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Effect of low light condition on the growth and carbon use of legume seedlings

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Abstract. *Qur'ani CG, Yoshimura K. 2020. Effect of low light condition on the growth and carbon use of legume seedlings. Asian J For 5: 51-59.* Plants exhibit flexible changes of morphological and physiological traits to adapt to low light environments. However, the interaction between growth, functional traits among plant organs, and non-structural carbohydrates (NSCs) concentration to determine the adaptation strategies remain unclear. Three legume- and shade-intolerant species, *Robinia pseudoacacia* (L.), *Falcataria moluccana* (Miq.), and *Acacia mangium* (Willd.) were grown under full light (open) and 15% of light availability (shade). Changes in shoot length, diameter, organ respiration rates, and NSCs concentration were observed throughout 6 months of the growing period. Only *R. pseudoacacia* developed longer (13.67%) and bigger (26.61%) shoots in open sites than shade sites. Specific Leaf Area (SLA) and Specific Root Area (SRA) were bigger in shade than in open site for all species (SLA=±2 times; SRA=±1-4 times). Dry mass, respiration rates, and NSCs in *R. pseudoacacia* were allocated more to the roots but were more to the leaves in *F. moluccana* and *A. mangium.* Based on the interactions among morphological and physiological parameters, our results show that different legume species develop specific growth, morphological traits and carbon use (NSCs) under shade conditions, which exhibit flexibility changes as part of adaptation strategy to the low-light environment.

Keywords: Growth, legume, non-structural carbohydrates, respiration rates, shade-intolerant.

INTRODUCTION

Leguminous wood plants are known as fast-growing and pioneer species with high survival rates in various environmental disturbances (Hughes et al. 2011; Masaka 2016; Osunkoya and Othman 2005). As a result of their ability to colonize and dominate new habitats, some leguminous woody plants are often seen as invasive species (Akamatsu and Makishima 2014). An increase in growth and subsequent secondary succession of leguminous wood species is attributed to the light intensity (Bush and Van Auken 1986), with a decrease in growth observed under shade conditions (Sprent 1999).

Generally, plants show flexible changes in morphological and physiological traits as the light intensity changes. The changes in leaf and root morphology with light conditions are common to establish relative growth rate (RGR) variation among light environments (Reich et al, 1998). Shade-intolerant species showed a higher specific leaf area (SLA) with less investment in carbon storage as part of adaptation to survive under shaded conditions. Seedlings of *Acacia koa* exhibited no differences in relative allocation of carbon to the roots under varying light intensities (Craven et al. 2010). Meanwhile, in the case of *Acacia implexa*, seedlings in higher light conditions exhibited higher relative allocation to roots (Forster and Bonser 2009). These cases show that legume species have various flexibility changes, which work as strategies to survive under the shade

Seedlings in open sites have better chance on capturing light for photosynthesis than seedlings in shade sites, resulting in higher carbon gain and carbon stock for metabolism (Pattison et al. 1998). High carbon gain corresponds to the needs for plant organ growth and correlates with higher carbon use in high light seedlings. Carbon balance can be achieved when each organ potentially uses its roles to support the whole-plant metabolic activity level, such as leaf for photosynthesis and roots for carbon stock. Although recognizing carbon balance within an individual plant is important for survival under the shade, carbon consumption within an individual is not associated with survival under the shade. The changes in functional traits of each organ represent the potential of using carbon stock (Bush and Van Auken, 1986), which we can determine as the parameters that support and affect the whole-plant activity level. Respiration and carbon investment for each organ is not considered simultaneously as a compartment of whole-plant carbon balance.

The marked products of plant high or low rates in photosynthesis can be recognized through the availabilities of non-structural carbohydrates (NSCs). NSCs are used as resources for metabolism among the stored carbon, which explains the breakdown of the metabolism process when the deficiency of NSCs occurs. Generally, the photosynthesis rates decrease as light decreases and reduce the NSCs (Xie et al. 2018). A positive correlation was found between biomass, NSCs concentration, and survival rates with light availability in shade-intolerant species (Zhou et al. 2020). These variations are due to the internal regulation between soluble sugars and starch depending on the adaptive strategies under different environmental scenarios (Dirk et al. 1999; Kami et al.2011; Xie et al. 2018). The amount of carbon stock corresponds to the stored carbohydrates that proportionally allocate for the needed organs under the shaded condition.

The interaction between morphological changes, organ potential on using the carbon stock, and the availability of NSCs have not been explored in shade-intolerant legume species, especially their response and characteristic changes under low light. We hypothesize that changes in carbon allocation,*i.e,* low carbon gain in shade conditions, results in the shift of whole-plant metabolic activity and biomass production in legume species. In this study, we focused on the effect of low light environments on the growth of legume species, and the connection on the ability of plant organs to use carbon stocks as well as the availability of NSCs concentration. From the results, we hope to understand the survival strategy of each species on their adaptation to the low light condition.

MATERIALS AND METHODS

Seedling origin

We used three leguminous tree species of *Robinia pseudoacacia* (L.), *Falcataria moluccana* (Miq.), and *Acacia mangium* (Willd.). *R. pseudoacacia* is a deciduous legume tree native to North America and grows in a temperature range of 2 - 13ºC for budburst(Cierjacks et al. 2013). *F. moluccana* is deciduous legume trees native to parts of Indonesia and Papua New Guinea, grown in the natural habitat of wet climate with optimal temperature 22 - 29ºC (Hughes et al. 2011). And *A. mangium* (Willd.), an evergreen leguminous tree native to Australia, Papua New Guinea, Indonesia and Mollucas islands, grown in a wet climate with average annual temperature 18 - 28ºC (Atipanumpai, 1989).

Planting

The seeds of *R. pseudoacacia* were collected in Yamagata Prefecture, Japan (38° 43' 2" N, 139° 51' 19" E), while *F. moluccana* and *A. mangium* seeds were collected from East Java (-7° 50' 21" N, 112° 13' 24" E) and Central Java (-7° 47' 35" N, 110° 55' 42" E) Province, Indonesia. Seeds were soaked in boiled water at 100ºC for 24 hours during which the water temperature decreased gradually up to room temperature, to remove the seed coats after water absorption. The seeds were then sowed in granite soil on May 18, 2018 (139 days of the year) and left under full sunlight. Before sowing, the soil was heated for 1.5hour in 550ºC in an oven to remove organic matter/contents. Seeds were germinated within 7 - 10 days and immediately transplanted to pots (9 cm × 9 cm × 9 cm) in the nursery of Faculty of Agriculture, Yamagata University, northern part of Japan (38° 43′ 59″ N, 139° 49′ 28″ E). The area of the experiment location has an annual temperature of 13.3 °C, and annual precipitation is 1620 mm (AMeDAS, Japan Meteorological Agency).

Shading treatment and measurement of growth rate

Two types of light regimes were used after the transplanting on 194 days of year (DOY); open site under the full sunlight and shade under a black shading net (90 cm × 60 cm × 120 cm) with 15 % of full sunlight maintained by measuring light intensity with the LI-190SA (Li-cor, Lincoln, NE) connected to a data logger (LI-1400, Li-cor, Lincoln, NE). The Relative Photosynthetically active Photon Flux Density (rPPFD) was automatically recorded every 5 minutes. We measured shoot diameter on the base of the aboveground part, shoot length between the basal position on the above-ground part, and the tip of the shoots of 30 seedlings for each species and light regime using a digital caliper and a ruler. These measurements were conducted once a week, from 195 to 295 DOY.

Organ respiration rates

Five or six seedlings for each species for each treatment were selected and separated into leaves, stems and roots on 289 DOY. We harvested the seedlings at the end of the growing season (6 months) when it is understood that seedlings growth is maximum as cell expansion had slowed or ceased (Ryan et al, 1995). We proved the theory by finding a slow increment of shoot length and diameter by the end of summer. However, root growth can still proceed well during fall (Lyr and Hoffmann, 1967). To investigate the metabolic activity for each treatment, each separated sample was put in a closed-air circulation chamber with the volume of 1.94×10^{-4} m^3 for small samples and 5.47×10^{-3} m^3 for bigger samples fitted with an Infrared Gas Analyzer (IRGA) (GMP 343, Vaisala, Helsinki, Finland) to measure the respiration rates. We carefully checked the air circulation, air temperature and no air leakage inside the chamber during the measurements through the observation of CO_2 concentration per second. Organ respiration rates (OR) were calculated using the following equation (Ideal Gas Law).

$$OR = \frac{1}{R} \times \frac{\Delta CO_2}{\Delta t} \times \frac{P_{atm} \times V_{cham}}{T_{cham}} \times 1 \qquad [1]$$

where OR is the organ respiration rate (nmol s^{-1}), R is the gas constant (8.31 Pa m^3 K^{-1} mol^{-1}), CO_2/t is the change of CO_2 concentration inside the chamber for one second (ppm s^{-1}), P_{atm} is atmospheric air pressure (101.3 kPa), V_{cham} is the chamber volume (m^3), and T_{cham} is the temperature inside the chamber (K).

Morphological measurements

After measuring respiration rates, leaf surface area was analyzed using the flat-head image scanner (GT-600, Epson, Tokyo, Japan) and image analysis software (ImageJ, NIH, Bethesda, Maryland, USA). While the root surface area was analyzed using flat-head image scanner (V800, Epson, Tokyo, Japan) and image analysis software (WinRHIZO, Regent instrument, Quebec, Canada). All harvested materials, including leaves, stem and roots, were dried in an oven at 65°C for 48 hours and the respective dry mass (DM) measured. Specific Leaf Area (SLA) and Specific Root Area (SRA) were calculated by total leaf area/total leaf DM and total root area/total root DM, respectively.

Non-structural carbohydrates (NSCs)

Samples were ground to very fine powder for the analysis of non-structural carbohydrates (NSCs). The powder was extracted with 80% ethanol and the extract was once desiccated with heat. We analyzed soluble-sugar content by adding water to the desiccated materials followed by phenol-sulfuric acid assay, which induces a color-producing reaction that can be measured spectrophotometrically at 490nm. After adding potassium hydroxide and acetic acid on the sediment of 80% ethanol extraction, starch was decomposed to glucose by the mixture of α-amylase and amyloglucosidase, we then estimated the starch content by analyzing the glucose content using a Glucose test kit (Fujifilm/Wako Chemical, Japan) and measured the colorimetric at 550nm.

Total NSCs concentrations were calculated as the sum of soluble sugar and starch concentration from the assays. Total NSCs pools were calculated as NSCs concentration multiplied by the total dry mass of the organ

Data analysis

Independent t-tests were used to examine the statistically significant differences between the two treatments within each species. All statistical analyses were performed with SPSS (version 25, *SPSS Inc*, Chicago, Illinois, USA). We also performed a Detrended Correspondence Analysis (DCA) to summarize the traits of carbon used for each species and each treatment. Dry mass, starch concentration per dry mass, soluble sugar concentration per dry mass, respiration rate per dry mass for each organ were used for this analysis, and multicollinearity was not seen among these traits.

RESULTS AND DISCUSSION

Growth rates and morphological traits in shoots and roots

All species showed a high increment of shoot length and diameter until mid-summer (from 231 DOY) in both open and shade sites, but the patterns varied among all species (Fig.1 and Fig.2). In *R. pseudoacacia*, shoot length did not differ between open and shade sites throughout the measurement periods (t-test *p*=0.248), but shoot diameter became smaller in the shaded site in the mid-summer (t-test *p*=0.029). In *F. moluccana*, shoot length increment in shade site was higher than in open site in early summer (t-test *p*≤0.001) but caught up with the shade site seedlings by mid-summer. The shoot diameter in *F. moluccana* in the open site was higher than the shade site in mid-summer (t-test *p*≤0.001). In *A. mangium*, shoot length increment in shade site was higher than the open site treatment in mid-summer (t-test *p*≤0.05) while shoot diameter showed a similar pattern as *F. moluccana* (t-test *p*=0.006). Regardless of the species, the ratio of shoot length to diameter was significantly higher in the shade site than in the open site (Fig.3).

In all species, SLA in shade site was twice as high as those in open site (t-test *p_R. pseudoacacia*=0.005; *p_F. moluccana*=0.001; *p_A. mangium*=≤0.001) (Table 1). *R. pseudoacacia* had the lowest SRA in the open site, while *F. moluccana* had the lowest SRA in the shade site. The highest SRA among all species in open and shade sites was observed *A. mangium*. SRA in *R. pseudoacacia* under the shade was five times higher than in open site (t-test *p*=0.028), while *F. moluccana* showed no differences between the two treatments (t-test *p*=0.184). SRA in *A. mangium* was 1.5 times higher in the shade than open site, but this was not statistically significant (t-test *p*=0.095).

Biomass production and allocation

At the overall organ level, DM in the open site was higher than the shade site in all species (Table 2). Leaf DM in open site was higher in *R. pseudoacacia* (t-test *p*=0.004) and *F. moluccana (*t-test *p*=0.032), and not significant but marginally higher in *A. mangium* (t-test *p*=0.065). Stem DM in open site was significantly higher in *R. pseudoacacia* (t-test *p*=0.009) and *F. moluccana* (t-test *p*=0.056), and marginally higher in *A. mangium* (t-test *p*=0.394). Root DM in the open site was higher than the shade site in all species.

Regardless of light condition, root and leaf DM were higher than the other two organs DM in *R. pseudoacacia* and *F. moluccana*. But, in *A. mangium*, root DM was higher in open site while leaf DM was more in shade site

Organ level carbon properties

Among all species, a significantly higher leaf organ respiration (OR) in the open site than shade site was noted in *F. moluccana* (t-test *p*=0.032) (Table 2) only. While, in *R. pseudoacacia* a significantly higher stem OR in open site than shade site was observed (t-test *p*=0.03). All species showed significantly higher root OR in open sites than shade sites. Regardless of the light condition, OR in *A. mangium* was lower than the other two species for all organs. OR was not different among species for all organs in the shade site. Roots in *R. pseudoacacia* and *A. mangium* had higher OR than other organs, whereas, leaves in *F. moluccana* had higher OR than other organs in open sites.

In all species, the NSC organ in the open site was higher than the shade site (Table 2). Leaf and stem NSCs in *R. pseudoacacia* and *F. moluccana* were significantly higher in open sites than shade sites, but not in *A. mangium*. Leaf and root NSCs in the shade site showed different amounts among species, but stem NSC in the shade site showed no differences among species. Root NSCs of all species were significantly higher in the open site than the shade site. In *R. pseudoacacia,* roots NSCs had the highest amount than the other two organs, but leaves in *F. moluccana* and *A. mangium* had higher NSCs than the other organs (stem and roots), regardless of light conditions.

Combination of carbon use properties among species and organs

Overall, leaf mass showed different direction from root mass and stem mass in the biplot (Fig. 4). Root starch content showed different direction from leaf and stem mass. Leaf sugar content showed different directions from root and stem mass. DCA 1 decreased on the sequence of respiration rates, sugar contents, starch contents and dry mass. DCA 2 decreased on the sequence of root, stem, and leaf traits, but showed opposite patterns in respiration rates. In all species, DCA 1 in open site was lower than shade site. DCA 2 was higher in *R. pseudoacacia* than other two species.

Discussion

Light regimes significantly correspond to the changes of morphology and carbon-use performances of current-year legume saplings (Chazdon and Pearcy 1986; Valladares et al. 1997). According to Madsen (1994), shade-stress constrains shoot growth and eventually the whole plant performance. In our study, none of the leguminous species under the shade conditions died throughout the experimental period. This agreed with our hypothesis that legumes adapt survival strategies under shade stress. Craven et al. 2010 observed significant positive growth response of legume *Acacia koa* to increasing irradiance (Photosynthetically Active Radiation, PAR, 21.28±13.06 µmol m^{-2} s^{-1}, 80.33±55.15 µmol m^{-2} s^{-1}, and 255.25±176.78µmol m^{-2} s^{-1}). Similarly, for our study, all three-tree species had growth traits of shoot length and diameter (Fig. 1 and Fig. 2) as morphological adaptation to light and is consistent with that other light-demanding pioneer species (Walters and Bartholomew 1984, Sanford et al. 2003, Markesteijn et al. 2007, Smith and Shackleton 2000). Seedlings in the shade site showed higher shoot length than in open site in *F. moluccana* and *A. mangium* (Figure 1).

Table 1. Specific Leaf Area (SLA) and Specific Root Area (SRA) in each species in open and shade sites. Statistical analysis using independent t-test of n = 5 in each treatment; p-value ≤0.05 is significantly different. Asterisk symbols are significant differences of open and shade sites using independent t-test (p<0.05)

Species	**Treatments**	**SLA(cm^2g^{-1})**		**SRA(cm^2g^{-1})**	
		mean±SE	***p***	**mean±SE**	***p***
R. pseudoacacia	Open	130.08 ± 3.12	0.005*	180.01 ± 54.12	0.028*
	Shade	257.55 ± 22.70		829.18 ± 198.64	
F. moluccana	Open	108.01 ± 8.91	0.001*	544.16 ± 100.30	0.184ns
	Shade	252.02 ± 26.51		708.94 ± 52.77	
A. mangium	Open	115.82 ± 12.18	<0.001*	970.16 ± 57.39	0.095ns
	Shade	231.87 ± 17.19		1307.08 ± 161.65	

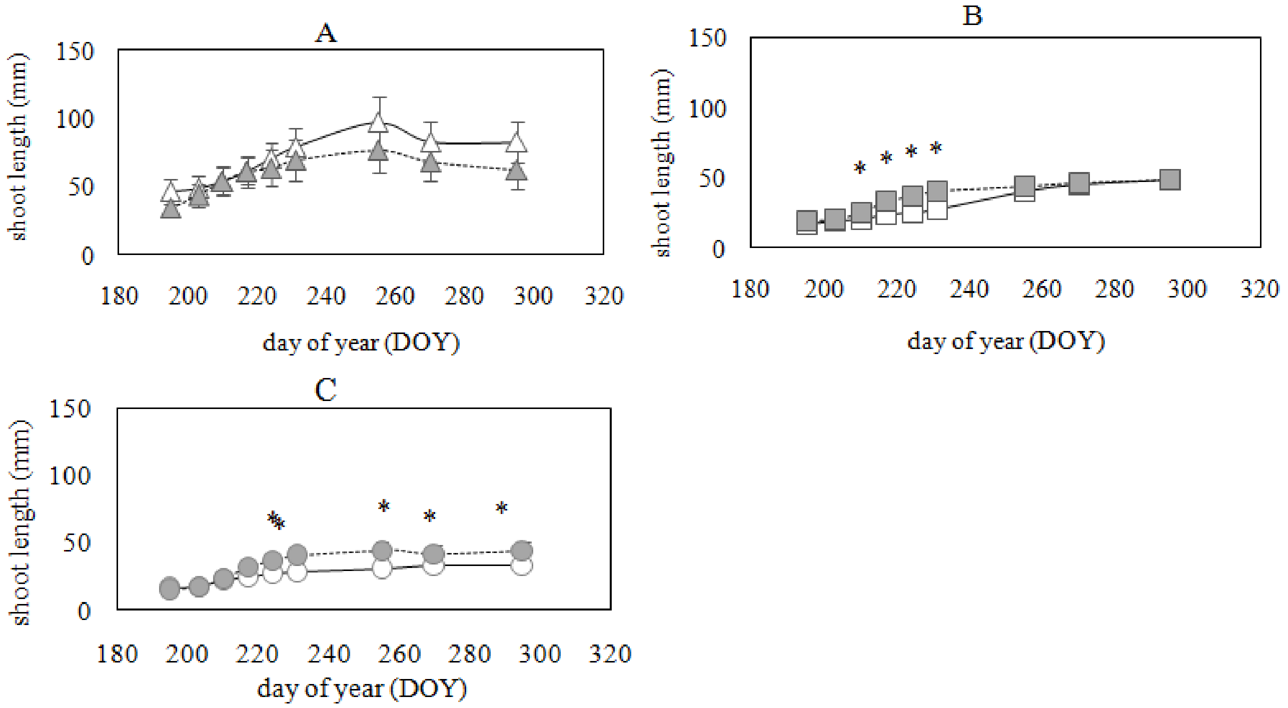

Figure 1. Changes in shoot length before and after the shading were applied in seedlings of *R. pseudoacacia* (A), *F. moluccana* (B), and *A. mangium* (C). Open symbols are seedlings in open sites (n=30) and close symbols are seedlings in shade sites (n=30). Error bars are standard errors. Asterisk symbols are significant differences of open and shade sites using independent t-test (p<0.05)

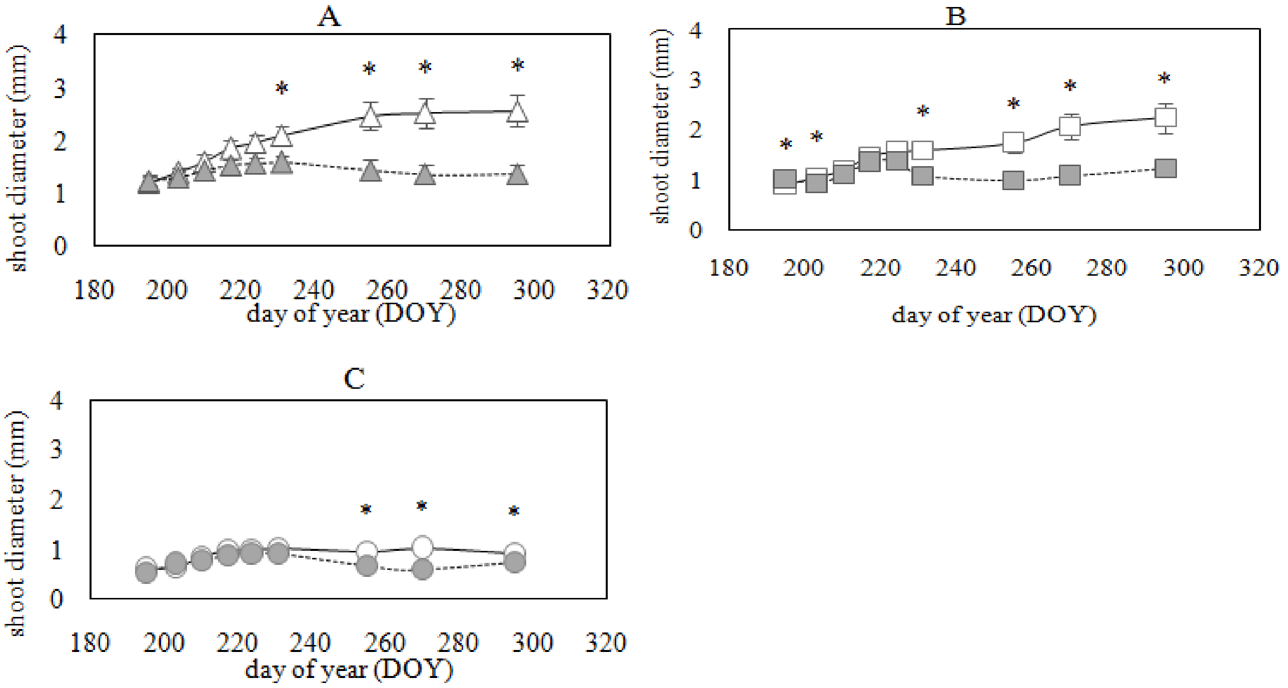

Figure 2. Changes in shoot diameter before and after the shading were applied in seedlings of *R. pseudoacacia* (A), *F. moluccana* (B), and *A. mangium* (C). Open symbols are seedlings in open sites (n=30) and close symbols are seedlings in shade sites (n=30). Error bars are standard errors. Asterisk symbols are significant differences of open and shade sites using independent t-test (p<0.05).

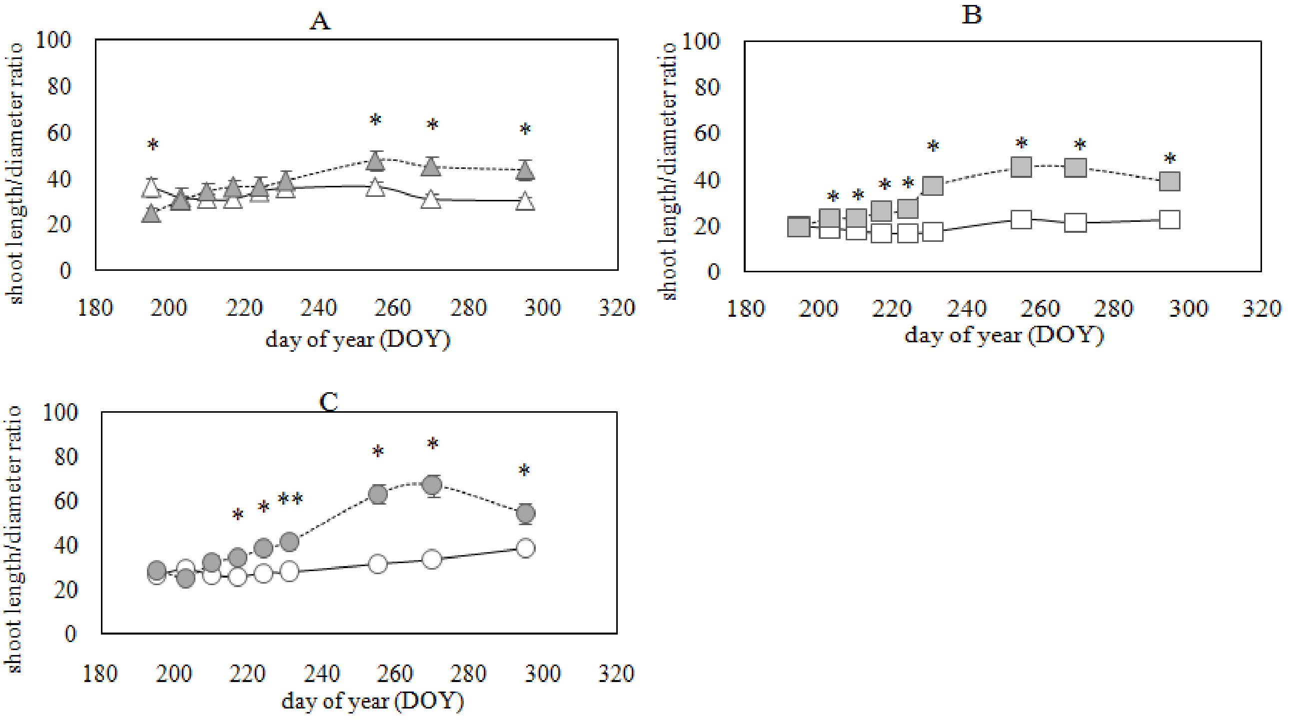

Figure 3. The atio of shoot length to shoot diameter before and after the shading was applied in seedlings of *R. pseudoacacia* (A), *F. moluccana* (B), and *A. mangium* (C). Open symbols are seedlings in open sites (n=30) and close symbols are seedlings in shade sites (n=30). Error bars are standard errors. Asterisk symbols are significant differences of open and shade sites using independent t-test (p<0.05))

Table 2. Dry mass (DM), respiration rates and the amount of non-structural carbohydrate (NSC) in three organs (leaf, stem, and root) and whole-plant of seedlings of three legume species (*R. pseudoacacia*, *F. moluccana*, *A. mangium*) grown in open and shade site. Mean values and p-values after the comparison between open and shade sites using Mann-Whitney U-tests are shown, and bold means significantly higher values (p<0.05) between open and shade sites. Different characters mean significant differences (p<0.05) among species after Holm's multiple comparisons of Kruskal-Wallis tests, and no characters mean no significant differences after the tests.

	Leaf			**Stem**			**Root**			**Whole-plant**		
	Open	**Shade**	**p**	**Open**	**Shade**	**p**	**Open**	**Shade**	**p**	**Open**	**Shade**	**p**
DM (g)												
R. pseudoacacia	**0.634** a	0.064	0.004	**0.503** a	0.104	0.009	**1.544** a	0.147	0.004	**2.681** a	0.314	0.004
F. moluccana	**1.030** a	0.152	0.032	0.321 a	0.064	0.056	**0.647** a	0.064	0.008	**1.998** a	0.281	0.016
A. mangium	0.078 b	0.035	0.065	0.027 b	0.018	0.394	**0.087** b	0.018	0.002	**0.193** b	0.071	0.009
Respiration rates (nmol s^{-1})												
R. pseudoacacia	3.343 a	0.924	0.052	**1.866** a	0.584	0.030	**6.268** a	1.211	0.004	**11.477** a	2.719	0.009
F. moluccana	**7.470** a	1.453	0.032	1.474 a	0.322	0.056	**4.313** a	1.700	0.032	**13.256** a	3.475	0.032
A. mangium	0.278 b	0.205	0.394	0.105 b	0.102	0.818	**1.255** b	0.360	0.026	**1.638** b	0.668	0.026
NSC (mg)												
R. pseudoacacia	**72.09** a	2.15 A	0.004	**88.20** a	8.94	0.004	**437.51** a	12.84 A	0.004	**597.80** a	23.93	0.004
F. moluccana	**156.94** a	15.72 B	0.008	**33.33** a	5.38	0.032	**24.75** b	4.29 A	0.032	**215.02** a	25.39	0.008
A. mangium	6.80 b	4.59 AB	0.329	2.02 b	1.16	0.177	**1.88** c	0.27 B	0.002	10.70 b	6.07	0.082

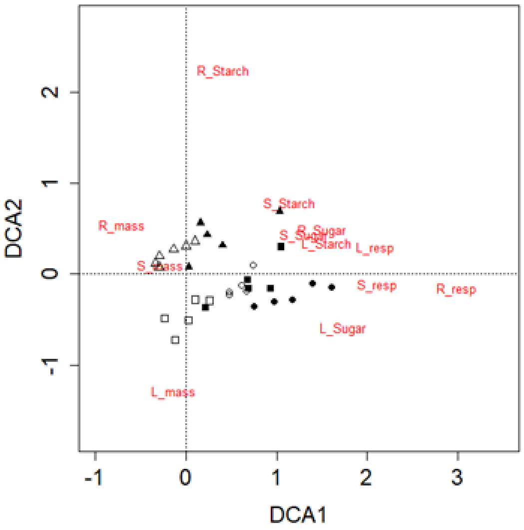

Figure 4. Detrended Correspondence Analysis (DCA) ordination of the entire data set parameters of all species materials in open (open symbols) and shade site (close symbols). The seedlings of *R. pseudoacacia* are in triangle symbols, *F. moluccana* are in square symbols, and *A. mangium* are in circle symbols. Note: L: leaf; S: stem; R: root; mass: dry mass; resp: respiration rates

Under low-light conditions, shade-intolerant species prioritize shoot length growth over diameter increase (Evans and Poorter 2001; Gommers et al. 2013; Liu et al. 2016; Noguchi et al. 2001). This enhances light absorption and reduces carbon use. We also found in our study that seedlings in shade site performed higher SLA than that in open site (Table1). We believe that plants respond against light stress by allocating larger surface areas to capture light (Catoni et al. 2015; Xu et al. 2009). From these findings, leaf is the most preferential organ for capturing light. Legner et al. 2014 showed that shade-tolerant species have higher plasticity on SLA than shade-intolerant species and this may be useful in species-specific N allocation patterns for supporting photosynthesis under the shaded conditions. From these findings, leaf is the most preferential organ for capturing light (Hanba et al. 2002).

Seedlings in the open site have a better chance of capturing light for photosynthesis than seedlings in shade sites, resulting in higher carbon gain and carbon stock for metabolism (Pattison et al. 1998). The NSC was highly allocated to the roots in *R. pseudoacacia*, and to the leaf in *F. moluccana* and *A. mangium* (Table 2). *R. pseudoacacia* can resprout from stump and horizontal roots after aboveground perturbations (Hoshino et al. 2021). It is a species with characteristic of high carbon storage in the roots because this species exhibits high maintenance respiration (Barbaroux and Breda 2002), high basal respiration rates in sapwood tissues, need access for the new leaf flush before leaf expansion in spring (Breda and Granier 1996; Landhäusser 2011), and resprout after experiencing aboveground damage (Cierjacks et al. 2013). Highlighting that *R. pseudoacacia* species have higher function on carbon storage than the other two species. Meanwhile, *F. moluccana* and *A. mangium* show better assimilation of carbohydrates by maximizing the carbon use for photosynthesis. Some invasive species such as *A.koa*, *F. moluccana*, and *P.cattleianum* contain high protein and amino acid represented N storage in leaves, allowing rapid growth in heterogenous light environments (Funk et al. 2013). Also, recent study supports idea that *Acacia* has high phenotypic plasticity in response to light availability that correlates with stored N that useful for adaptation under changing light conditions (Funk 2008). On the aspect of carbon use, leaves have a function to assimilate carbohydrates, so higher leaf mass achieves higher carbon gain and higher sugar contents necessary for or from the photosynthesis process (Jurik et al. 1979).

Most of dry mass of each organ consists of structural carbohydrates. Soluble sugar can be used for metabolism while starch cannot. Starch is, however, used for the stock of carbohydrates (DCA axis 1 means the activity of each organ). Categorized by DCA axis 2, root is the most important organ for carbon storage, and the amount of sugar does not contribute to the function of carbon storage, compared to the amount of starch. Along the gradient of light conditions, shaded seedlings invest their carbon resources into metabolism higher. On the other hand, seedlings in the open site allocate their carbon resources into structure or carbon stock. The results supported by our finding on the respiration rate, carbon stock, carbon use, and NSCs where seedlings in shade sites had smaller biomass production due to low ability of light capturing resulting in low carbon gain and carbon stock.

Throughout our findings, we understood that the strategy for legume trees for survival under shade conditions varies to ensure balanced carbon gain, carbon use, and carbon stock. In our results, we found the interactions between shoot growth (length and diameter), biomass, and NSCs concentration correlate positively with light availability (Figure 1, Figure 2, Table1, Table2). The optimum use of carbon stock by each organ supports the survival strategy in low light environment as we recognized in shade site seedlings. *R. pseudoacacia* allocated higher storage to the roots and a low elongation to aboveground shoots to relates to the ability of the species to recover after the death or damage of aboveground parts following disturbances such as flood and clear-cut. The *R. pseudoacacia* are able to produce new sprouts from the roots when the aboveground parts are under environmental disturbances, which cause the decrease of carbon gain (Masaka 2016, Nicolescu et al. 2020). On the other hand, *F. moluccana* and *A. mangium* invest high NSC to the leaves, which ensures a greater carbon use efficiency during photosynthesis production and respiration. The two species development mechanisms for higher light capture by large shoot elongation and high biomass deposition to leaves under the shaded conditions.

The basic silvics information on the legume species is important for restoration activities. The comprehensive information on morphological and physiological changes due to light intensity in our study will be useful in identifying light tolerant species. Our study found that morphological and physiological changes are part of adaptation to light conditions, including tolerance to low light. However, at the end of our investigation, the seedlings under shade conditions showed a low increment of biomass which we determined was due to low light intolerance. Many studies determined *R. pseudoacacia, F. moluccana,* and *A. mangium* as shade-intolerant species following observations on various light regimes (Hughes et al. 2011; Osunkoya and Othman 2005). This study examined the growth through the carbon allocation among organs to understand the survival behavior and adaptation strategies of legume species in low light conditions. Contrary to studies that stated that some legume species could not survive under the shade due to shade intolerance (Izaguirremayoral et al. 1995; Sprent 1999), we observed in our study that legume species perform an adaptation strategy through exhibit plasticity changes. ..

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