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Growth of Jackfruit Seedlings under Plant Growth Regulator (PGR) and Shading Treatments

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Authors' contributions

This work was carried out in collaboration among all authors. Author KK conceived and designed the study, performed the formal analysis, co-wrote the original draft of the manuscript, and contributed to reviewing and editing the manuscript. Author KS contributed to the study conceptualization, developed the methodology, and participated in reviewing and editing the manuscript. Author MRT contributed to the study conceptualization, developed the methodology, and participated in reviewing and editing the manuscript. Author AS conducted the field experiment, performed the formal analysis, prepared the original draft of the manuscript, and contributed to reviewing and editing the manuscript. All authors read and approved the final manuscript.

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Abstract

The success of jackfruit (*Artocarpus heterophyllus* Lam.) grafting is strongly influenced by the physiological quality of the rootstock prior to grafting. This study aimed to evaluate the effects of 75% shading and the individual application of 50 ppm α-naphthaleneacetic acid (NAA) and 15 ppm abscisic acid (ABA) on the vegetative growth and physiological characteristics of jackfruit rootstock seedlings. The experiment was

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conducted using a randomised complete block design with four treatments (control/untreated, 75% shade, 15 ppm ABA, and 50 ppm NAA), five replications, and five seedlings per experimental unit. Morphological parameters, including plant height, stem diameter, branch number, shoot number, and leaf number, were measured biweekly, whereas chlorophyll, glucose, and fructose contents were determined monthly. Stem anatomy was evaluated 7 days after treatment. The results showed that 75% shading consistently promoted vegetative growth by increasing stem diameter, branch number, shoot number, and leaf number while maintaining stable chlorophyll content and carbon metabolism. The application of 50 ppm NAA enhanced plant height and tended to maintain higher chlorophyll content, indicating improved photosynthetic performance and vegetative vigour. In contrast, 15 ppm ABA did not affect vegetative growth but increased soluble sugar accumulation, suggesting its role in maintaining physiological homeostasis and stress adaptation. Stem anatomical observations revealed darker tissues in ABA- and NAA-treated seedlings than in the control, which may indicate greater accumulation of lignin, phenolic compounds, and oxidised secondary metabolites associated with enhanced cell wall development and physiological responses induced by plant growth regulator application. Overall, 75% shading was the most effective treatment for improving the vegetative and physiological quality of jackfruit seedlings prior to grafting.

Keywords: Artocarpus heterophyllus; abscisic acid; α-naphthaleneacetic acid; shade; vegetative growth.

1. Introduction

Indonesia is one of the countries with a very high diversity of *Artocarpus* germplasm. Around 30 *Artocarpus* species have been recorded in Indonesia, with approximately 17 of these found on the island of Kalimantan (Mursyidin & Makruf, 2020). This wealth of germplasm constitutes an important genetic resource for the development of high-yielding varieties of tropical fruit crops. However, the majority of *Artocarpus* genetic resources are still found in forest areas, the existence of which is increasingly under threat due to land-use change and habitat fragmentation; consequently, efforts are needed to conserve these resources whilst also utilising them through the development of cultivation practices.

Jackfruit (*Artocarpus heterophyllus* Lam.) is a tropical fruit species in the family Moraceae with high economic value and considerable development potential in Indonesia. It is native to the Western Ghats of India, with Bangladesh recognised as a centre of diversity (Witherup et al., 2019). Every 100 g of ripe fruit contains 88–410 kJ of energy, 1.2–1.9 g of protein, 16.0–25.4 g of carbohydrates, and various essential vitamins and minerals such as vitamin A, vitamin C, and calcium (Nansereko & Muyonga, 2021; Barros-Castillo et al., 2023). High-quality jackfruit seedlings are commonly produced through vegetative propagation, particularly grafting, because it preserves the genetic characteristics of superior cultivars and shortens the juvenile phase compared with seed propagation. However, grafting success largely depends on the physiological quality of the seedlings, especially rootstock vigour, as poor early growth, weak root systems, and low vigour can limit cambial activity, callus formation, vascular tissue development, and the transport of water and photosynthates required for successful graft union (Melnyk, 2017; Serivichyaswat et al., 2024). Therefore, improving seedling growth before grafting is essential for successful propagation.

One promising approach is the exogenous application of plant growth regulators (PGRs) combined with environmental manipulation. Among these, the synthetic auxin α-naphthaleneacetic acid (NAA) promotes cambial cell division, lateral root formation, and root system development, thereby enhancing water and nutrient uptake (Du & Scheres, 2017), whereas abscisic acid (ABA) improves water balance, water-use efficiency, and tolerance to environmental stresses through stomatal regulation (Cutler et al., 2010). Application of the two PGRs is expected to enhance seedling vigour and physiological quality prior to grafting. In addition to PGR application, regulating light intensity through shading is also an important strategy for improving seedling quality. A 75% shading treatment, or light intensity of 1075 lux, creates a more favourable microclimate by reducing solar radiation, ambient temperature, and transpiration rate, thereby minimising water loss from plant tissues. Such conditions help maintain cell turgor, preserve tissue water balance, and alleviate heat stress that may otherwise inhibit physiological activities. Although light intensity is reduced with 75% shading, this level is sufficient to sustain photosynthesis, allowing adequate production of photoassimilates to support vegetative growth, cambial activity, and root system development (Arévalo-Gardini et al., 2021). Furthermore, shading has been reported to enhance plant sensitivity to auxin, promoting cell elongation and stem growth while creating favourable physiological conditions before grafting (Mditshwa et al., 2019; Bantis et al., 2021).

The effectiveness of PGR application and shading management has been demonstrated in several tropical fruit crops. Auxin application has been reported to support root development, cambial activity, tissue attachment, and vascular reconnection during graft healing (Melnyk, 2017; Serivichyaswat et al., 2024). ABA application has been shown to maintain plant water status, improve tolerance to environmental stress, and enhance the physiological quality of tomato seedlings during the early stages of growth (Cutler et al., 2010). Likewise, shading levels of approximately 70–75% have been reported to improve seedling growth and grafting success by maintaining plant physiological status, preserving tissue hydration, and reducing environmental stress during graft union formation (Mditshwa et al., 2019; Bedoya-Ramírez et al., 2024).

Recent evidence from crop and nursery systems indicates that plant growth regulator treatments can modify early seedling vigour, while nursery practices that improve rootstock growth may support subsequent grafting operations (Bhattacharya & Hembram, 2025; Getachew et al., 2025).

Photoselective shade netting has also been shown to alter rootstock diameter, biomass accumulation, gas exchange, and water-use efficiency in avocado seedlings, indicating that light management can influence both morphological and physiological seedling quality (Bedoya-Ramírez et al., 2024).

At the graft union, auxin signalling in cambial and procambial tissues contributes to tissue attachment, cell division, and vascular differentiation, whereas ABA regulates growth-stress trade-offs and physiological responses to adverse conditions (Serivichyaswat et al., 2024; Mo et al., 2024).

However, evidence remains limited on how 75% shading and the individual application of NAA or ABA affect the integrated vegetative, chlorophyll, soluble sugar, and stem anatomical responses of jackfruit rootstock seedlings under nursery conditions. This research gap restricts the selection of pre-grafting treatments specifically suited to jackfruit.

This study was conducted to investigate the effects of 75% shading and the individual application of the plant growth regulators α-naphthaleneacetic acid (NAA) and abscisic acid (ABA) on the vegetative growth and physiology of jackfruit seedlings.

2. Materials and Methods

2.1 Time and Study Site

The study was conducted from October 2025 to June 2026. Jackfruit seedlings of the 'Madu' cultivar, selected as rootstocks for their relatively low, slow-coagulating latex production, were obtained from Kertamaya Orchard, South Bogor, West Java, Indonesia. Seedling transplanting, plant maintenance, plant growth regulator (PGR) application, morphological observations, and grafting were conducted in the screenhouse of the Leuwikopo Experimental Farm, IPB University, Bogor, Indonesia (6°33′51″ S, 106°43′28″ E), while physiological analyses of leaf chlorophyll, glucose, and fructose contents were performed at the Seed Biology and Biophysics Laboratory, Department of Agronomy and Horticulture, IPB University.

2.2 Materials and Equipment

Plant materials consisted of two-month-old seed-propagated jackfruit seedlings of the 'Madu' cultivar, selected for uniformity in age, plant height, stem diameter, and physiological health. Healthy seedlings free from pests, diseases, and mechanical damage were transplanted into polyethylene bags (30 × 20 cm) containing a homogeneous mixture of topsoil and rice husk (2:1, v/v) supplemented with dolomitic lime. Plant growth regulator (PGR) treatments consisted of 15 ppm abscisic acid (ABA) and 50 ppm α-naphthaleneacetic acid (NAA) from Merck KGaA, Darmstadt, Germany. Physiological analyses of leaf chlorophyll, glucose, and fructose contents were performed using methanol, ethanol, distilled water, chloroform, and a D-Fructose/D-Glucose Assay Kit from Megazyme K-FRGLQR according to the Megazyme protocol for the Sucrose/Fructose/D-Glucose Assay Kit (300 assays).

2.3 Experimental Design

The experiment was arranged in a randomised complete block design (RCBD) with a single factor consisting of four treatments: 75% shade provided by paranet, application of 15 ppm abscisic acid (ABA), application of 50 ppm α-naphthaleneacetic acid (NAA), and an untreated control (without plant growth regulator application or shade). Each treatment was replicated five times, with each experimental unit consisting of five jackfruit seedlings. Consequently, the experiment comprised 20 experimental units and a total of 100 jackfruit seedlings.

2.4 Experimental Procedures

2.4.1 Seedling Preparation and Maintenance

The experiment began with the selection of healthy, uniform, two-month-old, seed-propagated jackfruit seedlings free of visible pests and diseases. The seedlings were transplanted into 20 × 30 cm polyethylene bags containing a 2:1 (v/v) mixture of soil and rice husk and then acclimatised under 60% shade netting before being transferred to the respective treatment screenhouses. Throughout the experiment, seedlings received routine maintenance, including daily manual irrigation, monthly fertilisation with Growmore (NPK: 20–20–20) applied as a soil drench at 0.5 g L^{-1} (500 mL per plant). Pest and disease control was conducted manually as needed.

2.4.2 Preparation of Solutions and PGR Application

Plant growth regulator (PGR) treatments consisted of 15 ppm abscisic acid (ABA) and 50 ppm α-naphthaleneacetic acid (NAA). Stock solutions were prepared by dissolving the active compounds in methanol and diluting them with distilled water to the required concentrations. The PGRs were applied once after seedling acclimatisation using the soil drench method, with 10 mL of solution applied around the base of each seedling. Control plants received an equal volume of distilled water to ensure treatment consistency.

2.4.3 Installation and Calibration of 75% Shading

A 75% shading treatment was applied throughout the experimental period using paranet installed over the designated treatment area in the screenhouse. The shading level was calibrated using a lux meter before the experiment to ensure uniform light conditions. The average light intensity measured under ambient conditions (without shading) was 4,110 lux, whereas the 75% shade treatment reduced light intensity to 1,072 lux, allowing approximately 25% of the available light to reach the seedlings throughout the experimental period. Light intensity was measured at several locations to confirm uniform shading, and the netting remained in place throughout the study to maintain consistent microclimatic conditions.

2.5 Growth Measurements

2.5.1 Environmental Condition Observations

Environmental conditions inside the screenhouse were monitored throughout the experiment using an Elitech GSP-6 Temperature and Humidity Data Logger. Temperature and relative humidity were automatically recorded at 15-minute intervals, and the collected data were processed to illustrate the environmental conditions during the experimental period.

2.5.2 Morphological Response Assessment of Seedlings

Seedlings were subjected to the designated shading treatments before morphological observations were conducted at two-week intervals throughout the experimental period. Growth parameters included plant height increment (measured from the stem base to the highest shoot), stem diameter (measured 10 cm above the stem base using a digital caliper), and the number of new branches, leaves, and shoots, which were recorded by direct counting. All measurements were performed on every experimental unit every two weeks.

2.5.3 Leaf Chlorophyll Content Analysis

Leaf chlorophyll content was determined monthly using the spectrophotometric method of Warren (2008). Five leaf samples were collected from the rootstock of each treatment, and leaf discs (0.56 cm^2) were homogenised in

100% methanol. The homogenates were centrifuged at 16,940 × g for 2 min, and the supernatants were transferred to a 96-well microplate. Absorbance was measured at 652 and 665 nm using a microplate spectrophotometer, and chlorophyll a and chlorophyll b concentrations were calculated according to the equations of Ritchie (2006):

Chl a (µg ml-1) = (−8,0962 x A652, 1 cm) + (16,5169 x A665, 1 cm)

Chl b (µg ml-1) = (27,4405 x A652, 1 cm) – (12,1688 x A665, 1 cm)

Where: A652, 1 cm : pathlength-corrected absorbance at 652, 1 cm A665, 1 cm : pathlength-corrected absorbance at 665, 1 cm

2.5.4 Leaf Glucose and Fructose Content Analysis

Glucose and fructose contents were determined monthly using leaf samples collected from the rootstock following the method of Lanoue et al. (2019). Leaf discs (0.56 cm^2) from fully expanded sun-exposed leaves were extracted with 80% ethanol, and the extracts were air-dried before being reconstituted with distilled water and 99% chloroform. After centrifugation at 2,200 × g for 3 min, the supernatant was analysed using a D-Fructose/D-Glucose Assay Kit (Megazyme, K-FRGLQR). Absorbance was measured at 340 nm with a Multiskan Sky Microplate Spectrophotometer. Glucose and fructose concentrations were determined using the D-Fructose/D-Glucose Assay Kit (Megazyme, K-FRGLQR) according to the manufacturer's instructions. Briefly, 40 µL of Reagent 1 was mixed with 160 µL of distilled water and 3 µL of either the sample or standard solution (163 µL distilled water for the blank), and the absorbance (A_1) was measured after 3 min. Subsequently, 20 µL of Reagent 2 was added, mixed thoroughly, and the absorbance (A_2) was recorded after approximately 5 min. Finally, 20 µL of Reagent 3 was added, mixed thoroughly, and the final absorbance (A_3) was measured after approximately 10 min. After all reagents had been added and thoroughly mixed, the glucose and fructose concentrations were automatically calculated using the following equations:

D-Glucose (µg ml-1) = A2 - (A1 x 203/223)

D-Fructose (µg ml-1) = A3 - (A2 x 223/243)

Where : A1-A3 represent the absorbance values measured at a wavelength of 340 nm.

2.5.5 Stem Tissue Anatomical Evaluation

Stem anatomy was evaluated qualitatively at the end of the experiment to compare jackfruit seedlings treated with 15 ppm ABA, 50 ppm NAA, and the control. Thin transverse hand sections were prepared using a razor blade and observed without histological staining under a light microscope (Olympus CX23). Observations focused on tissue colouration, relative tissue thickness, and the visibility of vascular tissue boundaries as qualitative indicators of anatomical responses to plant growth regulator treatments. Thin transverse hand sections were prepared using a sharp razor blade following the free-hand sectioning procedure described by Soukup & Tylová (2019).

2.6 Data Analysis

Data compilation and visualisation were performed using Microsoft Excel. Quantitative data were analysed using analysis of variance (ANOVA) with SAS OnDemand for Academics software. When the ANOVA indicated significant treatment effects, mean comparisons were performed using Tukey's honestly significant difference (HSD) test at a significance level of $\alpha = 0.05$.

3. Results and Discussion

3.1 Temperature and Relative Humidity Monitoring

Air temperature showed a typical diurnal pattern, with lower values in the morning, rising toward midday, and peaking in the afternoon. Maximum temperature increased from 31.03°C in December to 35.21°C in March, likely reflecting greater solar radiation during the transition to the dry season. This pattern is consistent with the environmental monitoring reported by Prasetyo et al. (2021). Temperature and relative humidity are important environmental factors that regulate plant growth by affecting photosynthesis, respiration, enzymatic activity, transpiration, and plant water balance (Ferrante & Mariani, 2018; Sawan, 2018).

The maximum temperatures recorded in Table 1 (31.03–35.21°C) may reduce photosynthetic efficiency and increase transpiration, potentially inducing heat stress (Ferrante & Mariani, 2018; Song et al., 2014; Sadok et al., 2021). The 75% shade treatment likely moderated the microclimate by reducing solar radiation and helping maintain plant water balance. Minimum temperatures remained relatively stable (21.70–22.65°C), thereby minimising the risk of cold stress and supporting normal respiration and metabolic activity (Yadav, 2010). Overall, the mean daily temperature (23.92–25.69°C) indicated that the screenhouse provided suitable conditions for jackfruit seedling growth and for evaluating vegetative responses to different plant growth regulator treatments and shade levels.

Relative humidity followed an inverse pattern to temperature, with higher values at night and lower values during the day. This occurs because rising temperatures increase the saturation vapour pressure and the air's capacity to hold water vapour; as a result, relative humidity decreases even as the actual water vapour content remains constant (Lawrence, 2005). During the experiment, minimum relative humidity varied by 12.45% across the observation period, reflecting substantial daytime microclimatic fluctuation in the screenhouse. These changes were mainly associated with solar radiation and air temperature, which increased evapouration and transpiration. As defined by Hao and Lu (2022), relative humidity is the ratio of the actual water vapour content in the air to the maximum amount the air can hold at a given temperature. Air circulation within the screenhouse may also have contributed to temporal variation in humidity by affecting water vapour distribution.

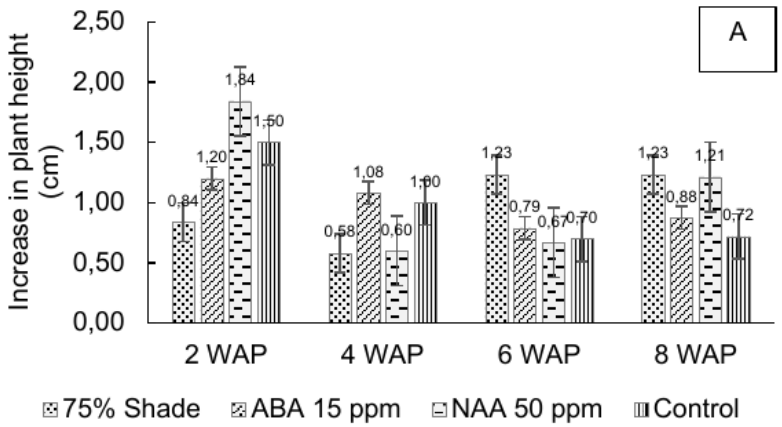
Table 1. Temperature and relative humidity in the experimental screenhouse

Month	Average Temperature (°C)			Average Relative Humidity (%)		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
December	21.67 ± 0.54	23.92 ± 0.60	31.03 ± 2.24	79.00 ± 7.47	97.54 ± 1.51	100.00 ± 0.00
January	22.65 ± 1.24	25.68 ± 1.75	32.75 ± 3.54	78.03 ± 10.21	95.58 ± 3.13	100.00 ± 0.00
February	22.14 ± 0.65	25.69 ± 0.84	33.65 ± 2.26	72.97 ± 7.67	93.63 ± 3.46	100.00 ± 0.00
March	21.98 ± 0.40	25.57 ± 0.77	35.21 ± 2.73	85.42 ± 15.06	96.57 ± 3.93	100.00 ± 0.00

Notes: Value are mean ± SE

3.2 Morphological Responses of Jackfruit Seedlings

Jackfruit seedling height responded differently to shade and plant growth regulator (PGR) treatments (Figure 1). Plant height generally increased at 2 WAP, declined at 4–6 WAP, and increased again by 8 WAP. The 75% shade treatment promoted greater height during the later observation period, likely by creating a favourable microclimate that reduced solar radiation, temperature, and transpiration while maintaining plant water balance. Similar responses have been reported in cocoa seedlings under shade. Shading also enhances auxin-mediated cell elongation and alleviates heat stress that can impair photosynthesis (Ma & Li, 2019; Tan et al., 2020). In contrast, 15 ppm ABA reduced plant height because ABA-induced stomatal closure limits CO_2 uptake, photosynthesis, and carbohydrate production, thereby restricting stem elongation (Assmann & Jegla, 2016; Verma et al., 2016). Conversely, 50 ppm NAA enhanced seedling height during 6–8 WAP by stimulating meristematic activity, cell division, and cell elongation, consistent with findings in wheat (Jeber & Khaeim, 2019). Control seedlings exhibited good early growth, but growth declined toward the end of the experiment, indicating that although jackfruit seedlings possess adequate natural vegetative growth, both shading and PGR application modified physiological responses and produced distinct growth patterns.



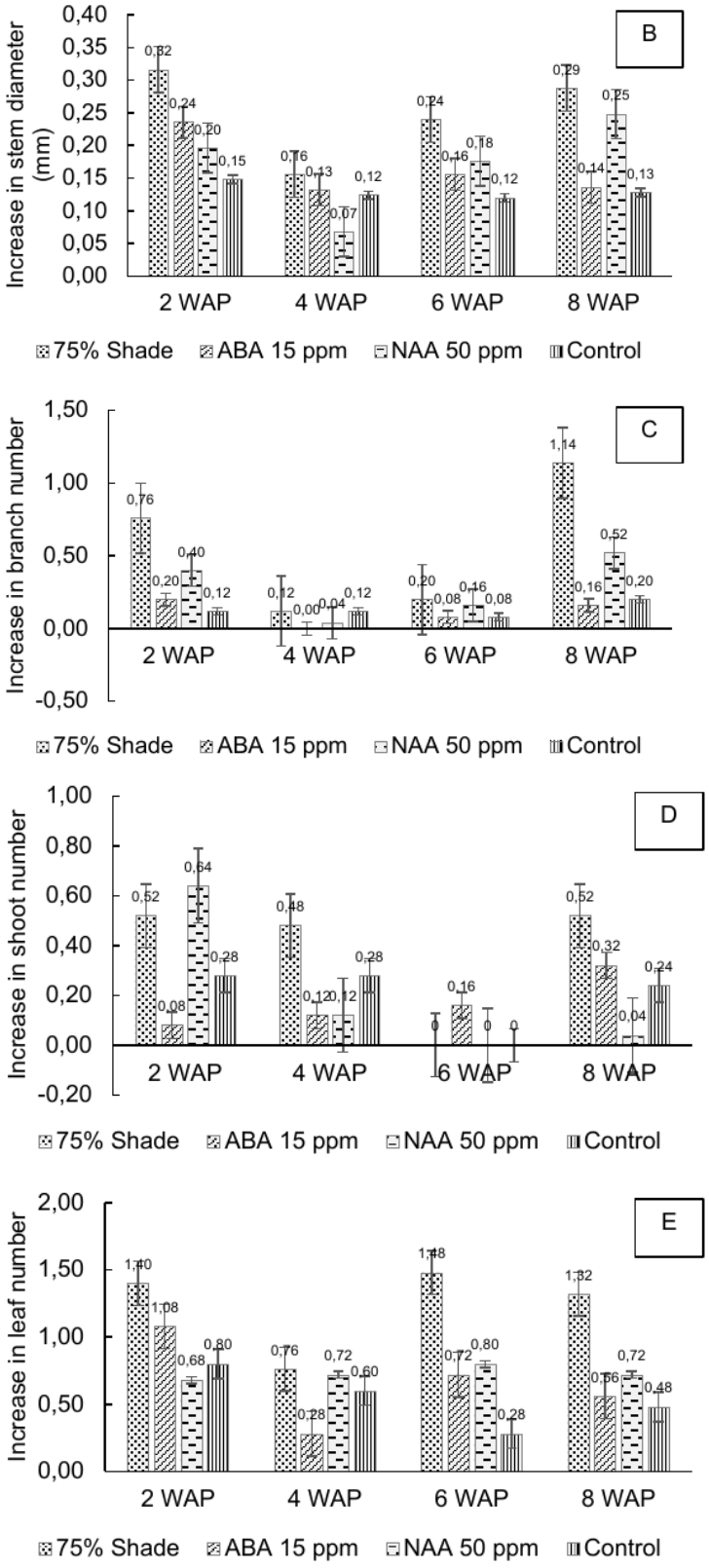


Fig. 1. Effect of 75% shading and plant growth regulator treatments on the increment of jackfruit seedling. A: plant height; B: stem diameter; C: branch number; D: shoot number; E: leaf number. Bars are standard errors (n: 25)

Stem diameter increment is an important indicator of seedling vigour because it reflects vascular cambium activity and secondary vascular development. The 75% shade treatment produced the greatest stem diameter increment, reaching 0.32 mm at 2 WAP, likely due to improved microclimatic conditions that reduced transpiration, maintained plant water status, and sustained cambial activity. Similar responses have been reported under 70–80% shade (Patil & Deshmukh, 2025; Fransson et al., 2021). In contrast, 15 ppm ABA resulted in relatively low stem diameter increment because ABA suppresses cambial cell division and redirects carbon metabolism toward soluble sugar accumulation rather than secondary growth (Brookbank et al., 2021; Liu et al., 2024; Park et al., 2021). The 50 ppm NAA treatment significantly enhanced stem diameter after application, reaching 0.25 mm at 8 WAP, reflecting auxin-induced stimulation of vascular cambium activity, cell division, and secondary xylem and phloem development (Liu et al., 2025). Control seedlings exhibited the lowest stem diameter increment, indicating slower natural secondary growth. Overall, 75% shade and NAA were more effective than ABA or the control in promoting stem thickening and seedling vigour.

Branch production is an important indicator of vegetative development because it reflects axillary meristem activity, apical dominance, and photoassimilate allocation to new vegetative organs (Guan & Jiao, 2020). The 75% shade treatment produced the highest branch increment, reaching 1.14 branches per plant at 8 WAP, likely because shading created a favourable microclimate that reduced transpiration, maintained plant water status, and promoted lateral bud outgrowth through reduced strigolactone signalling and light–hormone interactions (Tang et al., 2025). In contrast, 15 ppm ABA resulted in relatively low branch production because ABA reduces stomatal opening and photosynthesis while maintaining axillary bud dormancy through the BRC1–NCED3 pathway and antagonising cytokinin activity (Schneider et al., 2019). The 50 ppm NAA treatment produced the second-highest branch number by stimulating meristematic activity and vascular development, thereby improving water and photoassimilate transport to axillary buds (Siddik et al., 2015). Control seedlings exhibited the lowest branch increment, indicating limited natural branching. Overall, 75% shade and NAA were more effective than ABA or the control in promoting branch formation through improved hormonal regulation and axillary meristem activity.

Shoot production is an important indicator of vegetative growth because it reflects shoot apical meristem activity, hormonal regulation, and the allocation of photoassimilates to new organ formation (Guan & Jiao, 2020). The 75% shade treatment produced the most consistent increase in shoot number, likely because reduced light intensity induced shade-avoidance syndrome (SAS) while improving the microclimate by lowering radiation, temperature, and transpiration, thereby maintaining metabolic activity and meristem growth (Pierik & de Wit, 2014). Similar responses were reported by Fan et al. (2022), who observed enhanced shoot production under shaded conditions. Although 50 ppm NAA produced the highest shoot number at 2 WAP, ABA and NAA were applied only at 6 WAP, indicating that early shoot development reflected the seedlings' initial physiological condition rather than treatment effects (Domagalska & Leyser, 2011). After application, 15 ppm ABA resulted in relatively low shoot production because elevated ABA promotes bud dormancy, reduces stomatal conductance, and limits carbohydrate availability for new shoot formation (Kishor et al., 2022). Likewise, 50 ppm NAA produced only limited shoot initiation after application, suggesting that auxin primarily promoted stem elongation while maintaining apical dominance and suppressing lateral shoot development (Shimizu-Sato et al., 2009; Sosnowski et al., 2023). Control seedlings showed stable but lower shoot production than shaded seedlings. Overall, 75% shade was more effective than ABA or NAA in promoting shoot development by optimising shoot apical meristem activity and canopy growth.

Treatment with ABA at 15 ppm resulted in relatively low leaf production after application because ABA promotes stress adaptation by inducing stomatal closure, reducing photosynthetic carbon assimilation, suppressing cell division and expansion, and accelerating leaf senescence (Brookbank et al., 2021; Park et al., 2021). In contrast, 50 ppm NAA maintained relatively stable leaf production and produced more leaves than ABA-treated and control seedlings by promoting leaf initiation through the regulation of the shoot apical meristem, cell differentiation, and coordinated hormone signalling (Woodward & Bartel, 2005; Traas, 2019; Xiong & Jiao, 2019). Control seedlings exhibited reduced leaf production, indicating slower natural vegetative growth in the absence of environmental or hormonal stimulation. Overall, 75% shade was the most effective treatment for enhancing leaf production, followed by NAA, whereas ABA tended to suppress leaf development because of its primary role in stress adaptation.

3.3 Leaf Chlorophyll Dynamics and Pigment Ratios

Exogenous plant growth regulator (PGR) applications and shade treatments did not exert statistically significant effects on the concentrations of leaf chlorophyll a, chlorophyll b (Table 2), total chlorophyll, or the chlorophyll a/b ratio (Table 3) across all sampling timelines ($P > 0.05$).

The 50 ppm NAA treatment consistently yielded the highest chlorophyll a (Table 2) and total chlorophyll values (Table 3), peaking at 88.78 μg mL^{-1} and 119.39 μg mL^{-1} in March, respectively (Tables 2 and 3). Conversely, the 15 ppm ABA treatment induced a downward trend in pigment accumulation, decreasing total chlorophyll to its lowest value (96.99 μg mL^{-1}) by the end of the study. Seedlings subjected to 75% shade maintained robust and highly stable pigment contents throughout the evaluation period (102.42–109.99 μg mL^{-1}). Across all treatments, chlorophyll a concentrations remained consistently higher than chlorophyll b concentrations, maintaining a stable chlorophyll a/b ratio between 2.59 and 2.97 (Table 3).

Table 2. Leaf chlorophyll a and chlorophyll b contents of jackfruit seedlings

Treatment	Leaf Chlorophyll a Content (μg mL^{-1})			Leaf Chlorophyll b Content (μg mL^{-1})		
	January	**February**	**March**	**January**	**February**	**March**
75% Shade	75.61 ± 11.95	74.62 ± 15.52	81.65 ± 12.34	26.80 ± 3.46	27.41 ± 5.66	28.33 ± 4.52
ABA 15 ppm	78.34 ± 11.30	70.63 ± 20.36	71.08 ± 21.76	28.49 ± 6.19	27.07 ± 6.66	25.90 ± 6.71
NAA 50 ppm	88.56 ± 10.36	76.54 ± 15.61	88.78 ± 19.19	30.06 ± 4.97	27.86 ± 5.93	30.60 ± 6.98
Control	82.33 ± 7.75	68.62 ± 17.83	72.35 ± 15.74	29.78 ± 2.82	26.08 ± 6.58	26.22 ± 5.43
CD (P=.05)	.39	.86	.50	.61	.95	.64
CV (%)	13.87	25.05	27.16	16.99	24.57	26.34

Notes: values are means ± SE (n = 5)

Table 3. Total chlorophyll content and chlorophyll a/b ratio of jackfruit seedling leaves

Treatment	Total Leaf Chlorophyll Content (μg mL^{-1})			Leaf Chlorophyll a/b Ratio		
	January	**February**	**March**	**January**	**February**	**March**
75% Shade	102.42 ± 15.26	102.03 ± 21.09	109.99 ± 16.55	2.81 ± 0.15	2.72 ± 0.11	2.89 ± 0.18
ABA 15 ppm	106.83 ± 17.34	97.71 ± 26.67	96.99 ± 28.27	2.78 ± 0.22	2.59 ± 0.31	2.70 ± 0.32
NAA 50 ppm	118.63 ± 14.86	104.40 ± 21.30	119.39 ± 25.99	2.97 ± 0.29	2.75 ± 0.20	2.91 ± 0.19
Control	112.11 ± 10.08	94.70 ± 24.25	98.58 ± 20.99	2.76 ± 0.18	2.63 ± 0.21	2.76 ± 0.19
CD (P=.05)	.46	.89	.53	.47	.72	.66
CV (%)	14.30	24.65	26.70	8.38	8.79	8.80

Notes: values are means ± SE (n = 5)

Chlorophyll content is an important factor for assessing the photosynthetic capacity and metabolic stability of jackfruit seedlings during early vegetative development (Baker, 2008). The relative pigment stability observed under 75% shade highlights a successful low-light acclimation strategy. By optimising the structural arrangement of the light-harvesting complex and improving quantum yield, the seedlings effectively mitigated light limitations, a response that reflects adaptive mechanisms documented in other tropical woody crops such as shaded cocoa (Arévalo-Gardini et al., 2021; Mensah et al., 2022).

The positive trend in pigment retention following exogenous NAA application is likely driven by auxin-mediated upregulation of GOLDEN2-LIKE (GLK) transcription factors and Auxin Response Factors (ARFs). These molecular pathways enhance nitrogen assimilation, preserve chloroplast structural integrity, and provide antioxidant protection against reactive oxygen species (ROS), thereby delaying natural foliar senescence (Guo et al., 2021; Yong et al., 2024; Jiang et al., 2025).

In contrast, the decline observed in ABA-treated plants underscores the classic role of abscisic acid in accelerating pigment catabolism. Exogenous ABA triggers stomatal closure and restricts intracellular CO_2 influx, subsequently downregulating primary carbon assimilation and upregulating chlorophyll degradation transcripts (Kuai et al., 2018; Gao et al., 2016; Abhilasha & Roy Choudhury, 2021).

Importantly, the maintenance of the chlorophyll a/b ratio within the 2.59–2.97 range suggests that the fundamental bioenergetic balance between Photosystem I (PSI) and Photosystem II (PSII) remained unimpaired

across all treatments (Voitsekhovskaja & Tyutereva, 2015; Hu et al., 2021). This structural preservation indicates that the core light-dependent reactions retained the functional capacity to generate the ATP and NADPH required to fuel downstream organogenesis and seedling establishment (Shevela et al., 2023).

3.4 Soluble Sugar Dynamics and Carbon Allocation

Exogenous plant growth regulator (PGR) applications and the 75% shade treatment did not induce statistically significant changes in leaf glucose concentrations throughout the January–March monitoring period, maintaining a stable baseline between 61.7 and 72.7 ng mL^{-1} (Table 4). However, distinct carbohydrate partitioning trends emerged over time. The 75% shade cohort exhibited a progressive linear increase in glucose accumulation from January to March. Concurrently, the 15 ppm ABA treatment resulted in the highest absolute glucose concentration in March (72.4 ng mL^{-1}). In contrast, the 50 ppm NAA group showed lower glucose levels prior to application, followed by a minor upward adjustment in March.

Leaf fructose concentrations showed greater phenotypic plasticity than glucose, with statistically significant treatment variation restricted to the January sampling window ($P<0.05$; Table 4). The 75% shade regime generated the highest fructose concentration during this initial phase. Following exogenous applications, the ABA-treated seedlings showed a moderate increase in fructose levels, whereas the 50 ppm NAA cohort exhibited a steady, gradual decline in absolute fructose content toward the end of the vegetative evaluation.

Quantifying soluble hexose dynamics provides a direct physiological window into the photosynthetic efficiency and carbon homeostasis of developing jackfruit seedlings (Stein & Granot, 2018). The steady elevation of both glucose and fructose under the 75% shade treatment indicates a favourable microclimatic mitigation strategy. By dampening excessive solar radiation, reducing canopy temperature, and minimising transpirational vapour pressure deficits, the shade treatment may have reduced photoinhibition. This may have preserved stomatal conductance and sustained steady-state carbon fixation, matching the non-destructive carbohydrate accumulation profiles observed in other shaded perennial crops, such as coffee (Campa et al., 2017; Murchie & Ruban, 2020).

The prominent accumulation of soluble sugars triggered by exogenous ABA reflects a stress-adaptive metabolic shift. Rather than boosting carbon fixation, ABA drives the enzymatic mobilisation of internal reserves by upregulating key starch-degrading transcripts such as *BAM1* and *AMY3*. This accelerated starch-to-sugar hydrolytic flux elevates intracellular hexose pools, providing the solute gradients required for osmotic adjustment and the maintenance of cell turgor while meeting basic metabolic energy requirements under chemically induced stress signalling (Chen et al., 2019; Siddiqui et al., 2020).

Conversely, the declining fructose profile and low glucose accumulation observed in the 50 ppm NAA group underscore an active, auxin-mediated change in sink demand. Instead of stockpiling free soluble sugars in source leaves, exogenous auxin enhances long-distance sugar transport and activates metabolic utilisation pathways, including the upregulation of hexokinase genes such as *MdHxK1*. This accelerates glycolytic flux to fuel active cell division, structural elongation, and cell wall biosynthesis through auxin response factors (ARFs), effectively driving source-to-sink carbon translocation into expanding vegetative biomass rather than foliar storage (Mishra et al., 2022; Batista-Silva et al., 2024).

Collectively, the preservation of steady hexose concentrations indicates that neither PGR manipulation nor structural shading disrupted the core carbon metabolism of the jackfruit seedlings, suggesting their physiological tolerance and adaptive plasticity during early establishment.

Table 4. Glucose and fructose concentrations in jackfruit seedling leaves

Treatment	Leaf Glucose Content (ng mL^{-1})			Leaf Fructose Content (ng mL^{-1})		
	January	February	March	January	February	March
75% Shade	65.3 ± 9	67.5 ± 5	69.1 ± 11	23.2 ± 7	20.1 ± 4	25.4 ± 9
ABA 15 ppm	64.5 ± 4	69.3 ± 5	72.4 ± 6	16.9 ± 6	21.4 ± 7	23.3 ± 8
NAA 50 ppm	61.7 ± 6	64.0 ± 3	69.1 ± 5	20.0 ± 5	19.4 ± 5	16.3 ± 10
Control	64.9 ± 6	67.6 ± 6	72.7 ± 6	16.3 ± 3	22.5 ± 6	26.6 ± 8
CD (P = .05)	0.88	0.41	0.88	0.08	0.91	0.43
CV (%)	9.85	6.37	10.30	23.04	26.26	38.93

Notes: values are means ± SE (n = 5)

3.5 Stem Tissue Anatomy

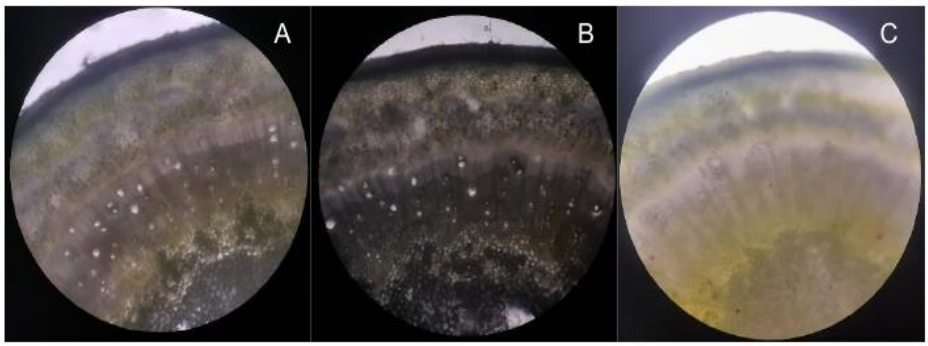


Fig. 2. Stem anatomical characteristics of jackfruit seedlings. A: 15 ppm ABA treatment; B: 50 ppm NAA treatment; C: control

Qualitative stem anatomical observations showed that seedlings treated with 15 ppm ABA and 50 ppm NAA exhibited darker stem tissues than the control (Fig. 2). This darker appearance is therefore more likely associated with the accumulation of phenolic compounds and metabolic changes induced by plant growth regulators rather than increased lignification. Phenolic compounds play important roles in plant defence, antioxidant activity, and tissue differentiation and are commonly enhanced by hormonal regulation and environmental stress (Taiz et al., 2015; Melnyk, 2017). These anatomical observations were consistent with the growth responses observed during the experiment, in which 50 ppm NAA likely promoted vascular cambial activity, vascular differentiation, and carbon metabolism, resulting in improved vegetative growth, whereas 15 ppm ABA primarily activated stress-adaptation mechanisms through secondary metabolism and water conservation, leading to comparatively lower vegetative growth. In contrast, control seedlings exhibited lighter stem tissues, indicating basal metabolic activity without hormonal stimulation. Overall, these findings suggest that plant growth regulator treatments influenced jackfruit seedling growth not only at the morphological level but also through physiological changes reflected in stem tissue appearance, although histochemical staining or biochemical analyses are required to confirm the underlying structural changes.

4. Conclusions

The 75% shade treatment was the most effective in promoting vegetative growth of jackfruit seedlings prior to grafting, as indicated by greater stem diameter, branch number, shoot number, and leaf number while maintaining physiological performance through stable chlorophyll content and carbon metabolism. The application of 50 ppm NAA tended to enhance seedling height and maintain higher chlorophyll content, whereas 15 ppm ABA primarily contributed to physiological homeostasis through soluble sugar accumulation rather than vegetative growth promotion. Overall, 75% shading was the most promising treatment for improving the physiological quality of jackfruit seedlings prior to grafting.

5. Limitations

This study evaluated one shade level and single concentrations of ABA and NAA under one screenhouse environment and with one jackfruit cultivar. Stem anatomy was assessed qualitatively without histochemical staining or biochemical confirmation, so the compounds responsible for darker tissues could not be determined. The study also focused on pre-grafting seedling responses and did not directly quantify graft union formation, graft survival or longer-term post-grafting performance.

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Declaration of AI Use

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Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Abhilasha, A., & Roy Choudhury, S. (2021). Molecular and physiological perspectives of abscisic acid-mediated drought adjustment strategies. *Plants, 10*(12), 2769. https://doi.org/10.3390/plants10122769

Arévalo-Gardini, E., Farfán, A., Barraza, F., Arévalo-Hernández, C. O., Zúñiga-Cernades, L. B., Alegre, J., & Baligar, V. C. (2021). Growth, physiological, nutrient-uptake-efficiency and shade-tolerance responses of cacao genotypes under different shades. *Agronomy, 11*(8), 1536. https://doi.org/10.3390/agronomy11081536

Assmann, S. M., & Jegla, T. (2016). Guard cell sensory systems: Recent insights on stomatal responses to light, abscisic acid, and CO_2. *Current Opinion in Plant Biology, 33*, 157–167. https://doi.org/10.1016/j.pbi.2016.07.003

Baker, N. R. (2008). Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annual Review of Plant Biology, 59*, 89–113. https://doi.org/10.1146/annurev.arplant.59.032607.092759

Bantis, F., Panteris, E., Dangitsis, C., Carrera, E., & Koukounaras, A. (2021). Blue light promotes vascular reconnection, while red light boosts the physiological response and quality of grafted watermelon seedlings. *Scientific Reports, 11*(1), 21754. https://doi.org/10.1038/s41598-021-01158-w

Barros-Castillo, J. C., Calderón-Santoyo, M., Rivera-Aguilar, J. O., & Ragazzo-Sánchez, J. A. (2023). High-value biological compounds in jackfruit (*Artocarpus heterophyllus* Lam.): Postulates of their possible anticancer mechanisms. *Revista Bio Ciencias, 10*, e1403. https://doi.org/10.15741/revbio.10.e1403

Batista-Silva, W., de Paiva Gonçalves, J., Siqueira, J. A., Martins, A. O., Ribeiro, D. M., Nunes-Nesi, A., Zsögön, A., & Araújo, W. L. (2024). Auxin metabolism and the modulation of plant growth. *Environmental and Experimental Botany, 226*, 105917. https://doi.org/10.1016/j.envexpbot.2024.105917

Bedoya-Ramírez, S. I., Loaiza-Ruiz, R. A., Barrera-Sánchez, C. F., & Córdoba-Gaona, O. de J. (2024). Impact of colored shade netting on growth and physiological traits in avocado creole rootstock seedling. *Revista de Ciencias Agrícolas, 41*(3), e3242. https://doi.org/10.22267/rcia.20244103.242

Bhattacharya, M., & Hembram, A. K. (2025). Influence of seed priming with plant growth regulators on seed germination and seedling quality in French bean (*Phaseolus vulgaris* L.). *Journal of Experimental Agriculture International, 47*(6), 589–596. https://doi.org/10.9734/jeai/2025/v47i63519

Brookbank, B. P., Patel, J., Gazzarrini, S., & Nambara, E. (2021). Role of basal ABA in plant growth and development. *Genes, 12*(12), 1936. https://doi.org/10.3390/genes12121936

Campa, C., Urban, L., Mondolot, L., Fabre, D., Roques, S., Lizzi, Y., Aarrouf, J., Doulbeau, S., Breitler, J.-C., Letrez, C., Toniutti, L., Bertrand, B., La Fisca, P., Bidel, L. P. R., & Etienne, H. (2017). Juvenile coffee leaves acclimated to low light are unable to cope with a moderate light increase. *Frontiers in Plant Science, 8*, 1126. https://doi.org/10.3389/fpls.2017.01126

Chen, T., Li, G., Islam, M. R., Fu, W., Feng, B., Tao, L., & Fu, G. (2019). Abscisic acid synergizes with sucrose to enhance grain yield and quality of rice by improving the source–sink relationship. *BMC Plant Biology, 19*(1), 525. https://doi.org/10.1186/s12870-019-2126-y

Cutler, S. R., Rodriguez, P. L., Finkelstein, R. R., & Abrams, S. R. (2010). Abscisic acid: Emergence of a core signaling network. *Annual Review of Plant Biology, 61*, 651–679. https://doi.org/10.1146/annurev-arplant-042809-112122

Domagalska, M. A., & Leyser, O. (2011). Signal integration in the control of shoot branching. *Nature Reviews Molecular Cell Biology, 12*(4), 211–221. https://doi.org/10.1038/nrm3088

Du, Y., & Scheres, B. (2017). PLETHORA transcription factors orchestrate de novo organ patterning during *Arabidopsis* lateral root outgrowth. *Proceedings of the National Academy of Sciences of the United States of America, 114*(44), 11709–11714. https://doi.org/10.1073/pnas.1714410114

Fan, L., Li, B., Han, Y., Chen, L., He, T., Zheng, Y., & Rong, J. (2022). Lower light intensities increase shoot germination with improved leaf biosynthesis in Ma bamboo (*Dendrocalamus latiflorus* Munro). *Forests, 13*(10), 1723. https://doi.org/10.3390/f13101723

Ferrante, A., & Mariani, L. (2018). Agronomic management for enhancing plant tolerance to abiotic stresses—High and low values of temperature, light intensity, and relative humidity. *Horticulturae, 4*(3), 21. https://doi.org/10.3390/horticulturae4030021

Fransson, P., Brännström, Å., & Franklin, O. (2021). A tree's quest for light—Optimal height and diameter growth under a shading canopy. *Tree Physiology, 41*(1), 1–11. https://doi.org/10.1093/treephys/tpaa110

Gao, S., Gao, J., Zhu, X., Song, Y., Li, Z., Ren, G., Zhou, X., & Kuai, B. (2016). ABF2, ABF3, and ABF4 promote ABA-mediated chlorophyll degradation and leaf senescence by transcriptional activation of chlorophyll catabolic genes and senescence-associated genes in *Arabidopsis*. *Molecular Plant, 9*(9), 1272–1285. https://doi.org/10.1016/j.molp.2016.06.006

Getachew, G., Tadele, T., Bekele, A., Sebsibe, S., & Tega, A. (2025). Effect of vermicompost on growth of avocado (*Persea americana* Mill.) seedlings in selected district of Sidama Region and Gedeo Zone, Ethiopia. *Asian Journal of Research and Review in Agriculture, 7*(1), 276–293. https://doi.org/10.56557/ajrra/2025/v7i1177

Guan, C., & Jiao, Y. (2020). Interplay between the shoot apical meristem and lateral organs. *ABIOTech, 1*(3), 178–184. https://doi.org/10.1007/s42994-020-00021-2

Guo, Y., Ren, G., Zhang, K., Li, Z., Miao, Y., & Guo, H. (2021). Leaf senescence: Progression, regulation, and application. *Molecular Horticulture, 1*(1), 5. https://doi.org/10.1186/s43897-021-00006-9

Hao, J., & Lu, E. (2022). Variation of relative humidity as seen through linking water vapor to air temperature: An assessment of interannual variations in the near-surface atmosphere. *Atmosphere, 13*(8), 1171. https://doi.org/10.3390/atmos13081171

Hu, X., Gu, T., Khan, I., Zada, A., & Jia, T. (2021). Research progress in the interconversion, turnover, and degradation of chlorophyll. *Cells, 10*(11), 3134. https://doi.org/10.3390/cells10113134

Jeber, B. A., & Khaeim, H. M. (2019). Effect of foliar application of amino acids, organic acids, and naphthalene acetic acid on growth and yield traits of wheat. *Plant Archives, 19*(Suppl. 2), 824–826. https://www.plantarchives.org/SPL%20ISSUE%20SUPP%202%2C2019/147__824-826_.pdf

Jiang, N., Wang, P., Yang, Z., Li, C., Xia, Y., Rong, X., Han, Y., & Yang, L. (2025). Auxin regulates leaf senescence and nitrogen assimilation to promote grain filling in maize (*Zea mays* L.). *Field Crops Research, 323*, 109787. https://doi.org/10.1016/j.fcr.2025.109787

Kishor, P. B. K., Tiozon, R. N., Fernie, A. R., & Sreenivasulu, N. (2022). Abscisic acid and its role in the modulation of plant growth, development, and yield stability. *Trends in Plant Science, 27*(12), 1283–1295. https://doi.org/10.1016/j.tplants.2022.08.013

Kuai, B., Chen, J., & Hörtensteiner, S. (2018). The biochemistry and molecular biology of chlorophyll breakdown. *Journal of Experimental Botany, 69*(4), 751–767. https://doi.org/10.1093/jxb/erx322

Lanoue, J., Zheng, J., Little, C., Thibodeau, A., Grodzinski, B., & Hao, X. (2019). Alternating red and blue light-emitting diodes allows for injury-free tomato production with continuous lighting. *Frontiers in Plant Science, 10*, 1114. https://doi.org/10.3389/fpls.2019.01114

Lawrence, M. G. (2005). The relationship between relative humidity and the dewpoint temperature in moist air: A simple conversion and applications. *Bulletin of the American Meteorological Society, 86*(2), 225–233. https://doi.org/10.1175/BAMS-86-2-225

Liu, H., Liu, D., Lv, S., Alam, S. M., Zhou, T., & Liu, Y. (2025). Auxin promotes stem secondary growth of *Poncirus trifoliata* seedling through ARF7 modulating xylem development. *Plant Science, 358*, 112574. https://doi.org/10.1016/j.plantsci.2025.112574

Liu, J., Carriquí, M., Xiong, D., & Kang, S. (2024). Influence of IAA and ABA on maize stem vessel diameter and stress resistance in variable environments. *Physiologia Plantarum, 176*(4), e14443. https://doi.org/10.1111/ppl.14443

Ma, L., & Li, G. (2019). Auxin-dependent cell elongation during the shade avoidance response. *Frontiers in Plant Science, 10*, 914. https://doi.org/10.3389/fpls.2019.00914

Mditshwa, A., Magwaza, L. S., & Tesfay, S. Z. (2019). Shade netting on subtropical fruit: Effect on environmental conditions, tree physiology and fruit quality. *Scientia Horticulturae, 256*, 108556. https://doi.org/10.1016/j.scienta.2019.108556

Melnyk, C. W. (2017). Plant grafting: Insights into tissue regeneration. *Regeneration, 4*(1), 3–14. https://doi.org/10.1002/reg2.71

Mensah, E. O., Asare, R., Vaast, P., Amoatey, C. A., Markussen, B., & Owusu, K. (2022). Limited effects of shade on physiological performances of cocoa (*Theobroma cacao* L.) under elevated temperature. *Environmental and Experimental Botany, 201*, 104983. https://doi.org/10.1016/j.envexpbot.2022.104983

Mishra, B. S., Sharma, M., & Laxmi, A. (2022). Role of sugar and auxin crosstalk in plant growth and development. *Physiologia Plantarum, 174*(1), e13546. https://doi.org/10.1111/ppl.13546

Mo, W., Zheng, X., Shi, Q., Zhao, X., Chen, X., Yang, Z., & Zuo, Z. (2024). Unveiling the crucial roles of abscisic acid in plant physiology: Implications for enhancing stress tolerance and productivity. *Frontiers in Plant Science, 15*, 1437184. https://doi.org/10.3389/fpls.2024.1437184

Murchie, E. H., & Ruban, A. V. (2020). Dynamic non-photochemical quenching in plants: From molecular mechanism to productivity. *The Plant Journal, 101*(4), 885–896. https://doi.org/10.1111/tpj.14601

Mursyidin, D. H., & Makruf, M. I. (2020). Keanekaragaman dan kekerabatan genetik *Artocarpus* berdasarkan penanda DNA kloroplas *matK* & *rbcL*: Kajian in silico. *Floribunda, 6*(5), 195–206. https://doi.org/10.32556/floribunda.v6i5.2020.322

Nansereko, S., & Muyonga, J. H. (2021). Exploring the potential of jackfruit (*Artocarpus heterophyllus* Lam.). *Asian Food Science Journal, 20*(9), 97–117. https://doi.org/10.9734/afsj/2021/v20i930346

Park, S. H., Lee, B. R., La, V. H., Mamun, M. A., Bae, D. W., & Kim, T. H. (2021). Drought intensity-responsive salicylic acid and abscisic acid crosstalk with the sugar signaling and metabolic pathway in *Brassica napus*. *Plants, 10*(3), 610. https://doi.org/10.3390/plants10030610

Patil, M. D., & Deshmukh, S. V. (2025). Shades and shapes: Influence of native shade tree canopies on internodal length, diameter and wall thickness in *Pseudoxytenanthera stocksii* (Munro) T. Q. Nguyen. *Advances in Bamboo Science, 12*, 100192. https://doi.org/10.1016/j.bamboo.2025.100192

Pierik, R., & de Wit, M. (2014). Shade avoidance: Phytochrome signalling and other aboveground neighbour detection cues. *Journal of Experimental Botany, 65*(11), 2815–2824. https://doi.org/10.1093/jxb/ert389

Prasetyo, S., Hidayat, U., Haryanto, Y. D., & Riama, N. F. (2021). Karakteristik suhu udara di Pulau Jawa kaitannya dengan kelembapan udara, curah hujan, SOI, dan DMI. *Jurnal Geografi, Edukasi dan Lingkungan, 5*(1), 15–26. https://doi.org/10.22236/jgel.v5i1.5971

Ritchie, R. J. (2006). Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. *Photosynthesis Research, 89*(1), 27–41. https://doi.org/10.1007/s11120-006-9065-9

Sadok, W., Lopez, J. R., & Smith, K. P. (2021). Transpiration increases under high-temperature stress: Potential mechanisms, trade-offs and prospects for crop resilience in a warming world. *Plant, Cell & Environment, 44*(7), 2102–2116. https://doi.org/10.1111/pce.13970

Sawan, Z. M. (2018). Climatic variables: Evaporation, sunshine, relative humidity, soil and air temperature and their adverse effects on cotton production. *Information Processing in Agriculture, 5*(1), 134–148. https://doi.org/10.1016/j.inpa.2017.09.006

Schneider, A., Godin, C., Boudon, F., Demotes-Mainard, S., Sakr, S., & Bertheloot, J. (2019). Light regulation of axillary bud outgrowth along plant axes: An overview of the roles of sugars and hormones. *Frontiers in Plant Science, 10*, 1296. https://doi.org/10.3389/fpls.2019.01296

Serivichyaswat, P. T., Kareem, A., Feng, M., & Melnyk, C. W. (2024). Auxin signaling in the cambium promotes tissue adhesion and vascular formation during *Arabidopsis* graft healing. *Plant Physiology, 196*(2), 754–762. https://doi.org/10.1093/plphys/kiae257

Shevela, D., Kern, J. F., Govindjee, & Messinger, J. (2023). Solar energy conversion by photosystem II: Principles and structures. *Photosynthesis Research, 156*(3), 279–307. https://doi.org/10.1007/s11120-022-00991-y

Shimizu-Sato, S., Tanaka, M., & Mori, H. (2009). Auxin–cytokinin interactions in the control of shoot branching. *Plant Molecular Biology, 69*(4), 429–435. https://doi.org/10.1007/s11103-008-9416-3

Siddik, M. A., Islam, M. M., Hoque, M. A., Islam, S., Parvin, S., & Rabin, M. H. (2015). Morpho-physiological and yield-contributing characters and yield of sesame with 1-naphthalene acetic acid (NAA). *Journal of Plant Sciences, 3*(6), 329–336. https://doi.org/10.11648/j.jps.20150306.16

Siddiqui, H., Sami, F., & Hayat, S. (2020). Glucose: Sweet or bitter effects in plants—A review on current and future perspectives. *Carbohydrate Research, 487*, 107884. https://doi.org/10.1016/j.carres.2019.107884

Song, Y., Chen, Q., Ci, D., Shao, X., & Zhang, D. (2014). Effects of high temperature on photosynthesis and related gene expression in poplar. *BMC Plant Biology, 14*, 111. https://doi.org/10.1186/1471-2229-14-111

Sosnowski, J., Truba, M., & Vasileva, V. (2023). The impact of auxin and cytokinin on the growth and development of selected crops. *Agriculture, 13*(3), 724. https://doi.org/10.3390/agriculture13030724

Soukup, A., & Tylová, E. (2019). Essential methods of plant sample preparation for light microscopy. In F. Cvrčková (Ed.), *Plant cell morphogenesis: Methods and protocols* (Methods in Molecular Biology, Vol. 1992, pp. 1–26). Humana Press. https://doi.org/10.1007/978-1-4939-9469-4_1

Stein, O., & Granot, D. (2018). Plant fructokinases: Evolutionary, developmental, and metabolic aspects in sink tissues. *Frontiers in Plant Science, 9*, 339. https://doi.org/10.3389/fpls.2018.00339

Taiz, L., Zeiger, E., Møller, I. M., & Murphy, A. (2015). *Plant physiology and development* (6th ed.). Sinauer Associates.

Tan, S. L., Yang, Y. J., Liu, T., Zhang, S. B., & Huang, W. (2020). Responses of photosystem I compared with photosystem II to the combination of heat stress and fluctuating light in tobacco leaves. *Plant Science, 292*, 110371. https://doi.org/10.1016/j.plantsci.2019.110371

Tang, X., Qin, S., Zhao, Y., Xu, M., Li, H., Ai, Y., Wang, Y., & Liu, W. (2025). Regulatory roles of seedling shading and strip planting on soybean branching and yield in relay intercropping systems. *Agronomy, 15*(12), 2756. https://doi.org/10.3390/agronomy15122756

Traas, J. (2019). Organogenesis at the shoot apical meristem. *Plants, 8*(1), 6. https://doi.org/10.3390/plants8010006

Verma, V., Ravindran, P., & Kumar, P. P. (2016). Plant hormone-mediated regulation of stress responses. *BMC Plant Biology, 16*(1), 86. https://doi.org/10.1186/s12870-016-0771-y

Voitsekhovskaja, O. V., & Tyutereva, E. V. (2015). Chlorophyll *b* in angiosperms: Functions in photosynthesis, signaling and ontogenetic regulation. *Journal of Plant Physiology, 189*, 51–64. https://doi.org/10.1016/j.jplph.2015.09.013

Warren, C. R. (2008). Rapid measurement of chlorophylls with a microplate reader. *Journal of Plant Nutrition, 31*(7), 1321–1332. https://doi.org/10.1080/01904160802135092

Witherup, C., Zuberi, M. I., Hossain, S., & Zerega, N. J. C. (2019). Genetic diversity of Bangladeshi jackfruit (*Artocarpus heterophyllus*) over time and across seedling sources. *Economic Botany, 73*(2), 233–248. https://doi.org/10.1007/s12231-019-09452-5

Woodward, A. W., & Bartel, B. (2005). Auxin: Regulation, action, and interaction. *Annals of Botany, 95*(5), 707–735. https://doi.org/10.1093/aob/mci083

Xiong, Y., & Jiao, Y. (2019). The diverse roles of auxin in regulating leaf development. *Plants, 8*(7), 243. https://doi.org/10.3390/plants8070243

Yadav, S. K. (2010). Cold stress tolerance mechanisms in plants: A review. *Agronomy for Sustainable Development, 30*(3), 515–527. https://doi.org/10.1051/agro/2009050

Yong, S., Chen, Q., Xu, F., Fu, H., Liang, G., & Guo, Q. (2024). Exploring the interplay between angiosperm chlorophyll metabolism and environmental factors. *Planta, 260*(1), 25. https://doi.org/10.1007/s00425-024-04437-8

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