Physiological Traits of Vanilla Plant (*Vanilla planifolia* Andrew) in Various Types of Shade Trees

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Sri Suryanti[1,*], Hangger Gahara Mawandha[1], Herawati Oktavianty[2]

[1]*Agrotechnology Study Program, Faculty of Agriculture, INSTIPER Yogyakarta, Jl. Nangka II, Maguwoharjo, Depok Sleman, Yogyakarta, 55281, Indonesia*
[2]*Agricultural Product Technology Study Program, Faculty of Agricultural Technology, INSTIPER Yogyakarta, Jl. Nangka II, Maguwoharjo, Depok Sleman, Yogyakarta, 55281, Indonesia*

[*]*Corresponding email: ntie@instiperjogja.ac.id*

ABSTRACT

Vanilla plants are CAM species and are very sensitive to direct sunlight. Shade plants are crucial for mitigating the intensity of sunlight to protect vanilla plants. The physiological properties of vanilla plants under different shade trees were studied to understand how shade trees affect vanilla plants. The research applied a randomized completely block design with four groups. Planting was carried out using four shade plants, including *Gliricidia sepium, Syzygium aromaticums, Erythrina variegata,* and *Leucaena leucocephala*. Microclimate conditions such as temperature, humidity, and sunlight intensity were observed three times a day (morning, afternoon, and evening). Physiological observation parameters include chlorophyll A, chlorophyll B, total chlorophyll, proline, and relative water content. The research results showed that temperature, humidity, and intensity of sunlight varied depending on the type of shade plant. Types of shade plants significantly influence chlorophyll A content, chlorophyll B levels, total chlorophyll, proline, and relative water content. The conclusion indicated that the type of shade plant affects the microclimatic conditions of the vanilla plant, thereby influencing the physiological traits of the vanilla plant.

Keywords: Chlorophyll; Microclimate; Proline; Water Content

INTRODUCTION

Vanilla plant (*Vanilla planifolia* Andrews) is a tropical plant widely cultivated in Madagascar, Indonesia, China, and Mexico (Rahman et al., 2019). High concentrations of phytochemical elements with high antioxidant activities in stems and leaves showed that *Vanilla planifolia* is a source of antioxidants (Yusuf et al., 2023). Vanilla is a plantation commodity with high economic value (Mudyantini et al., 2024). Vanilla plants grow optimally at temperatures between 20 and 30 °C (Parada-Molina et al., 2022), with a minimum rainfall of 2,000 mm per year, sunlight intensity of 30 – 50 %, air humidity of 60 – 75 % (Iftikhar et al., 2023), and in the warmest, driest environment (Parada-Molina et al., 2022). The average rainfall of 2,050 and 2,070 mm gradually reduces the suitable growing area for vanilla species. There is a need to rearrange the vanilla agricultural production strategies by adopting sustainable and climate-smart practices and implementing a national strategy for conserving genetic diversity (Armenta-Montero et al., 2022).

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Vanilla plants are susceptible to direct sunlight, so they need a shade tree to reduce the intensity of sunlight. Excessive shading can destroy vanilla plants, significantly influencing the number of branches produced (Nugraha et al., 2024). Land and climate suitability, especially light intensity, are crucial factors, so the adjustment to land, climate, and cultivation techniques are necessary (Rosman, 2020).

The chlorophyll fluorescence, P700 redox state, and electrochromic shift signals were measured to examine photosynthetic characteristics under FL in *Vanilla planifolia*. The light use efficiency was high in the morning but was limited in the afternoon, indicating that the pool of malic acid dried down in the afternoon. During morning photosynthetic enhancement, electron flow through photosystem I quickly reached 95% of its maximum value within 4–6 min, indicating that V. planifolia exhibits a faster photosynthetic enhancement compared to C3 and C4 plants reported previously. Upon a sudden transition from dark to actinic light, *Vanilla planifolia* displayed a rapid re-oxidation of P700, indicating a swift outflow of electrons from PSI to alternative electron acceptors, which was attributed to the O2 photo-reduction mediated by the water-water cycle. The quantum photochemical yield of PSI and PSII of vanilla plants was mostly reduced in the afternoon compared to the morning. This suggests that CO_2 assimilation is very low in the afternoon. Meanwhile, the non-photochemical quantum in PSII and PSI increased markedly to protect PSI and PSII (Wang et al., 2022). The high relative humidity due to excessive shading decreased the yield of *Vanilla planifolia* (Andrade et al., 2023).

Vanilla plants do not require full sun (*shade-loving plants*). Therefore, protective plants are essential for vanilla cultivation. The diverse types of protective plants used for vanilla cultivation can significantly impact the intensity of sunlight the plant receives. The light intensity received by vanilla plants varied depending on the shading. Teak and jackfruit trees can be used as shading options in vanilla cultivation as they provide optimal sunlight intensity, resulting in 36% and 46% of yields, respectively (Nugraha et al., 2024). The vanilla plant is a CAM plant. High solar radiation can inhibit the process of photosynthesis and the growth of vanilla plants. However, in the long term, vanilla plants exhibit higher photosynthesis and growth at intermediate radiation levels (Sanchez, 2021). In CAM plants, stomata open at night when conditions are relatively cold and moist. PEP carboxylase operates at night, binding inorganic carbon to C_4 acid stored in large vacuoles. At noon, the stomata close to saving water, and the C_4 acid is decarboxylated to release CO_2, which is then fixed by Rubisco in the C_3 photosynthesis pathway.

Colored photoselective shade netting (CPSN) can alter the spectral light quality. The research result showed that red and blue CPSN affect the physiology traits and increase the antioxidant activity of *Vanilla planifolia*. Red CPSN can accelerate plant growth and biomass production, possibly due to its higher efficiency. However, further research is needed to know if red CPSN can also increase reproductive development and fruit yield (Sanchez, 2021). At an altitude of 825 m asl, vanilla plants produce better generative growth and yield components, although vegetative growth decreases. Vanilla orchids are not frost-tolerant and require tropical climatic conditions (Arya & Lenka, 2019). The flowering *of Vanilla planivolia* requires strong sunlight (Kitai & Lahjie, 2016). The research showed that blue light with a wavelength of 460 nm and red color light with a wavelength of 660 nm markedly improved stem elongation and chlorophyll synthesis of vanilla plants. Blue light markedly improves root elongation, the number of roots, and the number of leaves of vanilla plants (Ramírez-Mosqueda et al., 2017).

Vanilla plants can adapt to their light environments through morphological and physiological traits (Zhang et al., 2018). Changes in the absorption of sunlight by plants result in morphological and physiological changes. Leaf adjustment is achieved through filtration effect, light distribution, and adaptation to environmental conditions. The difference in the chlorophyll content between shaded and unshaded plants affects the density of photosynthesis photon flow. The transmission of light is carried out through vacuoles to shorten the distance that electrons must travel in the electron transfer chain. Physiological acclimatization is done by changing the chlorophyll arrangement and PSII/PSI ratio. Sheltered plants have a high PS II/PSI ratio and a/b chlorophyll ratio to increase the light-capture complex for more efficient photosynthesis (Yustiningsih, 2019). Shade conditions can improve gas exchange, reduce leaf temperature, and promote chlorophyll synthesis (Gómez-Bellot et al., 2023). This research aimed to determine the influence of types of shade trees on the physiological traits of vanilla plants.

MATERIALS AND METHODS

Research Area

The research was carried out on vanilla farms in Sinogo, Pagerharjo, Samigaluh, Kulonprogo from May to November 2023. The location was 7◦ 66 S, 110◦ 16 E, and 700 m above sea level.

Experimental Design

The research applied a randomized completely block design with 4 blocks. The treatment involves a type of shading plant, which includes 4 types of shade trees and climbing plants, namely *Gliricidia sepium, Syzygium aromaticum, Erythrina variegata,* and *Leucaena leucocephala.* The vanilla plants were 2 years old, with a planting distance of 80 x 150 cm. There were 5 plant samples for each different type of shade tree. The physiological parameters observed included chlorophyll A content, chlorophyll B levels, total chlorophyll, proline, and relative water content. Data analysis was carried out using analysis of variance (ANOVA) at the level of 5% and continued with the Duncan Multiple Range Test (DMRT) and correlation regression analysis. Daily measurements of sunlight intensity, temperature, and air humidity under the canopy of shade trees were taken for each plant sample at 6.00, 12.00, and 18.00.

Chlorophyll Content Analysis

Chlorophyll content was measured by sampling fully opened leaves. Chlorophyll was extracted from fresh leaves using 80% acetone filtered and then read with Spectronic 21 at wavelengths of 645 and 663 nm (Lichtenthaler, 1987).

Proline Content Analysis

Proline content was measured using a modified method (Bonjoch & Tamayo, 2001). The plant material for measurement was fully opened leaves. The leaves were mashed using a grinder, with 0.5 g of the material finely ground with a mortar with 10 ml of a 3% sulfosalicylic acid solution. The impact results were filtered with the Whatman 2 filter paper. A solution of ninhydrin acid was prepared by heating 0.50 g of ninhydrin in 30 l of glacial acetic acid and 29 ml of 6 M phosphoric acid until the solution was mixed. 0.5 ml of filtrate was reacted with 2 ml of ninhydrin acid in a test tube, then shaken and heated at 100 ^{0}C for one hour. The mixture was extracted with 5 ml of toluene and then cornered with a stinger for 15 seconds. After about 24 hours, the absorbent layer separated at the top and was aspirated with a pipette. The absorbent of the solution was read spectronic 21 D at a wavelength of 520 nm.

Relative Water Content Analysis

The relative water content of the leaves was determined by first measuring the fresh weight of the sample leaves, which were then saturated in water for 24 hours, after which they were weighed to obtain the turgid weight. After soaking, the samples were dried quickly with filter/tissue paper and immediately weighed to get a fully turgid weight (TW). The samples were then oven-dried at 80^{0}C for 24h and weighed to obtain dry weight (DW).

The relative moisture content (RWC) was calculated by the formula:

$$RWC\ (\%) = \frac{\text{fresh weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \times 100\ \% \quad (1)$$

RESULTS AND DISCUSSION

Microclimate of Vanilla Plants

Vanilla plants should employ shade to reduce the intensity of sunlight. The influence of shade plants varies across different parameters, including temperature, air humidity, and sunlight intensity (Table 1). The measurements of microclimate conditions revealed differences in temperature, air humidity, and sunlight intensity. Shading plants meet the requirements for optimal growing temperatures, as the temperatures range from 25 to 29 ^{0}C. The highest temperature was observed under the shade of *Gliricidia sepium*, while the temperatures under *Syzygium aromaticum, Erythrina variegata,* and *Leucaena leucocephala* shade plants were the same. Air humidity ranges from 65 – 75%, so the use of four types of shade met the requirements for growing vanilla plants. The intensity of sunlight under the shade of *Erythrina variegata* was 31%, under *Leucaena leucocephala* was 49%, under *Gliricidia sepium* was 59%, and under *Syzygium aromaticum* plants was 62%. This indicates that *Erythrina variegata* and *Leucaena leucocephala* plants are suitable shade plants for vanilla cultivation because they provide 30-50% of the sunlight intensity required by vanilla plants. This result is in line with (Rosman, 2020), showing that *Erythrina variegata* and *Leucaena leucocephala* trees qualify as suitable shading plants for vanilla.

Table 1. Microclimate data under various types of shade (± SE)

Types of Shade	Temperature (^{0}C)	Air Humidity (%)	Intensity of sunlight (%)
Gliricidia sepium	29 ± 0.53	75 ± 4.64	62 ± 0.10
Syzygium aromaticum	25 ± 0.80	67 ± 4.23	59 ± 0.13
Erythrina variegata	25 ± 0.62	65 ± 4.75	31 ± 0.09
Leucaena leucocephala	25 ± 0.53	67 ± 4.42	49 ± 0.09

The intensity of sunlight is a crucial factor that influences the growth and production of vanilla plants. During the vegetative phase, a lower intensity of sunlight is required compared to the generative phase. The intensity of the ray influences the temperature and humidity. There is a close relationship between the intensity of sunlight received by vanilla plants and both humidity and temperature. This is indicated by the results of correlation analysis, where there is a positive correlation between the sunlight intensity and air humidity (r = 0.712) and between the intensity of sunlight and temperature (r = 0.56). The results of the correlation analysis between temperature and humidity also showed a positive correlation (r = 0.977). This shows a close relationship between temperature and humidity.

Chlorophyll Content

Chlorophyll level is one of the main factors affecting the photosynthetic ability of plants. Using *Erythrina variegata* plants as the shade can significantly increase chlorophyll A, chlorophyll B, and total chlorophyll. There was a marked difference in the level of chlorophyll A, chlorophyll B, and total chlorophyll when comparing shading with *Erythrina variegata* to shading with *Leucaena leucocephala, Syzygium aromaticums* and *Gliricidia sepium* (Table 2).

Table 2. The effect of shade on the physiological traits of vanilla plants

Types of Shade	Parameters				
	Chlorophyll A (unit)	Chlorophyll B (unit)	Total Chlorophyll (unit)	Proline content (μmol/g)	Relative water content (%)
Gliricidia sepium	14.087 b	3670.191 c	26.203 c	0.066 c	20.899 b
Syzygium aromaticum	13.568 d	1885.965 d	22.254 d	0.157 a	13.797 d
Erythrina variegata	14.607 a	7484.309 a	31.910 a	0.059 d	29.163 a
Leucaena leucocephala	14.401 c	4999.367 b	28.542 b	0.073 b	20.825 c

Note: Means followed by the same letters in the column show a significance difference in the confidence level of 5%.

The chlorophyll A, B, and total chlorophyll levels were opposite the intensity of sunlight the vanilla plant received. The results of correlation analysis indicate a negative correlation between the intensity of sunlight and levels of chlorophyll A (r = - 0.787), chlorophyll B (r = - 0.917), and total chlorophyll (r = - 0.865). The intensity of sunlight under the shade of *Erythrina variegata* was 31%, under *Leucaena leucocephala* was 49%, under *Syzygium aromaticums,* was 59% and under *Gliricidia sepium* was 62%. This result is in line with previous studies on pineapple plants. Pineapple plants are CAM plants like vanilla, and high intensity of light in pineapple plants also reduces chlorophyll levels (Rodríguez-Escriba et al., 2015; Wang et al., 2020). Different research results are found in *Aralia errata*, a C_3 plant, where pigment photosynthesis of chlorophyll A, chlorophyll B, and total chlorophyll significantly decreases as shading increases or intensity of light decreases (reduction in chlorophyll content is directly related to the decrease in intensity of light) (Gao et al., 2019). Environmental factors such as light intensity affect the arrangement and role of the photosynthetic organs from C3 and C4 species (Hu et al., 2023). The results of this study are the same as research conducted by (Juhaeti et al., 2020), indicating that chlorophyll levels increase by 50% with 50% shading but decrease when shading reaches 75%.

The results showed that in vanilla plants, chlorophyll A levels and chlorophyll B levels significantly increased at low intensity of light (*Erythrina variegata* tree shade). The intensity of sunlight received by plants decreases when using shade trees with denser or larger leaves. *Erythrina variegata* plants have wider leaves, so the intensity of sunlight received by vanilla plants is lower. Low light intensity causes air temperature and humidity to decrease (Table 1). To increase the efficiency of light capture at low intensity, plants will reduce the light transmitted by increasing the number of chloroplasts and the pigment content within each chloroplast. According to (Ko et al., 2020), *Vanilla planifolia* is a loving plant. Vanilla chloroplasts started to decrease when blue light was higher than 20 µmol $m^{-2}s^{-1}$. Shade plants reduced leaf temperature and increased the synthesis of chlorophylls (Gómez-Bellot et al., 2023).

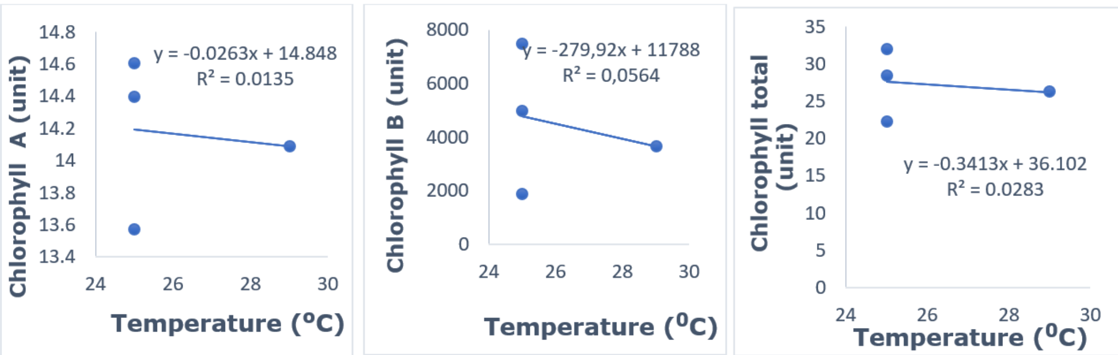

Figure 1. The correlation between temperature and content of chlorophyll A, chlorophyll B and total chlorophyll

The high intensity of sunlight increases the temperature. Increased temperature also decreases chlorophyll A, chlorophyll B, and total chlorophyll. This is shown by the results of regression analysis between temperature and levels of chlorophyll A (y = - 0.0263 x + 18.848), chlorophyll B levels (y = - 279.92 x + 11788), and total chlorophyll (y = - 0.3413 x + 36.102) (Figure 1). The results of this study differ from those of research on orchid plants, which are CAM plants. Most orchids, like vanilla plants, can adapt to their light environments through morphological and physiological traits (Zhang et al., 2018). Blue-red photoselective shade netting increased chlorophyll content and maximum quantum yield of photosystem II of the vanilla plant. In orchid plants, low temperatures further reduce chlorophyll A and chlorophyll B levels, while higher air temperatures lead to increased chlorophyll levels (Daems et al., 2022).

Proline Content

Proline is an osmolytic compound that helps plants resist drought stress (*drought tolerance*) through an osmotic adjustment mechanism. Light is a factor that greatly affects plants growth, development, and physiological processes. Plants can adjust their metabolism to environmental changes such as light by accumulating proline. When the intensity of light is very high, the accumulation of proline is three times greater than when the intensity is normal (Kovács et al., 2019). The results showed that *Syzygium aromaticum* shade obtained the highest levels of proline and significantly differed from *Erythrina variegata*, *Gliricidia sepium*, and *Leucaena leucocephala* shade. The intensity of sunlight received by vanilla plants was lower when under *Erythrina variegata* shade (31%), so that proline levels were lower. Conversely, the shade of *Syzygium aromaticum* resulted in a higher intensity of sunlight received by vanilla plants, leading to increased proline levels. High proline accumulation in response to increased temperatures was observed under the *Syzgium aromaticum* shade. According to (Raza et al., 2023), plants accumulate proline in response to temperature stress. There is a close relationship between the intensity of sunlight and proline levels. The results of the correlation analysis showed a positive correlation between the intensity of sunlight and proline levels (r = 0.484). According to (Zhang et al., 2022), free proline regulation is the main mechanism of plant adaptation to light stress. In CAM orchids, proline content in leaves increased after 7 weeks of drought under moderate light conditions (Tay et al., 2019).

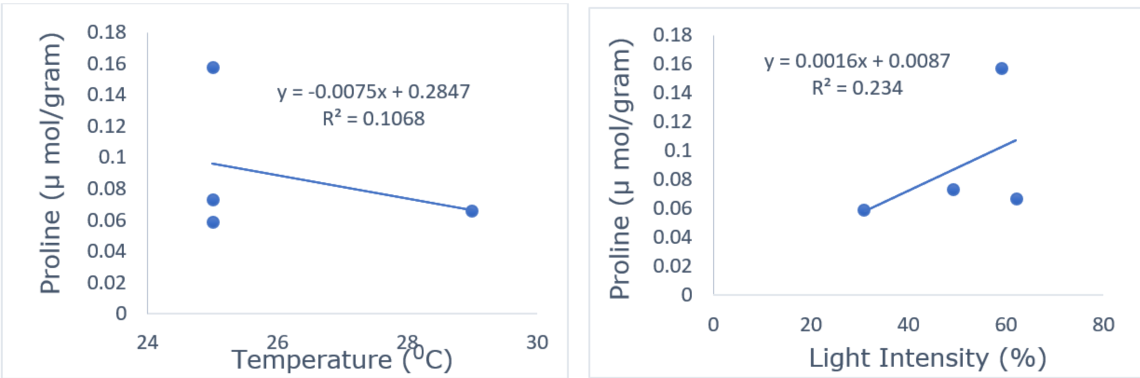

Figure 2. The correlation between temperature and light Intensity and proline Levels

The regression analysis results showed a positive linear regression between the intensity of light and proline levels (y = 0.0016x + 0.0087). This suggests that an increase follows an increase in the intensity of sunlight in proline levels. In contrast, a decrease in the intensity will be followed by a decline in proline levels (Figure 2). According to (Xie et al., 2023), slight shading significantly decreased the proline. On the contrary, plants accumulate proline in response to high-temperature stress (Raza et al., 2023).

An increase in air temperature, associated with higher light intensity, causes the proline levels of vanilla plants to decrease, even though the reduction is insignificant. This is shown by the regression analysis results between air temperature and proline levels (y = - 0.0075 x + 0.2847 (Figure 2). The study results are not in line with research on tomato plants, which are C3 plants where proline levels increase with higher temperatures (Suminar et al., 2021). This happens because C3 plants have a low saturation point for light intensity, leading to stress and increased proline levels as the intensity of light rises.

Relative Water Content

Relative water content is related to cell volume and can indicate a balance between the amount of water absorbed and that of water transpired. Plants that have a high relative water content are more resistant to drought stress. The results showed that the type of shade significantly affects the relative water content. The correlation analysis reveals a negative correlation between light intensity and relative water content (r = - 0.839), indicating that increased intensity of sunlight will reduce the leaf relative water content.

The regression analysis showed a negative linear regression between light intensity and relative water content (y = - 376.88 x + 40110). This shows that a decrease follows an increase in the intensity of light in relative water content, and conversely, a decrease in the intensity is followed by a rise in relative water content (Figure 3).

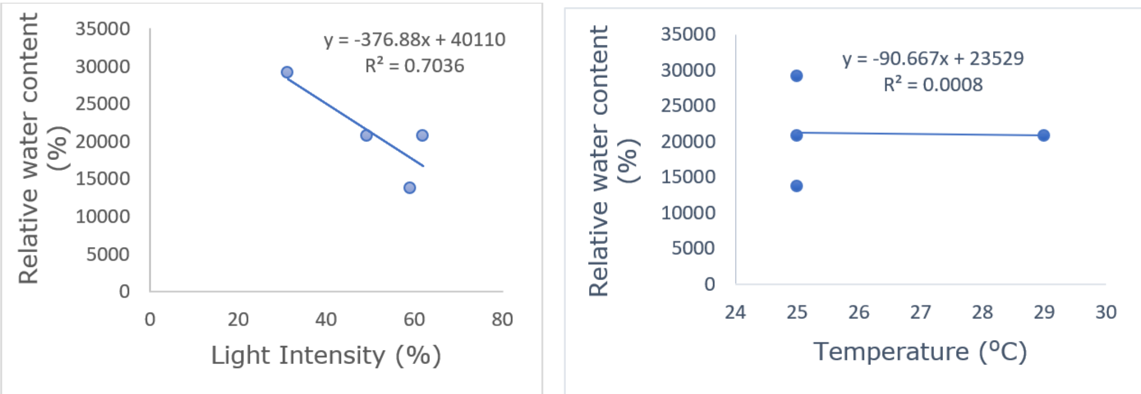

Figure 3. The correlation between light intensity and relative water content

In CAM plants with succulent leaves, such as vanilla plants, large vacuoles within the leaves enable them to store more water (Hu et al., 2023). It is a strategy of plants to store water in unfavorable conditions such as lack of water. The relative water content indicates the water status inside the plant. The higher the relative water content, the greater the amount of water stored in the tissues. The relative water content decreases under the conditions of lack of water (Arena, 2020). The intensity of sunlight received by vanilla plants under the shade of *Syzygium aromaticum* plants was 62%, and under *Gliricidia sepium* was 59 %. This condition can increase air temperature, leading to higher evaporation rates than under the shade of *Erythrina variegata*, consequently reducing the relative water content in the leaves. Conversely, under the shade of *Erythrina variegata*, the intensity of sunlight received by vanilla plants is low (31%), resulting in lower air temperatures, reduced evaporation, and higher moisture content in the leaves. The regression analysis shows these results between temperature and relative water content (y = - 90.667 x + 23539). The regression analysis shows the increase in air temperature causes the relative water content to be lower (Figure 3).

CONCLUSION

Erythrina variegata and *Leucaena leucocephala* are plants that qualify as shade and climbing trees for *Vanilla planifolia*. Using shading trees of *Erythrina variegata* increased chlorophyll A content, chlorophyll B levels, total chlorophyll, and relative water content but decreased vanilla plant proline levels. Higher intensity of sunlight decreases chlorophyll A, chlorophyll B, total chlorophyll, and relative water content, but high intensity increases vanilla plant proline levels.

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AUTHORS CONTRIBUTIONS

SS, HGM, and HO conducted the experiment. SS contributed to preparing the introduction and experimental design. HGM contributed to determined parameters. HO contributed to data analysis.

COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

REFERENCES

Andrade, A., Delgado, A., Herrera, C., Bustaman, G., Soto, H., & Guizar, G. (2023). Relative Humidity and Photosynthetically Active Radiation Influence the *Vanilla planifolia* Fruit Yield. *Tropical and Subtropical Agroecosystems*, *26*, 1–12.

Arena, C. (2020). (ADP-Ribose) Polymerase Activity in a Facultative CAM Plant Exposed to Long-Term Water Deprivation. *Plants*, *9*(1192), 1–14.

Armenta-Montero, S., Menchaca-García, R., Pérez-Silva, A., & Velázquez-Rosas, N. (2022). Changes in the Potential Distribution of *Vanilla planifolia* Andrews under Different Climate Change Projections in Mexico. *Sustainability, 14*(5), 2881. https://doi.org/10.3390/su14052881

Arya, S. S., & Lenka, S. K. (2019). (PDF) Vanilla Farming: The Way Forward. *Eden Horti*, *2*(3), 20–24. https://doi.org/10.13140/RG.2.2.18451.02087

Bonjoch, N.P., & Tamayo, P.R. (2001). *Handbook of Plant Ecophysiology Techniques: Protein Content Quantification by Bradford Method* (Ed. Manuel J. Reigosa Roger). Springer https://doi.org/10.1007/0-306-48057-3

Daems, S., Ceusters, N., Valcke, R., & Ceusters, J. (2022). Effects of chilling on the photosynthetic performance of the CAM orchid Phalaenopsis. *Frontiers in Plant Science*, *13*(November), 1–17. https://doi.org/10.3389/fpls.2022.981581

Gao, Z., Khalid, M., Jan, F., Saeed-ur-Rahman, Jiang, X., & Yu, X. (2019). Effects of light-regulation and intensity on the growth, physiological and biochemical properties of *Aralia elata* (miq.) seedlings. *South African Journal of Botany*, *121*, 456–462. https://doi.org/10.1016/j.sajb.2018.12.008

Gómez-Bellot, M. J., Sánchez-Blanco, M. J., Lorente, B., Vicente-Colomer, M. J., & Ortuño, M. F. (2023). Effects of Light Intensity and Water Stress on Growth, Photosynthetic Characteristics and Plant Survival of *Cistus heterophyllus* Desf. Subsp. carthaginensis (Pau) M. B. Crespo & Mateo. *Horticulturae*, *9*(8). https://doi.org/10.3390/horticulturae9080878

Hu, C., Mascoli, V., Elias, E., & Croce, R. (2023). The photosynthetic apparatus of the CAM plant Tillandsia flabellate and its response to water deficit. *Journal of Plant Physiology*, *282*, 153945. https://doi.org/10.1016/j.jplph.2023.153945

Iftikhar, T., Majeed, H., & Waheed, M. (2023). *Essentials of Medicinal and Aromatic Crops*: *Vanilla* (Eds. Zia-Ul-Haq, M., Abdulkreem AL-Huqail, A., Riaz, M., Farooq Gohar, U. 333). Springer. https://doi.org/10.1007/978-3-031-35403-8

Juhaeti, T., Setyowati, N., & Syarif, F. (2020). The chlorophyll contents and growth performances of west java (Indonesia) jobtears (*Coix lacryma*-jobi) accessions under low light intensity conditions. *Biodiversitas*, *21*(11), 5178–5185. https://doi.org/10.13057/biodiv/d211124

Kitai, K., & Lahjie, A. M. (2016). Sunlight environment for *Vanilla planifolia* cultivated by agroforestry system in East Kalimantan. *International Journal of Agroforestry and Silviculture*, *3*(10), 232–245.

Ko, S. S., Jhong, C. M., Lin, Y. J., Wei, C. Y., Lee, J. Y., & Shih, M. C. (2020). Blue light mediates chloroplast avoidance and enhances photoprotection of vanilla orchid. *International Journal of Molecular Sciences*, *21*(21), 1–17. https://doi.org/10.3390/ijms21218022

Kovács, H., Aleksza, D., Baba, A. I., Hajdu, A., Király, A. M., Zsigmond, L., Tóth, S. Z., Kozma-Bognár, L., & Szabados, L. (2019). Light Control of Salt-Induced Proline Accumulation Is Mediated by Elongated Hypocotyl 5 in Arabidopsis. *Frontiers in Plant Science*, *10*(December),

1–14. https://doi.org/10.3389/fpls.2019.01584
Lichtenthaler, H. K. (1987). Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. *Methods in Enzymology*, *148*, 350–382. https://doi.org/10.1016/0076-6879(87)48036-1
Mudyantini, W., Huda, Y. N., & Pitoyo, A. R. I. (2024). Growth of vanilla (*Vanilla planifolia*) roots in different internodes of stem cuttings with NAA (Naphthaleneacetic Acid) treatments. *Cell Biology & Development*, *8*(1), 13–21. https://doi.org/10.13057/cellbioldev/v080102
Nugraha, I. K., Suryanti, S., & Mawandha, H. G. (2024). Growth Optimization of Several Varieties of Vanilla Plants (*Vanilla Planifolia* Andrews) using Various Light Intensities. *Juatika*, *6*(2), 199–207.
Parada-Molina, P. C., Pérez-Silva, A., Cerdán-Cabrera, C. R., & Soto-Enrique, A. (2022). Climatic and microclimatic conditions of vanilla (*Vanilla planifolia* Jacks. ex Andrews) production systems in Mexico. *Agronomia Mesoamericana*, *33*(2). https://doi.org/10.15517/am.v33i2.48682
Rahman, K. U., Thaleth, M. K. Bin, Kutty, G. M., & Subramanian, R. (2019). Pilot scale cultivation and production of *Vanilla planifolia* in the united arab emirates. *Bulgarian Journal of Agricultural Science*, *25*(6), 1143–1150.
Ramírez-Mosqueda, M. A., Iglesias-Andreu, L. G., & Luna-Sánchez, I. J. (2017). Light quality affects growth and development of in vitro plantlet of *Vanilla planifolia* Jacks. *South African Journal of Botany*, *109*, 288–293. https://doi.org/10.1016/j.sajb.2017.01.205
Raza, A., Charagh, S., Abbas, S., Hassan, M. U., Saeed, F., Haider, S., Sharif, R., Anand, A., Corpas, F. J., Jin, W., & Varshney, R. K. (2023). Assessment of proline function in higher plants under extreme temperatures. *Plant Biology*, *25*(3), 379–395. https://doi.org/10.1111/plb.13510
Rodríguez-Escriba, R. C., Rodríguez, R., López, D., Lorente, G. Y., Pino, Y., Aragón, C. E., Garza, Y., Podestá, F. E., & González-Olmedo, J. L. (2015). High Light Intensity Increases the CAM Expression in "MD-2" Micro-Propagated Pineapple Plants at The End of The Acclimatization Stage. *American Journal of Plant Sciences*, *06*(19), 3109–3118. https://doi.org/10.4236/ajps.2015.619303
Rosman, R. (2020). Peran Teknologi Pembungaan dalam Menentukan Produski Tanaman Vanili (*Vanilla planivolia* Andrews). *Warta Balittro*, *37*(74), 1–3.
Sanchez, F. (2021). *Physiological, Biochemical and Growth Responses of Vanilla planifolia to Colored Photoselective Shade Netting* [Master Thesis, University of Florida]. University of Florida Digital Collections. https://original-ufdc.uflib.ufl.edu/UFE0058327/00001
Suminar, E., Mubarok, S., Nuraini, A., Ezura, H., & Fitriatin, F. W. (2021). Kandungan Prolin, Klorofil, dan Hasil Tanaman Tomat Mutan IAA9 pada Kondisi Cekaman Suhu Tinggi. *Agrikultura*, *31*(3), 280. https://doi.org/10.24198/agrikultura.v31i3.30924
Tay, S., He, J., & Yam, T. W. (2019). CAM plasticity in epiphytic tropical orchid species responding to environmental stress. *Botanical Studies*, *60*(1), 1–15. https://doi.org/10.1186/s40529-019-0255-0
Wang, H., Wang, X. Q., Xing, Y. Z., Zhao, Q. Y., Zhuang, H. F., & Huang, W. (2022). Regulation of Chloroplast ATP Synthase Modulates Photoprotection in the CAM Plant *Vanilla planifolia*. *Cells*, *11*(10), 1–13. https://doi.org/10.3390/cells11101647
Wang, L., Lee, M., Ye, B., & Yue, G. H. (2020). Genes, pathways and networks responding to drought stress in oil palm roots. *Scientific Reports, 10*(1), 1-13. https://doi.org/10.1038/s41598-020-78297-z
Xie, A., Lv, M., Zhang, D., Shi, Y., Yang, L., Yang, X., Du, J., Sun, L., & Sun, X. (2023). Effects of slight shading in summer on the leaf senescence and endogenous hormone and polyamine contents in herbaceous peony. *Scientific Reports*, *13*(1), 1–14. https://doi.org/10.1038/s41598-023-46192-y
Yustiningsih, M. (2019). Intensitas Cahaya dan Efisiensi Fotosintesis pada Tanaman Naungan dan Tanaman Terpapar Cahaya Langsung. *BIOEDU*, *4*(2), 43–48.
Yusuf, N., Masor, N. F., Zolkeflee, P., Zakaria, N. S., Abdul Wahab, N. H., Asari, A., & Aziz, A. N. (2023). Qualitative phytochemical analysis, enzymatic and non-enzymatic antioxidant activities in stems and leaves of *Vanilla planifolia* (Orchidaceae). *Food Research*, *7*(3), 165–172. https://doi.org/10.26656/fr.2017.7(3).008

Zhang, J., Ge, J., Dayananda, B., & Li, J. (2022). Effect of light intensities on the photosynthesis, growth and physiological performances of two maple species. *Frontiers in Plant Science*, *13*(October), 1–10. https://doi.org/10.3389/fpls.2022.999026

Zhang, S., Yang, Y., Li, J., Qin, J., Zhang, W., Huang, W., & Hu, H. (2018). Physiological diversity of orchids. *Plant Diversity*, *40*(4), 196–208. https://doi.org/10.1016/j.pld.2018.06.003