### Differences in Growth and Photosynthesis Performance of Two Dipterocarp Species Planted in Laguna, the Philippines

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#### Abstract

Plant growth and leaf photosynthesis were studied for saplings of two species in the Dipterocarpaceae family planted on open bare ground in the Philippines. The greatest rate of growth in height in the initial 14 months after planting was for *Shorea contorta*, followed by *Dipterocarpus grandiflorus*. The light-saturated photosynthetic rate ( $P_{max}$ ) for *S. contorta* and *D. grandiflorus* was  $9.9 \pm 0.29$  µmol m<sup>-2</sup>s<sup>-1</sup> and  $5.5 \pm 0.28$  µmol m<sup>-2</sup>s<sup>-1</sup>, respectively. Dark respiration and apparent quantum yield efficiency did not differ between them. The daily course of photosynthesis showed the existence of a midday depression in net photosynthesis for *S. contorta* and *D. grandiflorus* on open bare ground. When the leaf-to-air vapor pressure difference (L-AirVPD) was abruptly raised to 30 hPa, the decrease in the rate of photosynthesis was the same for potted saplings of *S. contorta* and *D. grandiflorus* in the nursery. One reason for the difference in growth between species is thought to be the difference in carbon gain depending on a difference in  $P_{max}$  between the species in the morning, before the leaves suffer from large L-AirVPD at midday.

Discipline: Forestry and forest products Additional key words: leaf-to-air vapor pressure difference, open bare ground planting, photosynthetic rate, tropical rain forest

#### Introduction

In the Philippines, Dipterocarp woodlands are distributed widely in lowlands (< 800 m a.s.l.). From the 1960's, these species rapidly decreased from felling for timber export. Large portions of the exploited land have been converted to plantations of other fast-growing tree species or to agricultural cropland or grassland. To restore the biological diversity and ecological function of degraded tropical forests, endemic tree species should be planted<sup>14</sup>. Then, Dipterocarps are of prime importance to the restoration of degraded bare ground, and techniques for planting Dipterocarp seedlings urgently need to be improved in the Philippines. The ecological features and morphological characteristics of these species have been examined in previous reports<sup>2,3</sup>. However, few studies have evaluated the eco-physiological features to environmental conditions in the Philippines.

The effects of light intensity, humidity and temperature on photosynthesis are especially important factors in biomass production and the survival of trees<sup>7,28</sup>. The low

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humidity of the air, which results from high light intensity and high temperature, depresses photosynthesis and stomatal conductance<sup>24</sup>. A midday reduction of photosynthesis is frequently observed in tropical and arid regions, and this may cause a decrease in CO<sub>2</sub> uptake and, potentially, a hindrance in biomass growth. A number of possible causes of photosynthetic reduction during midday have been suggested, including an increase in leaf-to-air vapor pressure difference (L-AirVPD)<sup>12,18,24,26</sup>.

It would appear that Dipterocarp saplings, which tend to be shade tolerant, are stressed easily from severe environmental conditions (e.g., high temperature and low humidity) on bare ground. However, some studies indicate that the initial growth of saplings on bare ground differs markedly among Dipterocarp species<sup>1,16</sup>, thus indicating intrinsic differences in photosynthetic ability. Ishida et al.<sup>10</sup> found that the light-saturated photosynthetic rate was higher in seedlings of fast-growing Dipterocarp species than in slow-growing Dipterocarp species, at an open site on the Malay Peninsula. They also found that stomatal conductance does not react to changes in L-AirVPD in slow-growing Dipterocarp species.

Bare ground near Mt. Maquiling in Los Baños, Laguna, the southern part of Luzon Island in the Philippines, was afforested with Dipterocarp species. In this study, we analyzed the increment of tree height and diameter for two Dipterocarp species, i.e., Shorea contorta Vidal, and Dipterocarpus grandiflorus Blanco. These two species are the main components of lowland Dipterocarp forests in the Philippines<sup>6</sup>. It has been reported that Shorea species have a relatively high light requirement, among Dipterocarps<sup>17</sup>. Research in Malaysia found that trees of Shorea species show higher light-saturated photosynthetic rate than trees of Dipterocarpus species<sup>7,13</sup>. In the Philippines, D. grandiflorus is known to be unsuitable for planting in locations of bare ground. Thus, we can assume that the growth and photosynthetic performance of seedlings planted on open bare ground differ greatly between S. contorta and D. grandiflorus.

We hypothesized that fast-growing species planted on open bare ground should have higher light-saturated photosynthesis and greater sensitivity to low humidity (high L-AirVPD) than slow-growing species. We tested this assumption by measuring the daily course of photosynthesis in the field, and by studying the photosynthetic response to light intensity and L-AirVPD using potted saplings in controlled experiments. We discussed how differences in photosynthetic properties contribute to the differences in growth between species.

#### Materials and methods

#### 1. Plant materials

Seeds of S. contorta and D. grandiflorus were collected at Quezon National Park in the southern part of Luzon Island, the Philippines in October and November 1995. These species are widely distributed in the lowland forests (0-750 m a.s.l.) of Luzon Island. All seeds were sown, germinated and grown under shaded conditions in a nursery for one month, then transplanted to ceramic pots and grown under non-shaded and well-watered conditions in the nursery. A total of 85 saplings for S. contorta and 88 saplings for D. grandiflorus were transplanted to open bare ground near the nursery in March 1996. The planting intervals were 2 m between lines and 3 m within lines. These sites are at the University of the Philippines (200 m a.s.l.) on the northern slope of Mt. Maquiling (1,090 m a.s.l., 14°13'N, 121°20'E) in Los Baños, Laguna. The average annual precipitation is approximately 2,200 mm. The rainy season begins in April and lasts until January. The saplings growing in the experiments were watered during the dry season.

#### 2. Sapling size increment

The tree height (H, cm) and diameter at 5 cm above the ground (D<sub>5</sub>, mm) of *S. contorta* and *D. grandiflorus* saplings growing on open bare ground were measured in January 1997, at the age of about 14 months.

## 3. Responses of photosynthesis to light intensity and humidity

The foliation of saplings begins in May, after the dry season (February to April). Leaf development is completed by the end of August. Thus, we were able to select completely mature leaves for the experiments in October and November. The responses of photosynthesis to light intensity (photosynthetic photon flux density, PPFD: µmol m<sup>-2</sup>s<sup>-1</sup>) and to humidity were examined for potted saplings of S. contorta and D. grandiflorus in October 1996. We selected 10 potted saplings for each species, which were brought into the laboratory immediately before the measurements. Apparent leaf photosynthesis per unit area of leaf was measured when each leaf was fully unfolded, using the SPB-H4 portable photosynthesis measurement system with a portable light unit with a halogen lamp (Analytical Development Corporation, Hoddesdon, UK). The air entering the chamber was taken from ambient air through buffer tanks of 20 liters. Using neutraldensity filters, the PPFD was decreased incrementally from 1,200 to 0  $\mu$ mol m<sup>-2</sup>s<sup>-1</sup>. Leaves experienced a high PPFD (approximately 1,000  $\mu$ mol m<sup>-2</sup>s<sup>-1</sup>) for 15 minutes before the measurement to eliminate the induction phase of photosynthesis. Humidity was above 80% and the L-AirVPD was kept below 15 hPa during measurement. The steady state photosynthetic rate was recorded before proceeding to the next lower PPFD. Leaf temperature changed only  $\pm 1^{\circ}$ C during one leaf measurement.

The shape of the light-photosynthesis ( $P_n$ ) curve was quantified by fitting the following equation to the data by an optimizing procedure<sup>8</sup> as follows:

$$P_{\rm n} = \frac{\phi \times PPFD}{\left(1 + \frac{\phi^2 \times PPFD^2}{P_{\rm max}^2}\right)^{\frac{1}{2}}} - Rd$$
(1)

where  $\phi$  is initial gradient of the curve (i.e., apparent quantum yield),  $P_{\text{max}}$  is the light-saturated photosynthetic rate (µmol m<sup>-2</sup>s<sup>-1</sup>) and  $R_d$  is the dark respiration (µmol m<sup>-2</sup> s<sup>-1</sup>). After the measurement of the light-photosynthesis curve, the photosynthetic response to dry air was measured under saturating light for *S. contorta* and *D. grandiflorus*. The air flow into the chamber was maintained at a given vapor pressure deficit using desiccant. The steady-state light-saturated photosynthetic rate ( $P_{\text{sat}}$ , µmol m<sup>-2</sup>s<sup>-1</sup>) and leaf temperature were recorded, and the L-AirVPD was calculated. The highest L-AirVPD obtained in this measurement was 40 hPa.

## 4. Response of photosynthesis to an abrupt change in L-AirVPD

The photosynthetic response to controlled L-AirVPD in S. contorta and D. grandiflorus were measured in situ using an LI-6400 portable gas analyzer (LI-COR Inc., Lincoln, Nebraska, USA) in November 1997. There were seven samples of the former species and six of the latter species. The potted saplings for each species were brought into the laboratory immediately before the measurements. Attached fully expanded leaves were exposed to air (L-AirVPD < 10 hPa) under saturating light (approximately 1,000  $\mu$ mol m<sup>-2</sup>s<sup>-1</sup>) for 15 minutes. When a steady-state photosynthetic rate was obtained, humidity-controlled dry air flowed into the chamber to maintain an L-AirVPD of 30 hPa. The time courses of changes in photosynthetic rate  $(P_{vpd})$  were recorded every 20 seconds. The rate of decrease in  $P_{\rm vpd}$  with time was determined by the following equation:

$$P_{\rm vpd} = a \cdot \exp(\beta \cdot t) \tag{2}$$

where *t* is seconds elapsed from the start of  $P_{vpd}$  decrease, and  $\alpha$  and  $\beta$  are constants. The CO<sub>2</sub> concentration of supplied air and the leaf temperature were kept at 365 ppm and 30°C, respectively.

#### 5. Diurnal course of leaf gas exchange in the field

The diurnal course of the photosynthetic rate, stomatal conductance ( $G_s$ , mol m<sup>-2</sup>s<sup>-1</sup>), leaf temperature, PPFD inside the chamber, and L-AirVPD were measured, using the LI-6400 portable gas analyzer, for intact leaves of S. contorta and D. grandiflorus growing on open bare ground from 0400 h to 1700 h at five-minute intervals. The saplings of S. contorta were measured on 20, 22 and 23 October 1997, and the saplings of D. grandiflorus were measured on 21, 24 and 28 October 1997. Ambient air was supplied to the leaves during measurement. PPFD inside the chamber was regulated automatically using a red/blue LED light source (6400-02B, LI-COR Inc., Lincoln, Nebraska, USA). PPFD of the LED light source was synchronized with the PPFD value measured at the top of the canopy. The leaves were selected from the relatively large saplings, as tall as approximately 2 m for S. contorta and approximately 0.6 m for D. grandiflorus. There were occasional squalls on 18 and 19 October 1997, and the saplings were watered every evening while measurements were taken.

#### 6. Statistical analysis

A non-linear least-squares method was used to calculate the light-photosynthesis curves (Eq. 1) and the  $P_{vpd}$  decrease rate (Eq. 2). The t-Test was used to compare mean values of H, D<sub>5</sub>, photosynthetic parameters and  $\beta$ . Means were reported  $\pm$  standard error. All the statistical analyses were performed using STATISTICA 5.1J (StatSoft, Inc. 1996 Statistica for Windows, Tulsa).

#### Results

#### 1. Sapling height and diameter at open bare ground

The mean sapling height of *S. contorta* was significantly greater than that of *D. grandiflorus*, which was 51% less than that of *S. contorta*, in January 1997 (p < 0.01, Table 1). D<sub>5</sub> of *D. grandiflorus* was significantly smaller than that of *S. contorta* (p < 0.01, Table 1). The mortality

Table 1. The sapling height and diameter at ground level (5 cm; D<sub>5</sub>) for *S. contorta* and *D. grandiflorus* growing on open bare ground on January 1997, at the age of about 14 months

| Species         | Height<br>(cm) | D <sub>5</sub><br>(mm) |
|-----------------|----------------|------------------------|
| S. contorta     | 94.7±2.6       | 21.8±7.6               |
| D. grandiflorus | 29.4±0.7       | 6.5±0.1                |

Means are reported  $\pm$  standard error. The mean sapling height and D<sub>5</sub> of *S. contorta* was significantly greater than that of *D. grandiflorus* (p < 0.01).

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of *S. contorta* and *D. grandiflorus* was 0% and 4% during the experiments, respectively.

#### 2. Response of photosynthesis to PPFD and L-AirVPD

The PPFD required for saturated photosynthesis in *S.* contorta was approximately 600–800 µmol m<sup>-2</sup>s<sup>-1</sup>, while that in *D. grandiflorus* was between 300 and 400 µmol m<sup>-2</sup>s<sup>-1</sup> (Fig. 1). Mean value of  $P_{\text{max}}$  for *S. contorta* and *D. grandiflo*rus was 9.9 ± 0.29 µmol m<sup>-2</sup>s<sup>-1</sup> and 5.5 ± 0.28 µmol m<sup>-2</sup>s<sup>-1</sup>, respectively, and these values differed significantly (p <



Fig. 1. The relationship between photosynthetic rate  $(P_n)$ and photosynthetic photon flux density (PPFD) for potted saplings of *S. contorta* and *D. grandiflorus* in the nursery





Fig. 2. The relationship between a steady-state light saturated photosynthetic rate  $(P_{sat})$  and leaf to air vapor pressure difference (L-AirVPD) for potted saplings of *S. contorta* and *D. grandiflorus* in the nursery

Vertical error bars indicate standard error.  $\bigcirc: S. \ contorta, \diamondsuit: D. \ grandiflorus.$  0.01). Mean value of  $R_d$  and  $\phi$  did not differ among the species (p > 0.1). When the data were pooled for *S. contorta* and *D. grandiflorus*, the mean value of  $R_d$  and  $\phi$  was  $0.42 \pm 0.04 \mu$ mol m<sup>-2</sup>s<sup>-1</sup> and  $0.032 \pm 0.001$ , respectively.

Increases in L-AirVPD caused decreases in  $P_{sat}$  for S. contorta and D. grandiflorus (Fig. 2). When  $P_{sat}$  began to decrease, the L-AirVPD was roughly 20–30 hPa, and increases in L-AirVPD of  $P_{sat}$  produced greater decreases for S. contorta than for D. grandiflorus. As a result, the difference in  $P_{sat}$  between S. contorta and D. grandiflorus decreased with increases in L-AirVPD.

### 3. Response of photosynthesis to an abrupt change in L-AirVPD

A decrease in  $P_{vpd}$  set in immediately at 30 hPa of L-AirVPD (Fig. 3(I)). The decrease continued for several seconds before leveling off. The rate of decrease ( $\beta$ ) in



Fig. 3. (I) The effect of an abrupt increase in L-AirVPD on the light-saturated photosynthetic rate  $(P_{vpd})$  and (II) the comparison of the relative decreasing rate  $(\beta)$  calculated in Equation 2 for potted saplings of *S. contorta* and *D. grandiflorus* in the nursery

> (I): An example of time course of  $P_{vpd}$  (solid circles) and artificially controlled L-AirVPD (solid triangles) for a potted sapling of *D. grandiflorus* in the nursery. Base air is non-treated natural air (L-AirVPD < 10 hPa) from outside of the laboratory.

> (II): Vertical error bars indicate standard error. They are not significantly different (p > 0.1).

 $P_{\text{vpd}}$  in Equation 2 does not significantly differ between *S. contorta* and *D. grandiflorus* (Fig. 3(II), p > 0.1). The mean elapsed time during  $P_{\text{vpd}}$  decrease was about 27.1 ± 9.1 minutes for *S. contorta* and 11.5 ± 1.9 minutes for *D. grandiflorus*.

#### 4. Daily course of photosynthesis and L-AirVPD

Figures 4 and 5 show the daily time course of  $P_n$ ,  $G_s$ , L-AirVPD, PPFD and leaf temperature of *S. contorta* and *D. grandiflorus*. The L-AirVPD rose to 30–60 hPa in the afternoon. The daily variations in L-AirVPD and leaf temperature showed the same trends on all experiment

days. In the early morning, the  $P_n$  increased rapidly with increases in PPFD; PPFD rose beyond 500 µmol m<sup>-2</sup>s<sup>-1</sup> at about 0800 h, and the  $P_n$  leveled off or decreased. The maximum  $P_n$  of *S. contorta* and *D. grandiflorus* reached 10 to 13 µmol m<sup>-2</sup>s<sup>-1</sup> and 4 to 10 µmol m<sup>-2</sup>s<sup>-1</sup> before noon, respectively.

On 21 and 22 October, days on which the L-AirVPD exceeded 40 hPa at midday, considerable decreases in the  $P_n$  were observed in *S. contorta* and *D. grandiflorus* when the L-AirVPD rose beyond approximately 15 hPa. On 20 October, the  $P_n$  for *S. contorta* reached a plateau at about 0800 h, but the L-AirVPD continued to increase.



Fig. 4. Diurnal courses of photosynthetic rate  $(P_n)$  and stomatal conductance  $(G_s)$  for *S. contorta* on 20, 22 and 23 October 1997 in open bare ground

The microclimatic parameters are leaf to air vapor pressure difference (L-AirVPD), photosynthetic photon flux density (PPFD) and leaf temperature (Ltem).



Fig. 5. Diurnal courses of photosynthetic rate (P<sub>n</sub>) and stomatal conductance (G<sub>s</sub>) for D. grandiflorus on 21, 24 and 28 October 1997 in open bare ground The microclimatic parameters are the same as Fig. 4.

After midday, the direction of change for  $P_n$  was opposite that for L-AirVPD. On 24 and 28 October, the  $P_n$  of *D*. *grandiflorus* began to decrease when the L-AirVPD rose beyond 20 hPa, but only before 0800 h. On 24 October, the  $P_n$  of *D*. *grandiflorus* decreased with increases in L-AirVPD. On 28 October, the direction of change for  $P_n$ was opposite that for L-AirVPD. No midday depression of photosynthesis of *S*. *contorta* occurred on 23 October; nevertheless the L-AirVPD exceeded 30 hPa at midday.

From the data recorded in daily course of photosynthesis, we extracted  $P_n$  and L-AirVPD on the days when the PPFD exceeded 600 µmol m<sup>-2</sup>s<sup>-1</sup>. From the extracted data, a strong correlation was found between  $P_n$  and L-AirVPD. That is, the  $P_n$  of *S. contorta* and *D. grandiflorus* on those days decreased with increases in L-AirVPD (p < 0.001), excluding the observation on 23 October for *S. contorta* (Fig. 6). The slope and intercept of linear regressions between  $P_n$  and L-AirVPD varied by species and experimental day. The slope of regression lines differed significantly among the experiments (p < 0.05, ANCOVA).

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Fig. 6. The effect of leaf to air vapor pressure difference (L-AirVPD) on photosynthetic rate (P<sub>n</sub>) measured at PPFD above 600 μmol m<sup>-2</sup>s<sup>-1</sup> during the day course experiment at open bare ground for *S. contorta* on 20, 22 and 23 October 1997 and for *D. grandiflorus* on 21, 24 and 28 October 1997

The lines are derived from the linear least squares model and  $r^2$  is the regression coefficient.

#### Discussion

The growth rate of Dipterocarps is limited by sunlight availability at all stages of tree development<sup>20</sup>. Nevertheless, as saplings, Dipterocarps are commonly able to survive under the canopy<sup>27</sup>, i.e., they are shade-tolerant and they grow best at relative light intensities of 30-50%<sup>23</sup>. In contrast, recent studies indicate that some of the Dipterocarp saplings grow better in the open than in the shade<sup>1,16</sup>. S. contorta appeared to grow better than D. grandiflorus in the initial stage of growth on open bare ground in our study. The light-saturated photosynthesis of S. contorta was obviously higher than that of D. grandiflorus. We observed that D. grandiflorus planted in the shade grew to the same size as D. grandiflorus planted on open bare ground (authors' unpublished observations). These reports and observations imply that saplings of S. contorta are more light-demanding than saplings of *D. grandiflorus*.

 $P_{\text{max}}$ ,  $R_{\text{d}}$  and  $\phi$  of the two species examined in the potted saplings were within the ranges observed in other

rain forest trees<sup>7,28</sup>. The low  $P_{\text{max}}$  (ca. 5–7 µmol m<sup>-2</sup>s<sup>-1</sup>) and the lower light saturation level (approx. 300–400 µmol m<sup>-2</sup>s<sup>-1</sup>) of *D. grandiflorus* imply that saplings of this species are better at adjusting to the shaded conditions than are the other species examined. Larcher<sup>15</sup> reports that  $P_{\text{max}}$  and light saturation of shade leaves for tropical forest trees range from 5–10 µmol m<sup>-2</sup>s<sup>-1</sup> and 200–300 µmol m<sup>-2</sup>s<sup>-1</sup>, respectively.

The measurements of the daily course of photosynthesis showed the existence of a midday depression of photosynthesis for *S. contorta* and *D. grandiflorus* on the bare ground plantation. A midday depression of photosynthesis is frequently observed in Mediterranean, arid, semiarid, and tropical regions<sup>12,19,22,26</sup>, and numerous explanations have been proposed, including a large L-AirVPD<sup>18,21</sup>. Strong PPFD incidence to the leaf raises leaf temperatures<sup>5</sup>, and this consequently leads to a large L-AirVPD. The maximum PPFD observed at open bare ground (Figs. 4 & 5), which was three to four times the light saturation PPFD of Dipterocarp species, may adversely affect the H. Utsugi et al.

photosynthetic rate of wild leaves.

In the potted saplings, the photosynthetic depression of the two species began after a critical L-AirVPD (20-30 hPa) had been exceeded (Fig. 2). This is in agreement with previous reports for semiarid and tropical regions<sup>21,26,28</sup>. In the tropical rain forest canopies of Cameroon, photosynthesis in Dialium pachyphyllum correlates inversely to L-AirVPD when PPFD exceeded the light saturation point (approx. 500  $\mu$ mol m<sup>-2</sup>s<sup>-1</sup>)<sup>12</sup>. Even with a low PPFD of 600 umol m<sup>-2</sup>s<sup>-1</sup> or less, light-saturated photosynthesis was observed for S. contorta and D. grandiflorus (Fig. 1). The S. contorta and D. grandiflorus growing on open bare ground showed a correlation between L-AirVPD and photosynthetic rate at PPFDs of greater than 600 µmol m<sup>-2</sup>s<sup>-1</sup> (Fig. 6). Ishida et al.<sup>11</sup> found the same relationship between L-AirVPD and photosynthesis for Shorea siamensis Miq. in Thailand. These observations suggest that the midday depression in an individual leaf is associated with L-AirVPD. However, significantly different relationships were observed between L-AirVPD and photosynthetic rate (Fig. 6), and S. contorta did not show the midday depression of photosynthesis on 23 October (Fig. 4). This implies the existence of other factors affecting photosynthesis, such as xylem cavitation<sup>25</sup> and root-produced abscisic acid<sup>4</sup>.

The rate of decrease in photosynthesis ( $\beta$ ) induced in S. contorta by abrupt changes in L-AirVPD did not differ significantly from that induced in D. grandiflorus (Fig. 3). This observation suggests that the difference in light saturated photosynthetic rate between S. contorta and D. grandiflorus when the L-AirVPD is low in the morning narrows abruptly when the L-AirVPD rises at midday. This indicates that photosynthesis responds more sensitively to low humidity (high L-AirVPD) in S. contorta than in D. grandiflorus. The value of 30 hPa of L-AirVPD was commonly attained for leaves under field conditions (Figs. 4 & 5). During October to February, the air vapor pressure deficit was lower than other months in Laguna<sup>9</sup>. This means that the L-AirVPD above 30 hPa probably occurs throughout the year. Thus, the daily carbon gain is expected to increase with increases in photosynthesis in the morning on a bright day. One reason for the difference in growth between S. contorta and D. grandiflorus at open bare ground can be assumed to be the difference in carbon gain depending on a difference in  $P_{\text{max}}$  between the species in the morning, before the leaves suffer from large L-AirVPD at midda.

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