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Morphological Responses of a Light-Demanding *Alstonia scholaris* and a Shade-Tolerant *Eusideroxylon zwageri* to the Air Humidity and Light Intensity

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Abstract

The response of tropical trees to the change of light intensity has been reported to be varied among different species. Some reports argued that the growth was increasing parallel to the increasing of light intensity, but other reports mentioned that the sensitivity to the light intensity was depending on the species. Another environmental factor that has been scientifically proven to affect tree growth is humidity. While humidity itself also directly affected by the light intensity in the forest ecosystems. Therefore, it is possible that the growth pattern of trees under different light intensities is also affected by air humidity under the canopy. This research aimed to study the growth response of a light-demanding Alstonia scholaris and a shade-tolerant Eusideroxylon zwageri to the different levels of air humidity and light intensity. The experiment was conducted in Jambi, Indonesia from April to November 2019. The experiment was carried out using split plot design with factorial treatments. The main plot was the air humidity with three levels and the sub plots was light intensity with five levels. Four replicates were applied. In general, the A. scholaris tends to be more sensitive to the humidity and light intensity compared to E. zwageri. In particular, A. scholaris tends to be more sensitive to the light intensity while, E, zwageri is more sensitive to the humidity. However, there is also strong indication that the effects of light intensity to the growth, especially for A. scholaris, was affected by the humidity level.

Keyword: *environmental factors, growth pattern, intolerant tree species, tolerant tree species, tropical tree species*

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Introduction

The tree growth is not only influenced by genetic factors but also by the environmental factors. Many studies have been conducted in recent years to study the causal relationships between trees and local environmental factors in tropical forests (Rao & Rajput, 1999; Ogata et al., 2001; Schongart et al., (2002); Yanez-Espinosa et al., 2006). Furthermore, Yanez-Espinosa et al. (2006) reported that each tropical species adapts to the different environmental conditions especially to the microclimatic factors. The mechanisms of the adaptation of each species to varying microclimatic factors determine the position of the species to the particular vertical strata and coexist in the subtropical and tropical rainforest.

Among environmental factors, light intensity and humidity are two primary environmental factors that determine the physiological processes of trees. Whitmore (1996) classified the tree species of rain forest into two main functional groups according to their growth and light requirements. Shade-tolerant species are able to germinate, survive, and grow in low light conditions. While light-demanding species require a high-light environment for their growth and establishment. Similar classification was also proposed that forest tree species have been divided into two: (1) pioneers, which regenerate only in open conditions, and (2) non-pioneers, which can germinate and establish under the shade of forest canopy (Swaine & Whitmore, 1988).

Experiment conducted by Veenendaal et al. (1996) supporting this classification. Pioneers showed markedly different responses in growth and biomass allocation to variation in irradiance, compared with non-pioneer shade-bearers. Pioneers were able to increase RGR up to full irradiance. Thus, pioneers continue to increase RGR from light-limited to light-saturated RGR over a wider range of irradiance and show a lower convexity of the response curve than shade- bearers. The highest relative growth of pioneer species was obtained by the irradiance level below 8% of their ambient. The shade-bearer species (non-pioneer species) showed intermediate responses to light intensity differences.

However, different results reported by Osunkoya et al. (1994) who conducted research on 12 rainforest tree species. The species were chosen representing a wide array of taxa, ecological and morphological characteristics. They found that all species showed reduced growth with decreasing light intensity. Similar results also suggested by Denslow (1980) who found that light is one of the most limiting factors affecting the survival and plant growth in tropical rain forest. It is suggested that the rain-forest tree species are separated along the light gradient that determine niche differentiation among the plant species. Species of tropical rainforest should be specialized and adapted to the certain ranges of the gradient of light intensity, at which they may perform better than others. Implicitly, it is also assumed that in the low light, the growth performance of shade-tolerant species is hypothesized to be outgrown of pioneer species, whereas in high light intensity, the reverse is true. However, such changes in the growth performance ranks were not observed. For example, whether grow will be fast in the shade, as well as in high light intensity (Poorter, 1999). The same results were also reported that both species, large and small gap species, responded positively to increases in irradiance (Fetcher et al., 1983; Rincon & Huante, 1993). However, the highest light dependency was obtained by the pioneer species (Rincon & Huante, 1993).

Naturally, the light intensity and air temperature under forest ecosystem relate with the humidity levels. Research conducted by Georgi and Zafiriadis (2006) indicated that the air temperature decreases under the tree canopy while the air relative humidity increases. The tree canopy plays as one of major components that contribute towards microclimatic environments such as irradiation and wind velocity (Steven et al., 1986). The dense tree canopy can block over 95% of visible light from reaching the Earth's surface. While the amount of solar radiation absorbed by a tree canopy depends on its leaf area index (LAI) (Bonan, 2008). Parallel to this finding, the air humidity under the forest canopy usually has a higher relative humidity than air above forest canopy and in nearby open areas (Chen et al., 1993; Williams-Linera et al., 1998).

Hardwick et al. (2015) explained strong relationships between vegetation structures and microclimate. The plant canopies reduce the amount of energy that penetrate below-canopy air by absorbing, scattering, and reflecting the incoming solar radiation. A denser canopy should result in cooler air temperature beneath the canopy soil. The cooler environment will have a higher relative humidity than the hotter environment. Moreover, the transpiration by the plants within the forest will also help to keep the air humidity level.

Many publications reported that air humidity plays an important role on the growth of tree species (Niglas et al., 2014; Rosenvald et al., 2014). As reported by Park & Furukawa (1999) that the tropical tree species is more sensitive to the humidity compared to temperate ones. However, Lendzion and Leuzchner (2008) reported that the reduction of relative air humidity will also decrease the productivity and biomass of European beech (*Fagus sylvatica*) saplings. The biomass reduction was mainly due to a dramatically reduced leaf growth of beech under the elevated vapour pressure deficit (VPD) treatments. In fact, the global vapor pressure deficit has increased over recent decades and is expected to continue to rise in the future (Grossiord et al., 2020).

However, the understanding of tree growth responses to the change of humidity and light intensity especially on the tropical tree species is not well developed yet. The dichotomy between light demanding species and shade tolerant species still used as the main consideration for understanding this growth pattern. Even it is well understood that all tree species requires light for photosynthesis, and that the photosynthetic rate is increasing parallel to the increasing of light intensity. This research was conducted to study the growth response of a light-demanding *Alstonia scholaris* and a shade-tolerant *Eusideroxylon zwageri* to the different levels of air humidity and light intensity. This finding may contribute and enrich the understanding on this growth pattern theory. In fact, this knowledge is also urgent especially for determining the silvicultural techniques and species selection on restoration and rehabilitation of degraded forest as well as for natural forest management and cultivations.

Methods

The experiment was conducted over eight months from April 2019 to November 2019 at experimental station belongs to Forestry Department, University of Jambi. The experimental station is situated in S1°37'11.49" and E103°30'55.56". The altitude of the research location is ± 35 m above sea level. The average monthly temperature is between 26.7 °C and 28.0 °C with the average monthly air humidity is from 80% to 87%. The species studied included a light-demanding pioneer (*A. scholaris*) and a shade-tolerant old-forest species (*Eusideroxylon zwageri* Teisjm. & Binn.). *E. zwageri* belongs to Lauraceae is well-known as shade bearer tree species. *E. zwageri* is able to grow under the humid climate and under climate with short dry season (Koopman & Verhoef, 1938; Soedibja, 1952; Sidiyasa et al., 2009; Irawan, 2018). Soedibja (1952) reported that *E. zwageri* is a shade bearer species during immature stage. It is especially found in sandy soil and grows well under a fairly drained soil. Additionaly, Soerianegera (1974) reported that *E. zwageri* could grow in the habitat with dry sub-humid climate to humid climate with precipitation of 2,000 to 6,000 mm year^{-1}. While *A. scholaris* (L.) R. Br. belongs to Apocynaceae. *A. scholaris* is a medium-sized to large tree, that be able to grow up to 35 m in height (Ashton, 1988). The *A. scholaris* natural regeneration occurs preferentially in open areas at forest edges and in secondary forest. *A. scholaris* considered to be a light-demanding species (Ashton, 1988; Laumonier, 1996).

The experiment was carried out using split plot design with factorial treatments. The main plot was the air humidity with three levels namely humidity 50% (h50), humidity 70% (h70), and humidity 75% (h75) and the subplots was light intensity with five levels namely light intensity 100% (k_{100}), light intensity 75% (k75), light intensity 50% (k_{50}), light intensity 25% (k_{25}), and light intensity 0% (k_0). The intensity levels are created using three levels of shade net (25%, 50%, and 75%). The 100% of light intensity was created using clear and transparent UV plastics while for 0% of light intensity was created using 100 % black cloth. All seedlings were covered under clear and transparent UV plastics to avoid direct water drops from the rain. The humidity levels are created by blowing water vapour with different intensity to the seedling blocks. Four replicates were applied for the experiment therefore, total number of experimental plots was 60 plots. Six seedlings were used for each plot that consisted of three *E. zawgeri* seedlings and three *A. scholaris* seedlings. The total number of seedlings was 360. The average *height of E. zawgeri* seedlings was 65 cm with age of six months after germination, while the height of *A. scholaris* seedlings was 25 cm with the age of four months after germination. All seedlings were germinated and raised in the Nursery Center belongs to Forestry Department, University of Jambi. The seedlings were raised in the polybags. All seedlings were used as samples and one seedling for each

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treatment selected randomly as destructive sample for measuring the shoot and root dry weight.

The media that used for the seedlings was topsoil, sand, and organic matter with the ratio of 1:1:1 (Irawan, 2005). The different levels of air humidity in the main plot were established using mist spraying fans that located inside the plot for each replicate. The measurement of air humidity level had been conducted regularly using LogTrans 6 – GPRS produced by UIT Umweltleistungen, Germany. The surrounding area of plots and upper part of the plots were closed by transparent plastic to maintain the air humidity level. While different levels of shade net to the light penetration had been deployed to create different levels of light intensity.

Parameters and statistical analysis These parameters included: seedling height (cm), diameter (mm), leaf number, leaf area (cm²), shoot dry weight (g) and root dry weight (g). The measuring method of seedling height was using the tape that measured from the root collar to the shoot tips. While the diameter measurement was conducted by caliper at 5 cm above root collar. The leaf area was measured using the Irvan View Software while for the dry weight was measured using analytic balance after the samples were dried using oven till reaching their dry weight. The data were subjected to statistical analysis: a one-way analysis of variance (ANOVA) with humidity and light intensity as treatment factors. The statistical test for all components of variance was determined at 0.05 significance level of Duncan multiple range test (DMRT) (Gomez & Gomez, 1984).

Results and Discussion

Shade-tolerant old-forest species The F-values of six different parameters of *E. zwageri* and *A, scholaris* seedlings that treated by different levels of air humidity and light intensity at eight months after treatment was presented on Table 1. Table 1 shows that the effect of humidity is much pronounce to the *E. zwageri* compared to light intensity. Among six parameters, four parameters are highly significant different namely seedling height, diameter, leaf number and root dry weight while other two parameters are not significantly different. The light intensity only affected significantly on three parameters namely seedling height, diameter, and leaf number. While the interaction between humidity and light intensity is not significantly different for all parameters.

Table 2 shows that the humidity level of 75% provided

Table 1 The *F*-values of six different parameters of *E. zwageri* and *A. scholaris* seedlings that treated by different levels of air humidity and light intensity at eight months after treatments

Parameters	*E. zwageri*		*A. scholaris*	
	Source of variances	*F*-values	Source of variances	*F*-values
Height	Humidity	4.63**	Humidity	2.43
	Light intensity	3.21*	Light Intensity	19.12**
	Interaction between light intensity and humidity	1.18	Interaction between Light Intensity and Humidity	3.01**
Diameter	Humidity	6.97**	Humidity	4.15*
	Light intensity	2.68*	Light Intensity	54.02**
	Interaction between light intensity and humidity	1.19	Interaction between Light Intensity and Humidity	5.33**
Leaf number	Humidity	9.69**	Humidity	0.16
	Light intensity	2.84*	Light Intensity	11.39**
	Interaction between light intensity and humidity	2.03	Interaction between Light Intensity and Humidity	1.99
Leaf area	Humidity	2.25	Humidity	7.76**
	Light intensity	0.77	Light Intensity	5.27**
	Interaction between light intensity and humidity	0.95	Interaction between Light Intensity and Humidity	3.00*
Root dry weight	Humidity	3.25*	Humidity	1.29
	Light intensity	1.59	Light Intensity	39.45**
	Interaction between light intensity and humidity	0.64	Interaction between Light Intensity and Humidity	0.81
Shoot dry weight	Humidity	1.60	Humidity	2.40
	Light intensity	1.89	Light Intensity	29.37**
	Interaction between light intensity and humidity	0.80	Interaction between Light Intensity and Humidity	0.99

Note: * = significantly influenced on the 5% of variance analysis; ** = highly significantly influenced based on the 1% of variance analysis significant differences to other levels of humidity for all parameters except leaf area and shoot and root dry weight. The treatments of 50% and 70% of humidity did not providing significant different effect to the growth of *E. zwageri*. The results confirmed the results of some other researches that humidity plays an important role about the growth rate of trees (Kaufmann, 1976; Park & Furukawa, 1999; Lendzion & Leuschner, 2008; Niglas et al., 2014; Rosenvald et al., 2014; Grossiord et al., 2020). The humidity mostly influences the stomatal sensitivities of the leaves (Kaufmann, 1976; Aasamaa & Sõber, 2011) and helps maintaining cell turgidity, and hence helps in leaf expansion (Nataraja et al., 1998).

The optimum humidity level for the *E. zwageri* was around 50% to 70% and the growth rate is decreasing when reaching the humidity of 75% (Table 2). The ecological niche with high air humidity that needed by *E. zwageri* is confirming some reports (Koopman & Verhoef, 1938; Soerianegara, 1974). However, the range of optimum humidity is little bit different to the reports that provided by Sidiyasa (2011) and Arifin et al. (2014). Sidiyasa (2011) reported that the average humidity around *E. zwageri* was 69.2% to 95.3% while Arifin et al. (2014) reported that humidity of *E. zwageri* habitat ranged between 66.43% to 83.76%. The reports of both researchers were based on field measurement of microclimate around *E. zwageri* stand.

However, Lestari (2016) reported that when the humidity is decreasing under 50% (in her case 46.64%), the growth rate of *E. zwageri* is lower compared to *E. zwageri* seedlings that planted under humidity level of 53.86%. Lendzion and Leuschner (2008) also confirmed that the productivity of the trees that planted in the climate chambers reduced to 68% when the air humidity was reduced by 40%. Lendzion and Leuschner (2008) also confirmed that the plant biomass declined by 30% when relative air humidity was 15% lower for the experiment that conducted on the forest floor. Grossiord et al. (2020) explained that VPD conditions that appear under low air humidity reduce stomatal conductance and increasing plant water losses through transpiration associate with simultaneously reduce photosynthesis rate. These impacts vary across biomes and among plant functional types. However, they will influence in reducing primary productivity and amplifying drought-induced plant mortality worldwide. The same results were also performed by Yuan et al. (2019), showing that the decreasing of terrestrial gross primary production is due to increasing of VPD. Further explanation also reported by Niglas et al. (2014), saying that the low level of soil water availability during the dry years mitigated by the higher air humidity on broadleaved trees. The trees reduce the stomatal limitation to photosynthesis that allowing higher net photosynthetic rates and supporting higher growth rates.

The effect of light intensity to the growth of *E. zwageri* also presented on Table 2. Table 2 shows that all growth parameters of *E. zwageri* was significantly different among treatments except for leaf area. Among the treatments, light intensity of 50% and 75% performed better in influencing the growth of *E. zwageri*. The growth rate of *E. zwageri* mostly decreasing by increasing light intensity above 75% and below 50%. The response of *E. zwageri* to light intensity based on the results of this experiment mostly confirmed other research results (Swaine & Whitmore, 1988; Whitmore, 1996; Veenendaal et al., 1996; Eschenbach et al., 1998). However, the growth pattern of *E. zwageri* to the increasing light intensity does not confirm the research results that the growth of the trees will be increased parallel to the increasing of light intensity (Denslow, 1980; Fetcher et al., 1983; Rincon & Huante, 1993; Osunkoya et al., 1994; Poorter, 1999). Table 2 shows that the optimum light intensity to the growth of *E. zwageri* is around 50% to 75% which approximately similar to the findings of a study by Lestari (2016).

The interaction between humidity and light intensity was not significantly different to the growth of *E. zwageri*. It means that the effects of humidity on the growth of *E. zwageri* were not related or influenced by the changes of light intensity. Based on this result, the possibility of shade tolerant species *E. zwageri* to grow well under full sunlight as long as the level of air humidity is kept high, is not confirmed. Although all trees require light for photosynthesis, but since shade tolerant species has been adapted to the ecological condition with low light intensity, the increasing growth of those species does not necessarily correlate with increasing light intensity. The slow growth response that revealed by *E. zwageri* due to increasing of light intensity also confirmed research result that reported by Fetcher et al. (1983) The small gap tree species (shade tolerant species) tend to be less plastic compares to light demanding species under increased light intensities.

Tabel 2 Mean values of six traits of *Eusideroxylon zwageri* Teijsm. & Binn. seedlings that treated by different levels of air humidity and light intensity at eight months after treatments

Treatments	Height (cm)	Diameter (mm)	Leaf number	Leaf area (cm^2)	Root dry weight (g)	Shoot dry weight (g)
Humidity 50%	81.76a	7.587a	10.68a	12.80a	6.63ab	2.89a
Humidity 70%	80.04a	8.760a	14.05a	18.16a	8.02a	5.27a
Humidity 75%	49.09b	4.518b	4.60b	8.60a	2.31b	3.09a
Light intensity 100%	57.34b	6.16ab	10.28ab	14.52a	5.83ab	2.24b
Light intensity 75%	76.43ab	7.48ab	13.51a	15.62a	8.68a	6.71a
Light intensity 50%	100.97a	9.11a	11.81a	10.95a	4.43ab	4.18ab
Light intensity 25%	66.45b	7.60ab	8.50ab	16.80a	7.51ab	3.42ab
Light intensity 0%	50.30b	4.43b	4.79b	8.05a	1.81b	2.19b

Note: The mean values that are followed by the same letters are not significantly different based on 5% of Duncan multiple range test.

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Light-demanding pioneer species. On the other hand, the effects of light intensity are much pronounce to the growth of *A. scholaris* compared to air humidity. Table 1 shows that all six parameters are significantly influenced by light intensity while only two parameters are significantly affected by air humidity levels namely seedling diameter and leaf area. The interaction between humidity and light intensity is also significantly different for three parameters namely seedling height, diameter, and leaf area.

All growth parameters performed the same trend whereas the growth rate of *A. scholaris* is increasing parallel to the increasing of light intensity. The sensitivity of *A. scholaris* to the light intensity that revealed by this experiment confirmed some other research findings (Denslow, 1980; Fetcher et al., 1983; Rincon & Huante, 1993; Osunkoya et al., 1994; Poorter, 1999). Vincent (2006) reported that *A. scholaris* revealed more pronounce on the growth dynamics compared to *Durio zibethinus, Hevea brasiliensis,* and *Lansium domesticum*. *A. scholaris*, leaves produced by faster elongating main shoot. The main shoot leaves had life spans that were significantly shorter than those of leaves produced by the branches. Among the four studied species, the *A. scholaris* seedlings provided the maximum level of plasticity in leaf life span compared to other species. Additionally, the mean leaf emergence rate (LER) of *A. scholaris* appeared to reach a maximum level under full sunlight and to decrease parallel to the increase of shade intensity (Vincent, 2006), therefore, *A. scholaris* is considered as a light-demanding species (Ashton, 1988). However, there is a tendency that the light intensity is not an independent factor in influencing the growth rate of *A. scholaris*. The effects of light intensity tend to be depended on the humidity level. When the humidity is high (more that 70% in this case), the diameter growth rate is kept increasing until 100% of light intensity. While in the environment condition with low level of humidity, the trend of height and leaf number growth was decreasing at about 75% of light intensity or even below 50% of light intensity (Table 3).

The result of this experiment can be used to explain the behavior of some tree species that do not perform linearly to the increasing light intensity. Air humidity may play role as the limiting factor for the tree growth. It is the reason why some researchers reported differently on the responses of tree species to the light intensity.

The comparison between light-demanding pioneer and a shade-tolerant old-forest species. The response to the air humidity and light intensity between *E. zwageri* and *A. scholaris* tend to be different. In general, the *A. scholaris* tend more sensitive to the light intensity and interactive effect of humidity and light, compared to *E. zwageri*. It is indicated that the influence intensity of the humidity and light as well as interaction between both parameters on growth of both species were more pronounce on *A. scholaris* than *E. zwageri*. In particular, *A. scholaris* tend to be more sensitive to the light intensity, while *E, zwageri* is more sensitive to the humidity as shown in Table 1, Table 2, and Table 3.

The sensitivity of *E. zwageri* to the humidity is possibly related with the strategy of this species to the ecological habitat where *E. zwageri* mostly grows and adapts to the low light intensity. This tree species is adapted to grow under the shade environmental conditions (Soedibja, 1952). As explained by Aasamaa, and Sõber (2011) that the highly sensitive and strictly regulated responses of their stomata are the responsible adaptation capability of the slow grower species in their ecological niches. The adaptation of *E. zwageri* to the air humidity also reported by Sidiyasa et al. (2009) that air humidity may also have a significant effect on the presence and growth of the *E. zwageri*. *E. zwageri* will only grow well in locations where the surrounding vegetation is dense and in good condition. Due to the dense vegetation cover, the humidity level under the forest stands will be constant and relatively high. Conversely, in places where the vegetation has been severely damaged, the *E. zwageri* trees are no longer found.

Related to the light intensity, the growth pattern of *E. zwageri* and *A. scholaris* was also different. The *A. scholaris* mostly responded linearly to the increasing light intensity while *E. zwageri* was not. The different growth performance between pioneer tree species and gap tree species was reported also by Fetcher et al. (1983). They reported that growth of *Heliocarpus,* a pioneer or large gap species is more plastic than that of *Diptery* that is a small gap species in response to changes in irradiance. However, both species responded positively to increases in irradiance to specific extents. The results of this experiment also confirmed publication by Veenendaal et al. (1996).

Tabel 3 Mean values of six traits of *Alstonia scholaris* seedlings that treated by different levels of air humidity and light intensity at eight months after treatments

Treatments	Height (cm)	Diameter (mm)	Leaf number	Leaf area	Root dry weight	Plant dry weight
Humidity 50%	63.964b	5.220ab	27.242a	3.378a	2.499a	6.949a
Humidity 70%	72.583a	5.648a	26.202a	2.629b	1.931a	5.131b
Humidity 75%	66.458ab	4.826b	26.850a	2.501b	1.930a	5.824ab
Light intensity 100%	74.776b	7.639a	30.585a	2.859ab	5.435a	10.880a
Light intensity 75%	86.751a	6.858b	31.166a	3.437a	3.180b	9.958a
Light intensity 50%	73.661b	4.603c	30.168a	3.194a	0.915c	4.154b
Light intensity 25%	57.417c	3.567d	24.111b	2.490b	0.443c	2.103b
Light intensity 0%	45.787d	3.489d	17.793c	2.199b	0.625c	2.745b

Note: The mean values that are followed by the same letters are not significantly different based on 5% of Duncan multiple range test.

Conclusion

The conclusions of this study that the response to the air humidity and light intensity between *E. zwageri* and *A. scholaris* tend to be different. Generally, the *A. scholaris* tend to be more sensitive to the light intensity while *E. zwageri* is more sensitive to the humidity. There is a strong indication that the effects of light intensity to the growth was affected by the humidity level. When the humidity is high, the increasing light intensity increases the growth rate even when the light intensity reached to 100%. While in the environment condition with low level of humidity, the trend of growth is decreasing about 75% or even below 50% of light intensity.

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