Artificial shade shelters mitigate harsh microclimate conditions and enhance growth in tropical tree seedlings planted in degraded land

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ABSTRACT We evaluate the efficacy of artificial shade shelters in promoting seedling growth and ecophysiological traits in degraded tropical forest land. Seedlings of Dyera costulata were planted in an open control plot and two open-top shade shelters (2 and 3 m in height). Leaf traits, including nitrogen content, the ratio of variable to maximum fluorescence (Fv/Fm), and chlorophyll content (SPAD value) were assessed in the nursery prior to planting, and again at 2, 7, 12, and 16 months after planting. Seedling height, diameter, biomass, and leaf number were also assessed. Shade shelters reduced light intensity to approximately 70% and maximum temperature by up to 3.1 °C. Minimum daily air humidity was up to 12% higher in the shelters relative to the open control. Seedling growth was better under both shelters relative to the open control, but particularly for the 2 m shelter. Seedlings planted in the open lost roughly half their leaves immediately after planting due to environmental stress, whereas leaves were retained by seedlings under the shelters. A decrease in the Fv/Fm ratio was observed in the open control both 2 and 7 months after planting, indicating photoinhibition. The maximum photosynthetic rate decreased in all conditions immediately after planting, but seedlings under the shelters recovered faster, especially in the 2 m shelter. Decreases in leaf number and photosynthetic capability in the initial stages following planting may limit seedling growth in open conditions. The improved growth and ecophysiological parameters under the shelters persisted for up to 16 months after planting, indicating that shelters may be valuable tools for reforestation and rehabilitation in degraded tropical forests.

Key words: Climate change, degraded forest, photosynthesis, reforestation, rehabilitation

INTRODUCTION

Lowland areas in Malaysia were historically dominated by dipterocarp forest, but have been degraded by anthropogenic activity (Hansen and DeFries 2004; Wright 2005; Hansen et al. 2013). When tropical rainforest overstory is removed by human disturbance, strong sunlight penetrates to the forest floor, causing stressful drought conditions for tree seedlings due to increased temperature and decreased humidity (Lamb et al. 2005; Lamb 2011). High temperatures and drought are typically lethal to tree seedlings, which in turn delays the recovery of degraded forests (Appanah and Weinland 1993; Adjers et al. 1995, 1996). The mortality rate of tropical tree seedlings planted in Southeast Asia in degraded forest typically exceeds 50% within the first year (Adjers et al. 1996; Otsamo et al. 1997; Hattori et al. 2013). High seedling mortality is typically attributed to ecophysiological limitations in harsh environments, i.e., inhibition of photosynthesis under high light and temperature conditions, or drought stress due to excessive transpiration (Ishida et al. 1999; Kenzo et al. 2007, 2019). Climate change is also expected to increase temperatures and drought severity in tropical forests, which could further increase the influence of these stressors in the degraded forests of Southeast Asia (Corlett 2011, 2016).

Effectively recovering degraded tropical forests likely depends on mitigating the environmental stresses planted seedlings are subject to (Appanah and Weinland 1993). For example, instead of directly planting seedlings under open canopy, it may be advantageous to plant seedlings following the establishment of an early successional secondary forest (Appanah and Weinland 1993; Romell et al. 2008; Hattori et al. 2013). Secondary forest trees act as nurse trees, and their canopy both decreases light and temperature and increases humidity (Otsamo 1998; Tewksbury and Lloyd 2001; Padilla and Pugnaire 2006). Seedling survival is typically improved using this method, although the growth rate may be poor (Ashton et al. 1997; Norisada et al. 2005; Hattori et al. 2013). Thus, thinning upper layer canopy trees is often necessary to increase seedling growth following the
initial planting stage (Kuusipalo et al. 1996; Otsamo 1998). Another method to increase seedling survival, applied in semiarid lands and Mediterranean forests, is the use of artificial shade shelters (Sharew and Hairston-Strang 2005; del Campo et al. 2006; Defaa et al. 2015). This method effectively promotes short-term recovery of degraded land (Chirino et al. 2009). Shade shelters used in a semiarid setting were shown to reduce temperature and mitigate drought stress, which in turn improved the survival and growth of tree seedlings (Oliet and Jacobs 2007; González-Salvatierra et al. 2013). Improved growth performance of seedlings may be related to the enhancement of leaf functions, such as photosynthetic ability and water use efficiency, under the shade shelter (Oliet and Jacobs 2007). Artificial shade shelters may be a useful tool for recovering degraded tropical forests, although studies assessing their efficacy are rare in Southeast Asia (Yoneda et al. 2005).

Here, we assessed the potential of artificial shelters of different sizes to mitigate the effects of harsh microclimate conditions on the growth of planted tropical tree seedlings. We postulated that the shelters would cause changes in leaf functions, such as photosynthesis, as well as affect seedling growth. Since plant growth depends on the amount of leaves and the photosynthetic rate per unit leaf (Lambers et al. 1998), we measured leaf biomass and the leaf maximum photosynthetic rate ($A_{\text{max}}$) as an index of photosynthetic production. In addition, to determine the effects of the artificial shelter on $A_{\text{max}}$, we determined the stomatal conductance ($g_s$), leaf nitrogen ($N_{\text{mass}}$), and leaf mass per area (LMA), all of which are closely related to $A_{\text{max}}$. We focused on leaf ecophysiological parameters that indicate a response to environmental stress, such as the leaf instantaneous water use efficiency ($A_{\text{max}}/g_s$) for drought stress and the ratio of variable to maximum fluorescence ($F_{\text{v}}/F_{\text{m}}$) for photoinhibition. We postulated that mitigation of environmental stress by the shelter prevents photoinhibition and maintains a high $A_{\text{max}}$ with high $g_s$, and may increase the growth rate. By contrast, leaf biomass is expected to decrease to prevent water loss through transpiration under the high temperature and low humidity conditions outside the shelter, thus reducing growth. To test these hypotheses, we compared seedling growth and leaf ecophysiological traits for 16 months between shelters and open conditions.

MATERIALS AND METHODS

Study site and tree species

Our study was conducted in a bare, degraded pasture at the Universiti Putra Malaysia (N2° 59’ , E101° 43’) located in Selangor, Malaysia. The annual rainfall at the study site is approximately 2,700 mm and the average annual temperature is 25.3°C; the study site has a tropical rainforest climate (Kenzo et al. 2011). The soil is Ultisol and sandy loam to clay loam textures (Serdang soil series, Paramananthan 1998).

We studied seedlings of *Dyera costulata* (Miq.) Hook. f. (Apocynaceae), because this is a common fast-growing timber species and trial planting has been conducted in Southeast Asia (Appanah and Weinland 1993). This species is widely distributed in the lowland tropical forests of the Malay Peninsula, Sumatra and Borneo, occurring as a canopy species with a height of up to 60 m (Middleton 2004). *Dyera costulata* typically regenerates in canopy gaps with relatively high light conditions and requires adequate soil moisture (Aminuddin 1982; Whittmore 1984; Norwati 2002). The sap of this species is used for chewing gum, while its soft wood is often used for match shafts and plywood (Yap 1980).

Planting methods and microclimate measurements under artificial shade shelters

We used two sizes of open-top shade shelter (2 and 3 m in height), as well as an uncovered control (Fig. 1, Yoneda et al. 2005). The shelters were made from polyvinyl chloride pipes and a black-shade-net with a shading rate of 50%. The upper part of each shelter is not covered by the shade net, and opens at an angle of about 30 degrees over the planted seedlings (50–80 cm in height). The shelters allow direct sunlight to reach the seedlings for 2–3 hours.

![Fig. 1. Images of the 2 and 3 m shelters in the abandoned pasture 1 month after planting. Seedlings in the open control treatment are visible in the foreground.](image-url)
Shade shelter enhances growth performances per day. The shelters are about 1.5 m wide and 6 m long. The 2- and 3-m-high shelters costs about 50 and 90 USD, receptively. We set up the 2- and 3-m shelters at 10-m intervals on a relatively flat site. In November 2004, six seedlings were planted under each shelter and 13 seedlings were planted outside the shelter (uncovered). The planted seedlings were spaced about 1 m apart and did not apply fertilizer. The seedlings had been grown for roughly 10 months in plastic pots (diameter 10 cm, depth 18 cm) under low shade conditions (relative light intensity ~60%) in a nursery at Universiti Putra Malaysia, and were sufficiently irrigated twice daily. Those seedlings were also used for the ecophysiological measurements.

From 16 to 24 December 2004, the air temperature and humidity in all treatments were recorded every 10 minutes by a Hobo H8 Pro Series data logger (Onset Computer, Bourne, MA, USA), and the light intensity was recorded every 10 minutes by a Hobo Light Intensity Logger (Onset Computer).

Leaf ecophysiological traits and biomass estimation

The $A_{max}$ and $gs$ at light saturation were determined using a portable photosynthesis meter (LI-6400; LI-COR, Lincoln, NE, USA). Measurements were taken between 8 and 11 AM, to avoid the midday decrease in photosynthesis (Kenzo et al. 2008), from fully expanded leaves on four to five seedlings per condition. The measured light intensity was 1,500 µmol m$^{-2}$s$^{-1}$ and the temperature was approximately 30°C (Kenzo et al. 2011). The carbon dioxide (CO$_2$) concentration, vapor pressure deficit (VPD), and air humidity in the chamber were approximately 400 ppm, 1.7–2.0 kPa and 60 %, respectively. The instantaneous water use efficiency ($WUE$), which is the ratio of $A_{max}$ to $gs$ ($A_{max}/gs$), was also calculated. Following gas exchange measurements, the LMA, and leaf chlorophyll content were obtained. The LMA was calculated using a laser scanner (MP-640; Canon, Tokyo, Japan) and LIA32 software (Yamamoto 2004). The chlorophyll content was obtained using a SPAD-502 chlorophyll meter (Konica Minolta Holdings, Tokyo, Japan). SPAD values correlate with leaf chlorophyll content (Kenzo et al. 2008). $N_{max}$ was determined using an NC analyzer (Sumigraph NC-900; Shimadzu, Kyoto, Japan), on leaves that had been dried at 60°C for 3 days and had their dry mass measured.

The initial ($F_s$) and maximum fluorescence ($F_m$) were determined in the same leaves used for the photosynthesis measurements with a portable fluorometer (Mini-PAM; Walz, Effeltrich, Germany), and with saturating light for $F_m$ (Deming-Adams and Adams 1992). We then calculated the $F_s/F_m$ (where $F_s = F_m - F_o$) after overnight dark-adaptation, which represents the maximal photochemical efficiency of photosystem II (PSII). The leaf ecophysiological traits for four to six individuals from each treatment were assessed 2, 7, 12, and 16 months after planting, except for the 3-m shelter at 12 months. We also measured 10 seedlings under nursery conditions before planting.

We estimated aboveground biomass (AGB, g) and leaf biomass (g) based on the allometric relationship between seedling height (H, cm) and stem diameter at the base (D$_b$, cm), and the diameter at the lowest leaf (D$_l$, cm), respectively. Thirteen individuals were measured in the open condition and six were measured in each shelter, before planting and at 2, 7, 12, and 16 months after planting. The allometric relationships were determined by analyzing 10 harvested $D$. costulata seedlings ranging in height from 18 to 153 cm. The following formulas were used.

Leaf biomass = 0.35 × $D_l^2$ × $H^{0.73}$
Aboveground biomass = 0.37 × $D_b^2$ × $H^{0.80}$

Statistical analyses

The effects of the independent variables (treatment, sampling month, and their interaction as fixed effects) on the dependent variables (seedling size and ecophysiological traits) were evaluated using a linear mixed model (LMM) (Sokal and Rohlf 1995). Tree identity was included as a random effect. Type III tests were performed for fixed effects (Wald-type test; Sokal and Rohlf 1995). Differences between conditions were tested after Bonferroni correction for type I error (IBM 2014). The relationships of $A_{max}$ and $gs$ with $N_{max}$ and LMA were analyzed using linear regression. We used Fisher's exact test to identify differences in seedling survival among the treatments after 16 months. All analyses were conducted using SPSS for Windows software (ver. 23.0; IBM Corp., Armonk, NY, USA).

RESULTS

Microenvironment differences among conditions

Relative daily light intensity (RPFD) under the two shelters was significantly lower than in the open control, and there was no significant difference between the two
shelters (Table 1). RPFD under both shelters was nearly 70% of that of the open control (Table 1). Maximum daily temperature was significantly lower under the two shelters than in the open control (Table 1). The difference between the open control and 2 and 3 m shelters was $-1.4^\circ C$ and $-3.1^\circ C$, respectively. The difference in average daytime temperature from 8 AM to 6 PM was $-0.6$ to $-0.9^\circ C$ lower for the 2 and 3 m shelters, respectively, compared to the open control, and there was no difference between the two shelters (Table 1). Relative humidity was 6.6% and 12.2% lower in the open control relative to the 2 and 3 m shelters, respectively (Table 1). Average relative humidity was also significantly lower in the open control relative to both shelters, and did not differ between the shelters (Table 1).

**Seedling growth parameters**

The height of seedlings differed significantly between conditions (Table 2, Fig. 2A). Seedlings in the 2 m shelter were taller than those in the open control throughout the study period ($P<0.05$, Table 2), while the height of seedlings in the 3 m shelter was intermediate between the other two conditions. By contrast, seedling diameter did not differ significantly among conditions (Table 2, Fig. 2B). The height to diameter (H/D) ratio was largest for the 2 m shelter, followed by the 3 m one and the open control, throughout the study period (Table 2, Fig. 2C). Two months after planting, seedlings in the open control had half as many leaves as they had in the nursery; those in both shelters retained a greater number of leaves (Fig. 2D). Leaf biomass was also significantly lower in the open control relative to both treatments throughout the study period (Table 2, Fig. 2E). The total above ground biomass (AGB) differed among conditions, being greatest in the 2 m shelter, followed by the 3 m shelter and then the open control (Table 2, Fig. 2F). All seedlings under the two shelters survived, while approximately 85% of the seedlings under the open condition survived for 16 months after planting. The survival rate after 16 months did not differ among the treatments (Fisher’s exact test, $\chi^2 = 1.73$, $df = 2$, $P = 0.42$).

**Leaf ecophysiological parameters**

LMM results indicated significant differences in most leaf ecophysiological traits, including $Fv/Fm$, $A_{max}$, $gs$, $N_{max}$, LMA, and SPAD values, among conditions throughout the study period ($P<0.05$, Table 3). However, the leaf area-based nitrogen content ($N_{area}$) and WUE were not significantly different among conditions ($P>0.05$, Table 3).

Leaf $Fv/Fm$ values were $<0.46$ in the open control, whereas the values observed in the nursery and both shade shelters were all $>0.67$ (Fig. 3A). In the open control, this reduction continued until 7 months after planting, and then recovered to 0.68 at 12 months (Fig. 3A). One month after planting, $A_{max}$ was 3.2 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ in the 2 m shelter, 2.7 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ in the 3 m shelter, and 2.5 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ in the open control (Fig. 3B). These values were reduced from those recorded in the nursery (5.7 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$, Fig. 3B). In all conditions, $A_{max}$ values recovered 7 months after planting and were maintained at a higher level, i.e., $>8$ $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ (Fig. 3B). The greatest $A_{max}$ value was observed in the 2 m shelter and the lowest value was observed in the open control ($P<0.05$, Table 3). We observed a similar pattern in the $gs$ values, which decreased 2 months after planting relative to nursery conditions and then increased 7 months after planting (Fig. 3C). $gs$ was significantly higher in the 2 m shelter relative to the 3 m and open control throughout the study period ($P<0.05$, Table 3). $WUE$ values peaked 2 months after planting and then decreased for the remainder of the study period (Fig. 3D). $WUE$ did not differ significantly among conditions throughout the study period ($P>0.05$, Table 3).

SPAD values were lowest in the open control throughout the study ($P<0.05$, Table 4, Fig. 4A). By

| Treatment | RPFD (%) | $T_{max}$ ($^\circ C$) | $T_{av}$ ($^\circ C$) | RH$_{max}$ (%) | RH$_{min}$ (%) |
|-----------|---------|-------------------------|-----------------------|---------------|---------------|
| Open      | 100.0$^a$ | 0.0$^a$                | 0.0$^a$              | 0.0$^a$       | 0.0$^a$       |
| 2 m       | 70.3 ± 3.0$^b$ | −1.4 ± 0.3$^b$           | −0.9 ± 0.2$^b$       | 6.6 ± 0.7$^a$ | 4.6 ± 0.7$^a$ |
| 3 m       | 73.9 ± 3.1$^b$ | −3.1 ± 0.2$^b$           | −0.6 ± 0.4$^b$       | 12.2 ± 1.2$^c$ | 3.9 ± 1.9$^c$ |
Shade shelter enhances growth performances.

contrast, LMA was highest in the control 7 months after planting and remained high for the duration of monitoring ($P<0.05$, Table 4, Fig. 4B). For both shade shelters, LMA increased slowly following planting relative to the open control. $N_{\text{mass}}$ was highest in the 2 m treatment throughout the study ($P<0.05$, Table 4, Fig. 4C). $N_{\text{mass}}$ increased between 2 and 7 months after planting and then gradually decreased in all conditions. The $N_{\text{area}}$ showed a similar pattern to $N_{\text{mass}}$, albeit with smaller differences among conditions ($P>0.05$, Table 4, Fig. 4D). Finally, $A_{\text{max}}$ was positively correlated with $g_s$ in all conditions ($P<0.05$, Fig. 5A) and was positively related to LMA and $N_{\text{area}}$ (Fig. 5B, 5C).

**DISCUSSION**

*Seedling growth under artificial shade shelters*

*Dyera costulata* seedlings grew taller under shade
shelters relative to the open control when planted on degraded land, although seedling diameter did not differ among treatments. The increase in height may be related to biomass allocation, where seedlings allocated more biomass to height than diameter growth. Many tree seedlings allocate more resources to height under limited light conditions (Gaudio et al. 2011; Harja et al. 2012), and thus a similar shift in allocation may have been occurring in the seedlings of *D. costulata* under the shelters in this study. The increased H/D ratio under the shelters also supports this shift. Similar findings of increased height, rather than diameter, growth under shade shelters were also reported for semiarid tree species in the Mediterranean (Oliet and Jacobs 2007; Defaa et al. 2015). Increased height growth was also related to greater AGB under the shelter treatments in this study, especially in the 2 m shelter relative to the open control. The increase in height growth among seedlings under the shelters was consistent for up to 16 months after planting, indicating that shade shelters may promote faster and more effective restoration of native tree species in severely degraded tropical and semiarid lands (Sharew and Hairston-Strang 2005; del Campo et al. 2006; Chirino et al. 2009; Defaa et al. 2015).

### Ecophysiological traits and seedling growth

We found that the shade shelters mitigated stress on seedlings, which was related to increased photosynthetic ability at the initial planting stage, thus indicating that shelters may effectively promote growth in degraded land. Two months after planting, stomatal limitations related to water conservation may have induced the significant reduction in photosynthetic rate seen under all conditions (Lambers et al. 1998; Larcher 2003). Because root systems are not well developed in the initial stages after planting,
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Stomatal closure to limit water loss may have positive effects on survival (Díaz-López et al. 2012). Similar stomatal limitations have been reported for seedlings immediately following transplantation from shaded to open environments in the tropics (Ishida et al. 1999; Kenzo et al. 2008).

Our findings suggest that *D. costulata* may acclimate quickly to open conditions. Specifically, we saw an increase in *gs* 7 months after planting, which could be indicative of the development of root systems with greater water uptake capacity. In addition, the reduction in leaf number and biomass in the open control may contribute to lower water consumption by reducing transpiration during the initial period following planting (Larcher 2003; Wu et al. 2008). Defoliation is common among plant species that have suffered severe drought stress (Kramer 1983; Slot and Poorter 2007).

In addition to stomatal limitations, prolonged photoinhibition may also have been the cause of the reduction in photosynthesis in the open control between planting and 7 months thereafter (González-Salvatierra et al. 2013). The leaf *Fv/Fm* ratio was <0.5 until 7 months after planting, indicating that photosynthetic ability, especially in PSII, was strongly inhibited by strong sunlight (Deming-Adams and Adams 1992; Kamaluddin and Grace 1992; Kitao et al. 2006). Photoinhibition under strong light conditions is common for seedlings that have been moved from shaded to open conditions, and occurs more frequently in late successional species compared to pioneer species in tropical forests (Mulkey and Pearcy 1992; Lovelock et al. 1994; Kenzo et al. 2008, 2011). Given that *D. costulata* is considered to be somewhat of a pioneer species (Whitmore 1984), it is logical that seedlings appeared to adapt to high light conditions within the first year after planting. Lower chlorophyll content in leaves, as indicated by lower SPAD values, may also be related to the avoidance of photoinhibition by their lower catchment ability of photon flux (Tange et al. 1998; Yamashita et al. 2000; Shimizu et al. 2006; Quevedo-Rojas et al. 2018), although reduced chlorophyll content represents a trade-off with photosynthetic ability during periods of weak light, such as cloudy periods and the early morning (Lambers et al. 1998).

We found that higher LMA was correlated with higher

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Fig. 3. Changes in Fv/Fm (A), maximum photosynthetic rate (*A* max, B), stomatal conductance (*gs*, C), and instantaneous water use efficiency (*WUE*, D) from the nursery to 16 months after planting. Bars indicate standard error. The results of statistical analyses are shown in Table 3.
Leaves with a high LMA, i.e., thick leaves, typically have a well-developed palisade layer, which has high photosynthetic capability (Koike 1988, 2001; Kenzo et al. 2004, 2006). A similar correlation has been reported in many other plant species, including some tropical trees (Reich et al. 1991; Wright et al. 2004; Kenzo et al. 2012, 2015; Yoneyama and Ichie 2019). The increased LMA under the open control observed in this study may also have contributed to increased drought tolerance (Kramer 1983; Niinemets 2001). For example, leaves with a high LMA showed higher tolerance to dehydration in a study using dipterocarp species in Malaysia (Kenzo et al. 2007), and trees subjected to drought stress using an artificial drain had a significantly larger LMA than those in wet plots in an Indonesian tropical swamp forest (Ichie et al. 2019). A large LMA contributes to drought tolerance by increasing the strength of a leaf, because greater physical strength and a thick cell wall promote tolerance of the lower leaf water potential associated with drought stress (Niinemets 2001; Koch et al. 2004; Poorter et al. 2009). In addition, leaves with a larger LMA usually have thick cuticles and epidermal cell layers that prevent cuticle transpiration (Kramer 1983). By contrast, the increase in N concentration in leaves under the two shelters may also relate to higher $A_{\text{max}}$ and growth performance. Because N is directly related to the abundance of rubisco, which is the key enzyme for photosynthesis, leaves with a high nitrogen content generally have high $A_{\text{max}}$ (Field and Moony 1986; Evans 1989; Reich et al. 1991, 1997; Inoue et al. 2015).

The defoliation observed in our open control condition may have been related to the lower growth observed therein. Seven months after planting, all seedlings appeared to have acclimated to their environment; photosynthetic capacity increased in both the open and shelter conditions, but seedling growth may have been limited by low leaf biomass in the open treatment, even if photosynthetic capacity was similar to that in the shade treatments. The shelters mitigated drought and high temperatures conditions, thus preventing the defoliation of seedlings following planting. After their roots had developed, the associated increase in water supply enabled high rates of photosynthesis and transpiration, so seedlings under the shelters grew taller than those in the open control (González-Salvatierra et al. 2013). The differences in
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growth among treatments can be explained by classical plant growth analysis: because the plant growth rate can be expressed by multiplying the amount of leaves by the leaf photosynthetic rate (Lamberts et al. 1998), a larger leaf biomass with a similar \( A_{\text{max}} \) under the shelter condition leads to higher seedling growth compared to seedlings with a smaller leaf biomass in the open condition. The lower leaf biomass contributes to reduce water consumption via transpiration activity in the open condition under significant drought stress (Larcher 2003). The difference in growth between the open and shade shelter conditions persisted even 16 months after planting due to the difference in leaf

Table 4. Summary statistics for the Type III test performed for fixed effects in the linear mixed model (LMM), assessing differences in SPAD value, LMA, \( N_{\text{mass}} \), and \( N_{\text{area}} \) among treatments. Estimated values for each treatment throughout the study period are provided at the bottom of the table. ± indicate standard error. 'ns' indicates not significant (\( P > 0.05 \)) and different letters indicate significant differences among treatments (\( P < 0.05 \)).

|               | SPAD value | LMA | \( N_{\text{max}} \) | \( N_{\text{area}} \) |
|---------------|------------|-----|----------------------|----------------------|
| Fixed effect  |            |     |                      |                      |
| Month         | 10.6, <0.001 | 75.4, <0.0001 | 11.7, <0.001 | 59.8, <0.0001 |
| Treatment     | 12.0, <0.01 | 5.0, <0.05 | 6.0, <0.05 | 0.8, ns |
| Month × treatment | 2.2, ns    | 4.7, <0.05 | 2.4, ns | 3.3, <0.05 |
| Treatment     | Estimated value | Estimated value | Estimated value | Estimated value |
| Open          | 27.8 ± 1.5° | 75.9 ± 2.4° | 1.7 ± 0.1° | 1.3 ± 0.1° |
| 2 m           | 35.5 ± 1.6° | 64.8 ± 2.6° | 2.0 ± 0.1° | 1.3 ± 0.1° |
| 3 m           | 37.8 ± 1.7° | 70.9 ± 2.8° | 1.9 ± 0.1° | 1.4 ± 0.1° |

Fig. 5. \( A_{\text{max}} \) according to stomatal conductance (gs, A), leaf mass per area (LMA, B), and the area-based nitrogen concentration (\( N_{\text{area}} \), C) from the nursery to 16 months after planting. Regression analyses were conducted using pooled data.
biomass. These results show that shade is needed for optimal growth of *D. costulata* seedlings. Several studies also found that the optimal light conditions for *A. sesban* and growth in *D. costulata* were in large forest gaps with up to 60% canopy closure, rather than in full sun conditions (Lee et al. 1999; Kenzo et al. 2011).

**CONCLUSION**

Artificial shade shelters successfully mitigated drought- and high light and temperature-related stress, and protected seedlings from defoliation. Moreover, growth was maintained during the post-planting period, when seedlings are stress-sensitive. These positive effects persisted for more than 16 months following planting. Increased growth using artificial shelters could therefore enhance the rehabilitation and reforestation of degraded tropical forests comprising native tree species, which are typically more susceptible to stress than exotics such as *Acacia* and *Eucalyptus* species (Turner 2001; Osunkoya et al. 2005; Peh 2010). Heat and drought stress are expected to increase in tropical forests in Southeast Asia due to climate change (Corlett 2011, 2016). Although increased environmental stress may undermine effective rehabilitation and reforestation, the use of artificial shelters may mitigate the effects of stress on seedling survival and growth under future harsh conditions. We suspect that responses to shelter sizes may be species-specific due to the diversity of ecological traits among species and habitats (Whitmore 1998; Ashton 2014; Ghazoul 2016), although we found that the growth of *D. costulata* was best under the 2 m shelters. Thus, developing successful rehabilitation and reforestation techniques is likely to require additional work clarifying the effects of various shelter types on tropical tree species with different ecological traits.

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