterocarp ectomycorrhiza. This result has implications for the successful regeneration of seedlings in the rainforest understory. In future studies, we suggest understanding the responsibilities and relationships between plant litter as an organic mulch and forest ecosystems to attain conservation-oriented restoration of the studied species.

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