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Morphophysiological, anatomical, and biomass allocation responses of oil palm seedlings subjected to long-term waterlogging stress

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Abstract

Increasing rainfall variability and prolonged waterlogging due to climate change pose significant challenges to oil palm (Elaeis guineensis Jacq.) growth and physiological stability in lowland plantation areas. Therefore, this study aims to evaluate the morphophysiological, anatomical, and biomass allocation responses of oil palm subjected to long-term waterlogging stress. The experiment was arranged in a randomized complete block design with four replications, using four waterlogging treatments, namely 43 cm (control), 30 cm (shallow waterlogging), 15 cm (moderate waterlogging), and 0 cm (severe waterlogging) below the soil surface, applied to twelve-month-old seedlings for 26 weeks. The waterlogging level in each treatment was maintained at a constant level through daily checks and adjustments to compensate for evaporation. Observations included vegetative growth traits, leaf physiology and water status, leaf anatomical and stomatal behavior, root anatomical adaptations, and dry biomass allocation. The results showed that control and shallow waterlogging (43 and 30 cm) supported optimal growth, physiological performance, anatomical, and biomass accumulation. Moderate waterlogging (15 cm) initiated declines in growth and physiology, along with early signs of anatomical adaptation. Severe waterlogging (0 cm) reduced stomatal function, leaflet anatomical changes, lower shoot biomass, and enhanced aerenchyma and pneumatophore development. The correlation and principal component analyses confirmed that integrated morphophysiological and anatomical adjustments were critical for enhancing oil palm tolerance to waterlogging stress. The strong negative relationship between stomatal aperture and aerenchyma formation throughout the root depth suggests a coordinated response between physiological regulation and anatomical adaptation. These anatomical adaptations, particularly the formation of aerenchyma and pneumatophores, are recognized as key factors enhancing oil palm tolerance to severe waterlogging stress.

Keywords: abiotic stress; leaf anatomy; photosynthetic performance; respiratory adaptation; waterlogging tolerance

Abbreviations: AF0_aerenchyma formation at 0-15 cm soil depth; AF15_aerenchyma formation at 15-30 cm soil depth; AF30_aerenchyma formation at >30 cm soil depth; CDW_canopy dry weight; LL_leaflet length; LWC_leaf water content; NL_number of leaves; PCA_principal component analysis; PCO_percentage of open stomata; PH_plant height; PN_number of pneumatophores; RDW_root dry weight; ROS_reactive oxygen species; SD_stomatal density; SEM_scanning electron microscope; SRR_shoot-root ratio; SAWm_stomatal aperture width at 8:00-9:00 h, SAWmd_stomatal aperture width at 11.30-12.30 h; SAWn_stomatal aperture width at 15:00-16:00 h; TDW_total dry weight

Introduction

Oil palm (Elaeis guineensis Jacq.) is a major vegetable oil producer, accounting for over one-third of global edible oil production (Qaim et al., 2020). Crude palm oil (CPO), as the primary product of the oil palm industry, contributes significantly to the foreign exchange earnings of Southeast Asian countries, particularly Indonesia and Malaysia. Over the past few decades, oil palm plantations have expanded rapidly (Uning et al., 2020), driven by growing demand for edible oil, processed foods, and biofuels. Global vegetable oil demand is projected to increase significantly by 2050, with estimates indicating a 46-74% growth (Meijaard et al., 2020; Chiriacò et al., 2025) or nearly doubling from levels observed in 2009 (Meijaard et al., 2020). Meeting global palm oil demand faces various challenges, including a decrease in yield caused by abiotic stresses such as drought, heatwaves, salinity, and waterlogging. Among these stressors, waterlogging is particularly worrisome in lowland and poorly drained soil (Lim et al., 2023; Zhang et al., 2025), yet remains underexplored in oil palm research.

Waterlogging is one of the significant threats to global crop production and is projected to intensify in frequency and severity due to climate change (Kaur et al., 2020; Yang et al., 2023). Waterlogging imposes a multifaceted form of stress on plants, primarily by restricting oxygen availability in the root zone (hypoxia or anoxia), which disrupts root respiration and impairs energy production. It is estimated to affect approximately 10–15% of arable soil worldwide, resulting in substantial yield reductions, ranging from 20% to 50% in sensitive crops such as wheat (Manik et al., 2019; Pais et al., 2023). In addition to oxygen deprivation, prolonged soil saturation alters nutrient availability and uptake, accumulates toxic by-products such as ethylene and reduced iron compounds, and changes the composition of soil microbial communities (Tyagi et al., 2023). These physiological and biochemical disturbances collectively impair plant growth, reduce photosynthesis, and limit biomass accumulation. In oil palm, waterlogging stress has been reported to reduce the vegetative growth of oil palm seedlings as well as reduce their physiological activity (Rivera-Mendes et al., 2016). Although the impact of waterlogging has been well-documented in annual crops, less is known about how perennial tropical species, such as oil palm, respond to long-term waterlogging stress. Given that oil palm is often cultivated in lowland areas with high rainfall and poor drainage, understanding the effects of waterlogging is critical for sustaining productivity and guiding climate-resilient plantation management. Previous studies have reported that optimal oil palm growth is achieved when the groundwater level is maintained between 40–50 cm below the soil surface, while shallower water tables may begin to impose hypoxic stress on the roots (Akram et al., 2022).

Oil palm has several adaptive mechanisms that enable it to cope with waterlogged conditions, maintaining relative resilience compared to other tropical crops. Anatomically, this mechanism includes the development of lysigenous aerenchyma in the roots, facilitating internal oxygen transport under hypoxic conditions (Nuanlaong et al., 2021). Transcriptomic analyses at the molecular level have revealed significant changes in the stem core during waterlogging, characterized by the increased expression of genes associated with ethylene biosynthesis, cell wall alteration, and stress-related transcription factors (Nuanlaong et al., 2020; Lim et al., 2023). Waterlogging impairs seedling growth by reducing plant height, leaf area, and biomass (Rivera-Mendes et al., 2016). Comparative analyses indicate that oil palm exhibits greater tolerance under waterlogged conditions than rubber trees, as shown by relatively stable transpiration and water use patterns (Hardanto et al., 2017). However, existing studies have primarily focused on early developmental stages of seedlings or molecular-level responses under controlled conditions. There is a remaining knowledge gap in understanding how field-grown oil palm seedlings respond to varying levels of waterlogging stress. Considering climate change leads to greater rainfall variability, heightened floods, and waterlogging risks in areas where oil palm is cultivated, studies on waterlogging stress are increasingly important for supporting long-term crop sustainability and productivity (Sharma et al., 2021). Therefore, this study aims to investigate the morphophysiological, anatomical, and biomass allocation responses of oil palm seedlings subjected to long-term waterlogging stress.

Results and Discussions

Waterlogging in oil palm plantations typically arises from high and prolonged rainfall combined with compacted soil conditions and poor surface or subsoil drainage. These conditions cause soil saturation, where soil pores are filled with water, reducing atmospheric oxygen diffusion into the rhizosphere (Pan et al., 2021; Rupngam and Messiga, 2024). Since the oxygen diffusion rate in water is lower than in air, saturated soil rapidly becomes hypoxic or anoxic (Phukan et al., 2016). This leads to limitations in root respiration because aerobic metabolism requires oxygen as the final acceptor in the mitochondrial electron transport chain (Zahra et al., 2021). Consequently, roots experience energy deficits, inhibit nutrient uptake, and accumulate toxic anaerobic metabolites such as ethanol and lactic acid (Tyagi et al., 2023). Crops perceive this stress and initiate a range of responses that vary depending on the duration and severity of waterlogging and the developmental stage.

Vegetative growth

In this study, waterlogging significantly affected the vegetative growth of oil palm, with differences observed across water table depths (Fig 1). These results are consistent with previous studies stating that continuous waterlogging for 60 days suppresses the growth in height and number of leaves on oil palm seedlings (Rivera-Mendes et al., 2016). Oil palm grown under 43 cm, 30 cm, and 15 cm water table did not show any significant differences in height and leaflet length, ranging from 278.44 ± 30.72 cm to 293.56 ± 28.23 cm, and 48.37 ± 1.61 cm to 51.59 ± 0.91 cm, respectively. The best number of leaves was achieved at the 43 cm (24.87 ± 0.75 cm) and 30 cm (24.69 ± 1.48 cm) water table depths, while the best stem diameter was achieved at the 43 cm (137.22 ± 3.35 cm) treatment level. In contrast, severe waterlogging (0 cm below the soil surface) reduced plant height to 218.06 ± 6.91 cm, number of leaves to 21.87 ± 0.63, stem diameter to 115.81 ± 8.45 cm, and leaflet length to 42.97 ± 2.30 cm, with these values significantly lower ($p < 0.05$) than those in all other level treatments. Increasing waterlogging severity under 15 cm below the soil surface for six months suppressed vegetative growth, supporting the statement that prolonged root-zone hypoxia impairs cell division, elongation, and assimilate transport (Tong et al., 2021). Under these conditions, reduced oxygen diffusion to roots disrupts metabolic activity, limits uptake of essential nutrients (nitrogen and potassium), and suppresses growth (Manghwar et al., 2024; Zhang et al., 2025).

Leaf physiology and water content

Waterlogging significantly affected the gas exchange parameters of the oil palm. Changes in photosynthesis performance are frequently used to indicate productivity under abiotic stress due to its sensitivity to stress conditions (Pais et al., 2023). Exposure to waterlogging at 15 cm and 0 cm below the soil surface significantly reduced photosynthetic rate by 36.89% and 74.84%, respectively, compared to the control (Fig 2A). This result aligns with Bhusal et al. (2020), who reported that waterlogging for 75 days decreases the photosynthetic rate by more than 45% in apple trees. Waterlogging-induced hypoxia is known to suppress root respiration and reduce the uptake of water and nutrients, leading to stomatal closure, as shown in Fig 2D, and disrupts CO2 assimilation (Adegoye et al., 2023; Zhang et al., 2023). A similar trend was observed for transpiration rate, which declined by 24.83% and 56.21% under waterlogging at 15 cm and 0 cm below the soil surface, respectively (Fig 2B). These reductions indicate that prolonged exposure to hypoxic conditions impairs water absorption, leading to decreased transpiration (Yang et al., 2023). Gas exchange becomes limited and causes a decline in photosynthesis and transpiration performance. Stomatal closure was related to high internal CO2 concentrations at treatment levels 15 cm and 0 cm below the soil surface (Fig 2C). Such stress responses have also been reported in sago plants subjected to prolonged waterlogged conditions (Azhar et al., 2020), emphasizing the sensitivity of physiological processes in oil palm to water table fluctuations.

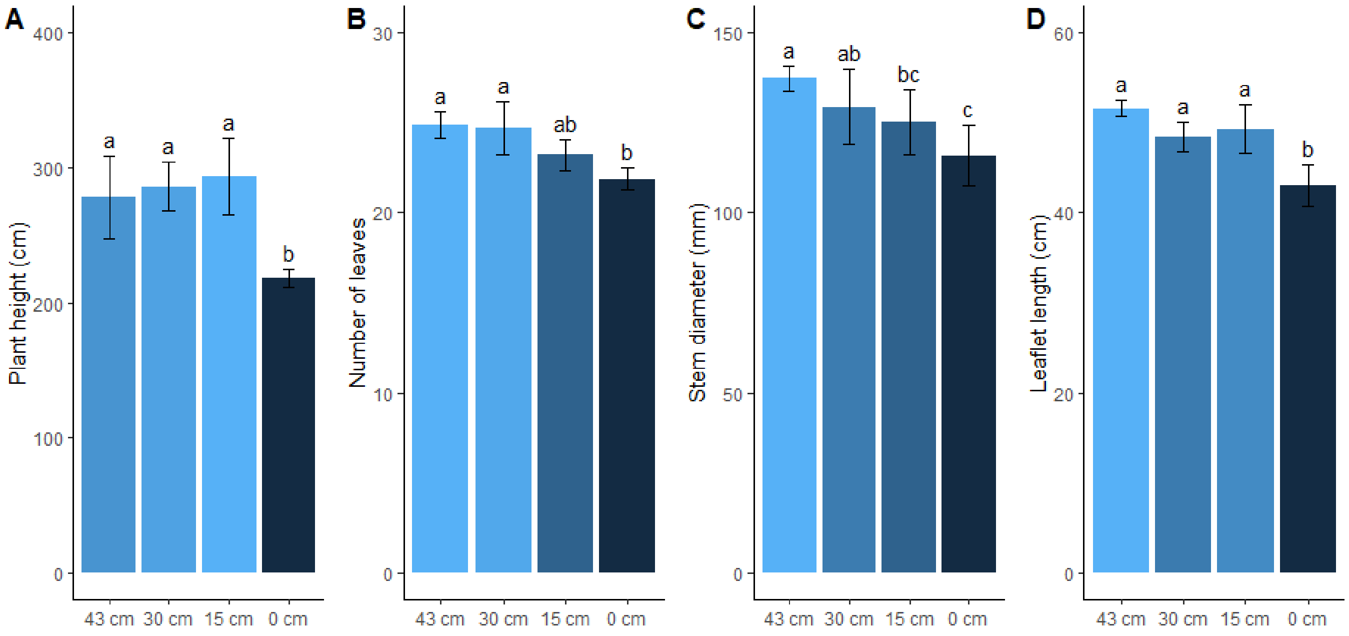


Fig 1. Plant height (A), number of leaves (B), stem diameter (C), and leaflet length (D) of oil palms subjected to long-term waterlogging stress. Data are the means of four replicates ± standard deviation. Means with different lowercase letters are significantly different according to Tukey's HSD test ($p \leq 0.05$).

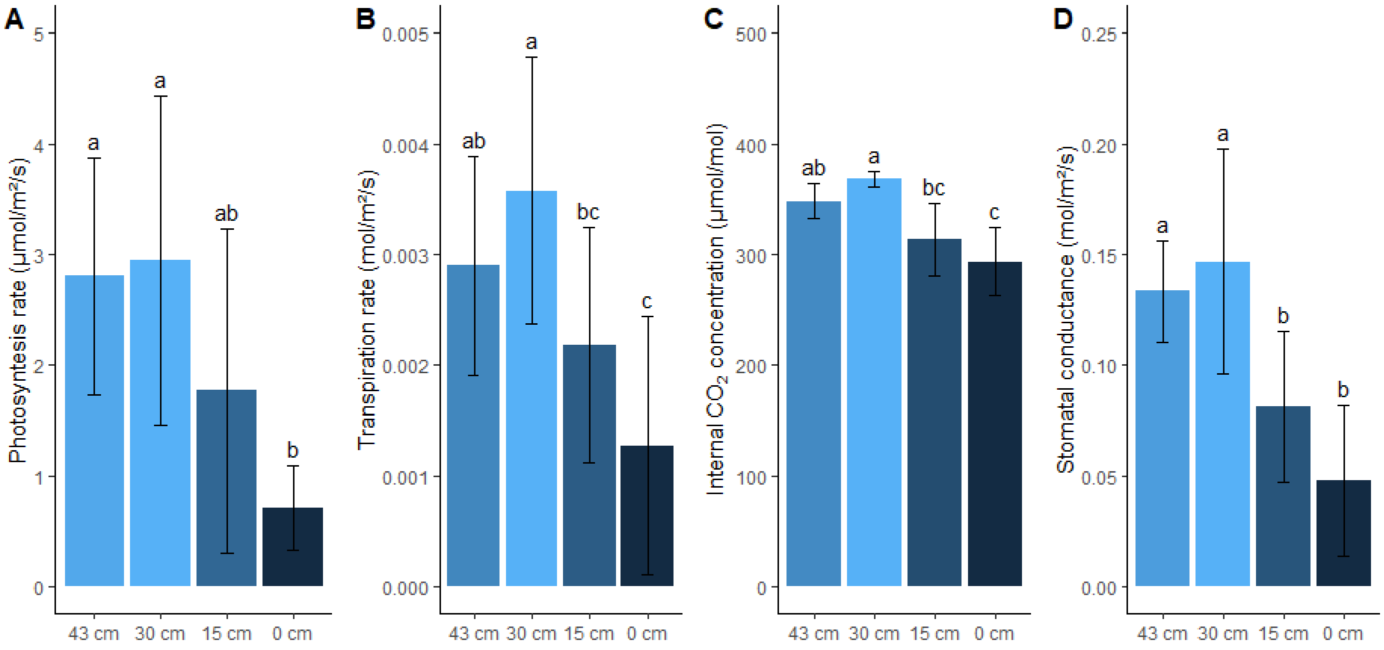


Fig 2. Photosynthesis rate (A), transpiration rate (B), internal CO2 concentration (C), and stomatal conductance (D) of oil palms subjected to long-term waterlogging stress. Data are the means of four replicates ± standard deviation. Means with different lowercase letters are significantly different according to Tukey's HSD test ($p \leq 0.05$).

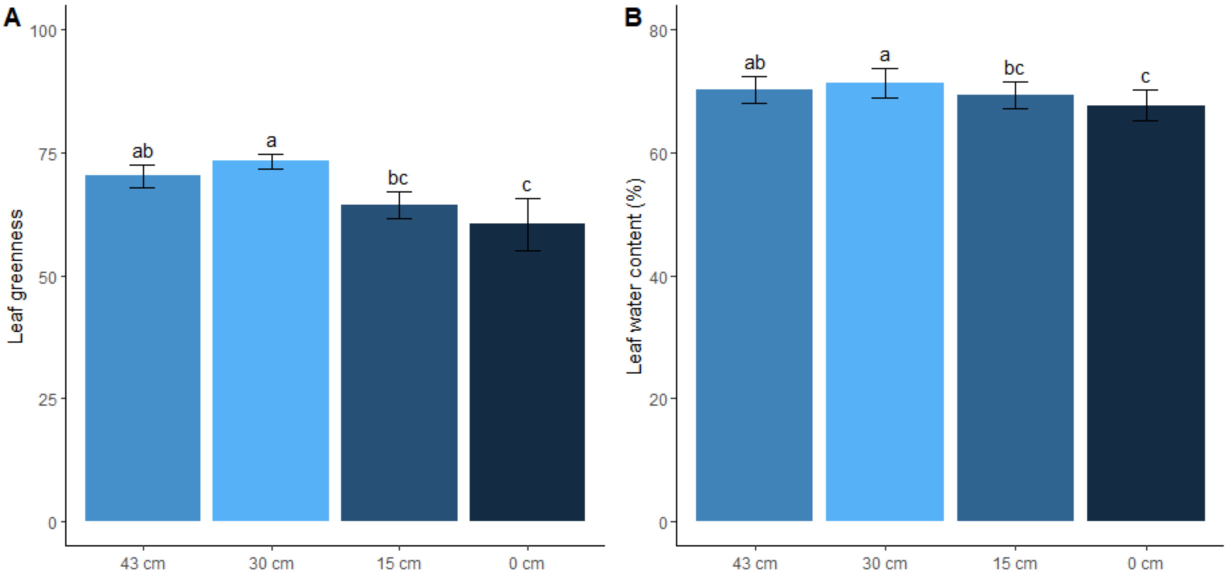


Fig 3. Leaf greenness index (A) and leaf water content (B) of oil palms subjected to long-term waterlogging stress. Data are the means of four replicates ± standard deviation. Means with different lowercase letters are significantly different according to Tukey's HSD test ($p \leq 0.05$).

Waterlogging also altered key leaf physiological traits in oil palm seedlings, particularly leaf greenness index and water content, which are proxies for photosynthetic capacity and water status. Leaf greenness index and water content varied significantly with water table depth (Fig 3). Based on the results, leaf greenness index (Fig 3A) was highest in oil palm subjected to the 30 cm water table depth (73.29 ± 1.46) and remained statistically similar to those at 43 cm water table depth (70.29 ± 2.33). The significantly higher values suggest that chlorophyll biosynthesis and retention remained functionally intact under non-waterlogging to shallow waterlogging, supporting continued photosynthetic activity. In comparison, a significant decline was observed at 15 cm water table depth (64.27 ± 2.67) and further at 0 cm water table depth (60.40 ± 5.37). This trend shows moderate (15 cm water table depth) to severe waterlogging (0 cm water table depth) reduced chlorophyll content or impaired photosynthetic function. The sharp decline shows a reduction in chlorophyll concentration, possibly due to oxidative stress and chloroplast degradation under prolonged hypoxic conditions (Goto et al., 2022). Similar declines in chlorophyll content under waterlogged conditions have been reported in oil palm by Andesmora et al. (2025) and sago palm by Azhar et al. (2020), where hypoxia restricts nitrogen assimilation, leading to chlorophyll breakdown. Similarly, leaf water content (LWC) was significantly affected (Fig 3B), with the highest values recorded at 30 cm water table depth (71.33 ± 2.44%), followed by 43 cm water table depth (70.16 ± 2.15%). Oil palm under 15 cm water table depth, specifically those with 0 cm water table depth, showed lower water retention. This reduction reflects the crop impaired ability to absorb and transport water due to restricted root permeability under low-oxygen conditions. Under hypoxia, water uptake becomes inefficient as root cells experience diminished metabolic energy, reduced hydraulic conductivity, and disconnection between leaves and stem (Haverroth et al., 2025). Moderate hypoxic stress, as indicated by a water table depth of 15 cm, is typically characterized by a partial reduction in leaf greenness index and leaf water content, accompanied by a decrease in photosynthetic efficiency while remaining functionally active. Early visual symptoms, including mild chlorosis and decreased leaf turgor without complete wilting, may also appear. These patterns correspond to the intermediate stage of root oxygen limitation, where aerobic respiration begins to decline while anaerobic pathways have not yet become dominant (Jethva et al., 2022). Under these conditions, limited ATP synthesis results in decreased chlorophyll formation and impaired water regulation.

Leaf anatomical and stomatal behavior

Electron microscopic observations of oil palm leaflets show changes in internal structure due to differences in water table depth. At water table depth of 45 cm and 30 cm below the soil surface, the mesophyll tissue appears compact and maintains the vascular system (Fig 4A and Fig 4B). At a higher water table depth, 15 cm below the soil surface, the mesophyll tissue enlarges and appears thickened (Fig 4C). Furthermore, intercellular spaces begin to form in the mesophyll tissue, which is considered to indicate the initiation of aerenchyma formation as a pathway for oxygen diffusion between leaves and roots. At more severe stress levels, the enlargement of the intercellular spaces becomes more pronounced, and the xylem undergoes deformation (Fig 4D). Consistent with the findings of Shi et al. (2023), prolonged exposure to waterlogging stress in Phoebe sheareri seedlings led to thicker leaves, with palisade tissue cells fusing together and exhibiting indistinct boundaries, a looser arrangement, and shrinkage in the spongy tissue cells.

Measured parameters further supported the impact of waterlogging on stomatal behavior (Fig 5). Stomatal aperture width measured at three different time points (8:00–9:00 h, 11:30–12:30 h, and 15:00–16:00 h; Fig 5A-C) showed a consistent decline with increasing waterlogging severity. Oil palm grown under the 0 cm water table had significantly narrower stomatal apertures at all time points compared to those under 30 cm and 43 cm treatments ($p < 0.05$), showing stress-induced stomatal closure to limit water loss. In general, stomatal closure is related to water status and has been reported in many species that grow under water stress. It is often mediated by reduced hormonal signaling, mainly abscisic acid, which restricts guard cell turgidity under waterlogging (Zhu, 2016). The narrower stomatal aperture observed at a 0 cm water table depth likely limits stomatal conductance, leading to lower CO2 uptake and suppressed photosynthetic activity. The percentage of open stomata (PSO) (Fig 5D) followed a similar trend, with the lowest values recorded at 0 cm water table depth, suggesting that prolonged exposure to waterlogged or flooded conditions inhibits stomatal functioning. Interestingly, stomatal density (Sde) did not differ significantly among treatments (Fig. 5E), indicating that waterlogging stress affects the physiological regulation of stomatal activity rather than stomatal formation. This suggests that the number of stomata per unit area remains stable, while functional regulation such as aperture control is more responsive to waterlogging stress.

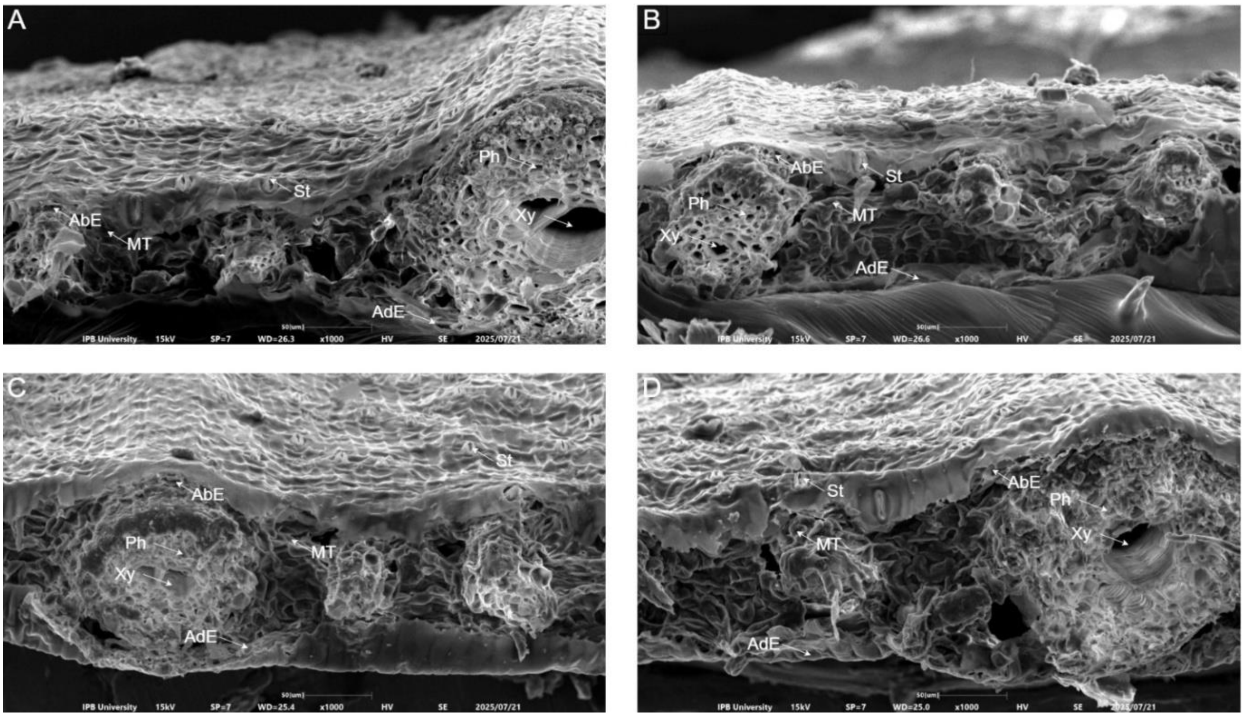


Fig 4. Changes in the anatomical structure of the oil palm leaflet subjected to long-term waterlogging: Under the 43 cm water table depth (A), under the 30 cm water table depth (B), under the 15 cm water table depth (C), and under the 0 cm water table depth (D). St: stomata, AbE: abaxial epidermis, MT: mesophyll tissue, Ph: phloem, Xy: xylem, and AdE: adaxial epidermis.

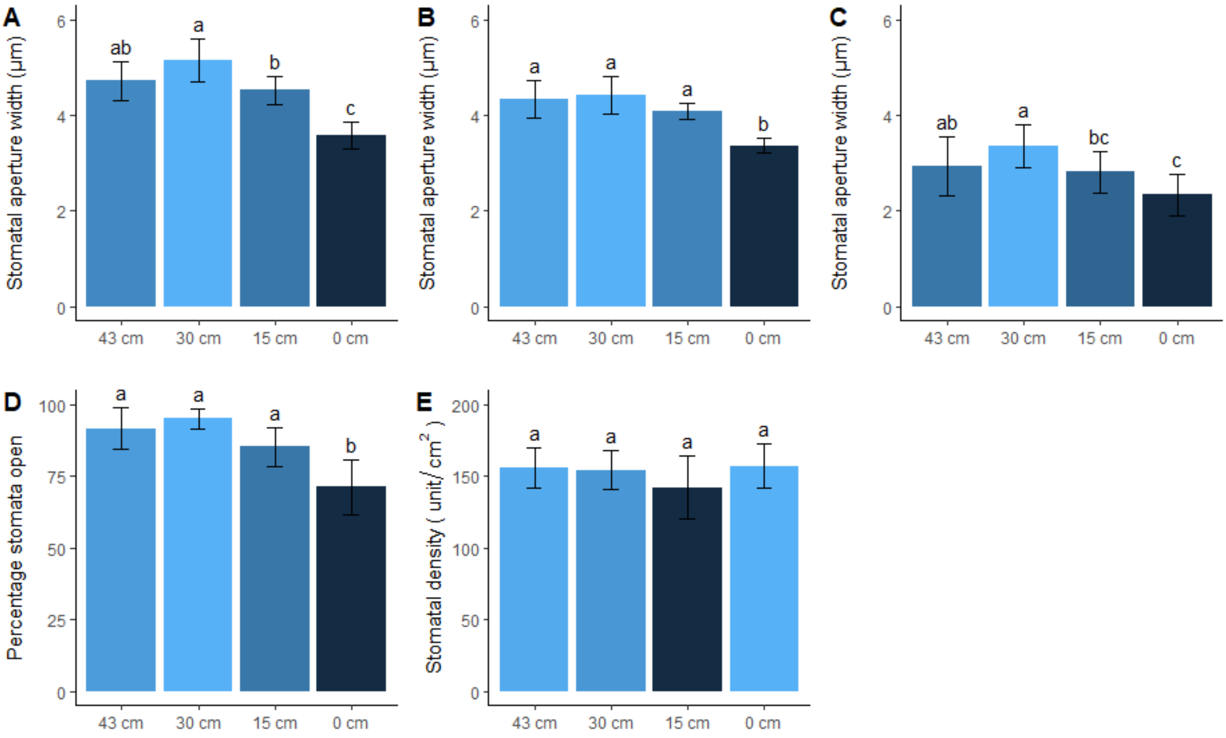


Fig 5. Stomatal aperture width at 8:00-9:00 h (A), stomatal aperture width at 11:30-12:30 h (B), stomatal aperture width at 15:00-16:00 h (C), percentage stomata open (D), and stomatal density (E) of oil palms subjected to long-term waterlogging stress. Data are the means of four replicates ± standard deviation. Means with different lowercase letters are significantly different according to Tukey's HSD test ($p \leq 0.05$).

Adaptive anatomical root responses

Adaptive anatomical responses of oil palm roots to waterlogging were evident through aerenchyma formation and the development of pneumatophores (Fig 6). Aerenchyma formation increased consistently with higher waterlogging severity across all three root zones observed (Fig 6A–C). Oil palm exposed to the 0 cm water table depth for six months had significantly higher aerenchyma percentages in the upper (11.83 ± 1.14%), middle (16.14 ± 4.97%), and lower (17.43 ± 2.14%) root segments compared to all other treatments ($p < 0.05$), showing a strong anatomical adaptation to low oxygen concentration conditions. Moderate aerenchyma formation was observed at 15 cm water table depths, while minimal development occurred at 43 cm and 30 cm. Oil palm can develop root aerenchyma and pneumatophores as adaptation mechanisms to waterlogging (Rivera-Mendes et al., 2016). The enhanced aerenchyma formation across all root zones in the 0 cm water table depth reflects a critical adaptive mechanism to cope with prolonged hypoxia. Ethylene and reactive oxygen species (ROS) induce programmed cell death and aerenchyma formation under hypoxia (Ni et al., 2019).

Aerenchyma provides an internal aeration pathway that facilitates oxygen diffusion from the shoot to the root tip, enabling continued root respiration under anaerobic soil conditions (Carbonare et al., 2023; Lin et al., 2024). This mechanism has been confirmed in oil palm by Nuanlaong et al. (2020), who observed significant lysigenous aerenchyma development in waterlogged seedlings, particularly in fibrous roots, as a key trait associated with tolerance. Similarly, the number of pneumatophores (Fig 6D) increased dramatically under the 0 cm water table depth, with significantly fewer or no pneumatophores formed under 15–43 cm water table depth. These aerial roots serve as supplementary channels for gas exchange with the atmosphere and are typically induced when aerenchyma alone is insufficient to meet the crop oxygen demands. The absence of pneumatophores at 43 cm and 30 cm water table depth, as well as limited occurrence at 15 cm, suggests that oil palm only activates energy-intensive morphological changes under critical stress levels. This structural adjustment is consistent with da Ponte et al. (2019), who documented aerial root formation as a long-term survival strategy under waterlogging stress. Adaptive anatomical responses can be helpful to markers in evaluating waterlogged or flooded tolerance during the growth stage and may inform selection strategies in breeding.

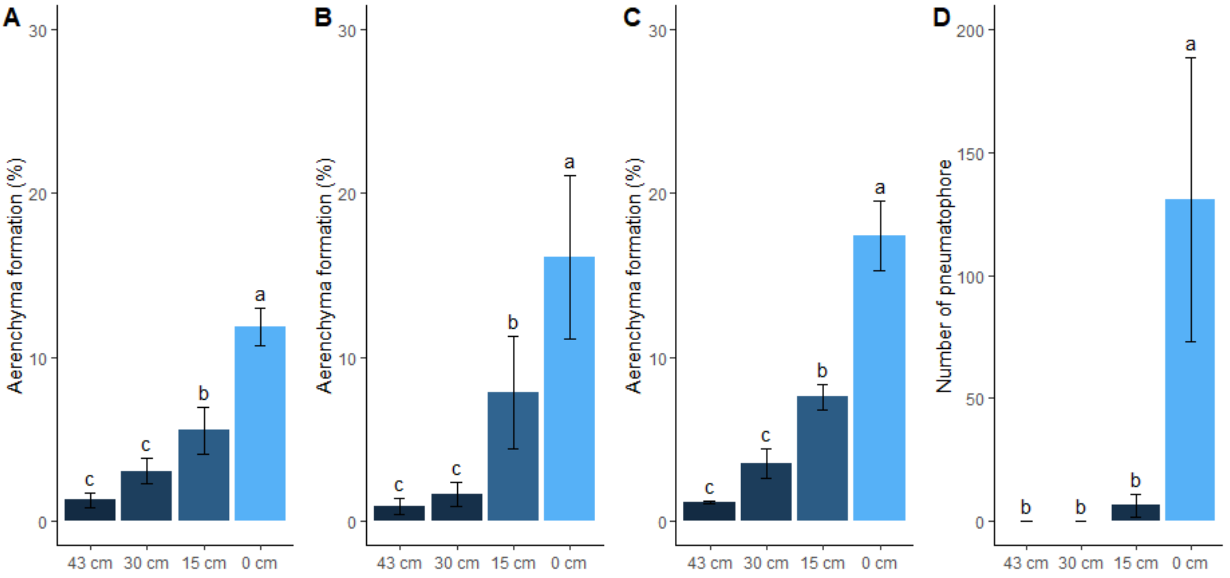


Fig 6. Aerenchyma formation at 0-15 cm soil depth (A), aerenchyma formation at 15-30 cm soil depth (B), aerenchyma formation at >30 cm soil depth (C), and number of pneumathophore (D) of oil palms subjected to long-term waterlogging stress. Data are the means of four replicates ± standard deviation. Means with different lowercase letters are significantly different according to Tukey's HSD test ($p \leq 0.05$).

Biomass allocation

Waterlogging significantly affected biomass allocation in oil palm, as shown in Fig 7. Canopy dry weight (CDW) (Fig 7A) was highest under the 43 cm (2,42 ± 0.88 kg) and 30 cm (2,62 ± 0.42 kg) water table depths, while oil palm subjected to deeper waterlogging (15 cm and 0 cm) showed significantly lower shoot biomass ($p < 0.05$) of 1,82 ± 0.39 kg and 1,62 ± 0.28 kg, respectively. The result is consistent with Fadila et al. (2024), who reported that oil palm affected by flooding produced poor biomass. The decrease in biomass under waterlogged conditions is caused by a reduction in photosynthetic capacity, triggered by increased production of ROS that interfere with cellular and photosynthetic processes (Hanif et al., 2024). This finding is supported by the strong positive Pearson correlation (Fig 8) between total dry weight (TDW) and photosynthesis rate ($r = 0.76$), indicating that higher photosynthetic activity is closely associated with greater biomass accumulation under non-stress conditions. The highest shoot biomass was maintained under control and shallow waterlogging (43 cm and 30 cm water table depths), while deeper waterlogging (15 cm and 0 cm water table depths) led to substantial declines, showing that aboveground growth is susceptible to hypoxic stress. Although lower than canopy biomass, root dry weight (RDW) (Fig 7B) did not vary significantly across treatments, showing a limited root growth response to waterlogging. The TDW (Fig 7C) followed a similar pattern to CDW, with substantial reductions observed at 15 cm and 0 cm water levels. Conversely, the shoot-root ratio (SRR) was statistically unaffected across all treatments (Fig 7D), suggesting that absolute biomass decreased under waterlogging stress. Oil palm can still maintain the allocation proportion between shoots and roots under conditions of waterlogging stress. These results show that waterlogging primarily suppresses overall plant growth rather than altering the relative distribution of biomass between aboveground and belowground parts.

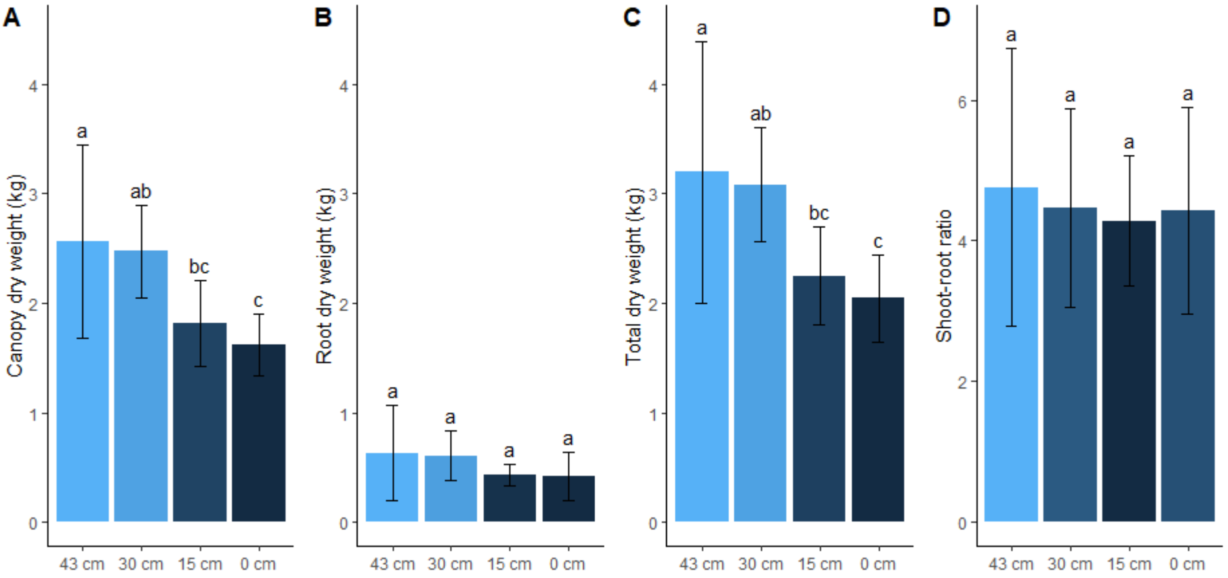


Fig 7. Canopy dry weight (A), root dry weight (B), total dry weight (C), and shoot-root dry weight (D) of oil palms subjected to long-term waterlogging stress. Data are the means of four replicates ± standard deviation. Means with different lowercase letters are significantly different according to Tukey's HSD test ($p \leq 0.05$).

Correlation analysis and principal component analysis (PCA)

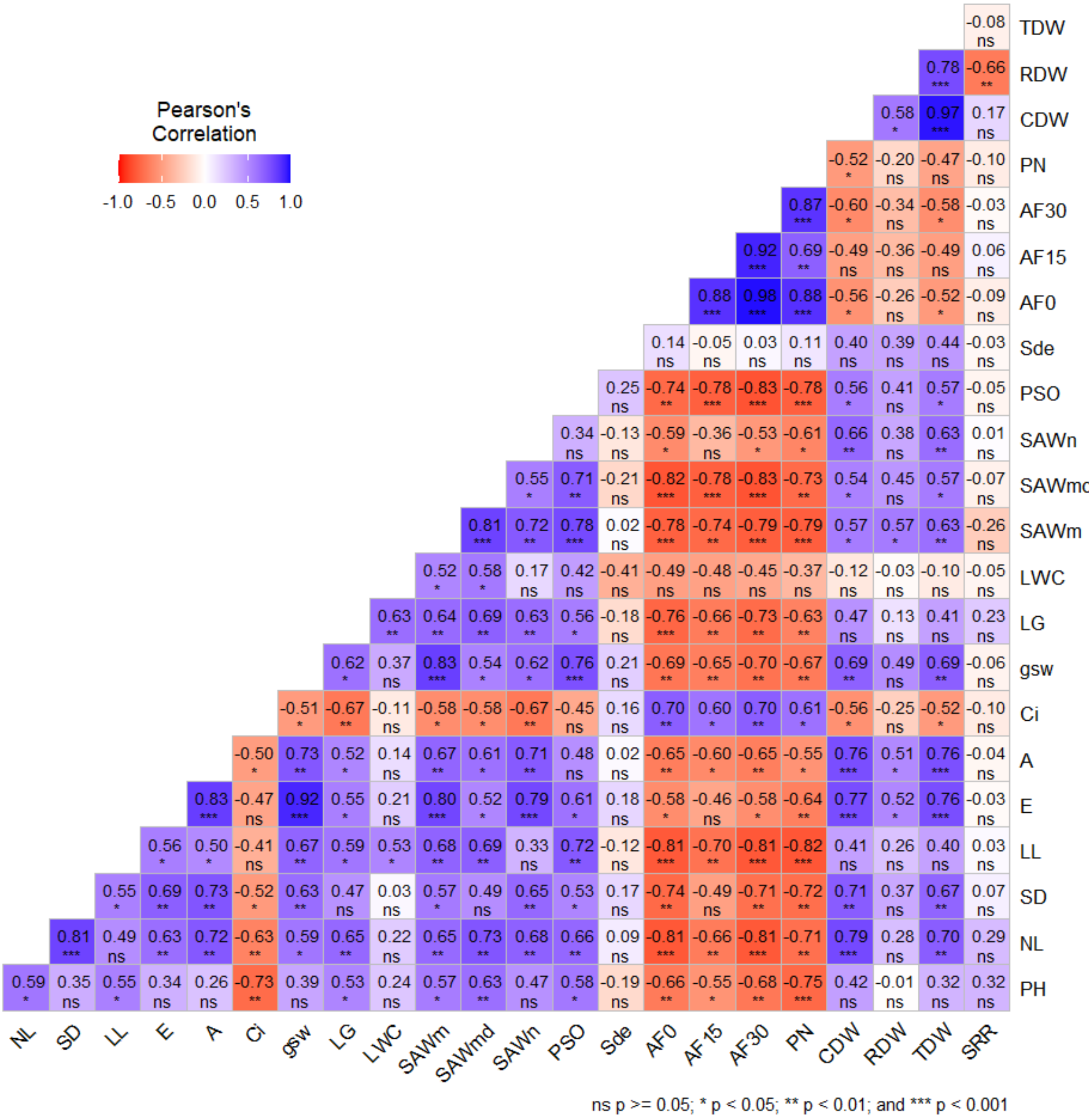
Pearson correlation analysis was conducted to understand the interrelationships among key morphophysiological, anatomical, and biomass allocation variables (Fig 8). This method was selected to evaluate the strength and direction of linear associations between variables measured across different water table depths. The results showed several significant correlations that helped explain the coordinated responses of oil palm to waterlogging stress. Stomatal aperture measured in the morning (SAWm) and midday (SAWmd) showed a moderate positive correlation to LWC, with correlation values of 0.52 and 0.58 ($p < 0.05$), respectively. This shows that wider stomatal opening is associated with improved leaf hydration under moderate stress. Similar associations between stomatal behavior and leaf water status have been reported in other crops (Peters et al., 2025). In contrast, stomatal aperture was strongly negatively correlated to aerenchyma formation at all measured root depths (AF0, AF15, AF30), with SAWmd showing the strongest correlation ($r = -0.78$ to -0.83, $p < 0.001$).

The result suggests a trade-off between gas exchange regulation and internal oxygen transport mechanisms under hypoxic conditions, comprising morphological and anatomical changes (Mohammed et al., 2019). However, stomatal density (SD) did not correlate significantly with most variables, suggesting that functional changes (e.g., aperture width) rather than structural stomatal traits are more responsive to waterlogging stress. A strong negative correlation between aerenchyma formation and the PSO was also observed ($r = -0.74$ to -0.83), reinforcing the role of stomatal closure as a key waterlogging stress response.

The number of pneumatophores was also strongly correlated with all morphological traits, photosynthetic performance, stomatal aperture, and aerenchyma formation. In terms of growth, TDW was positively correlated with stomatal aperture (SAWm, SAWmd, SAWn, and PSO). This is consistent with the results in oil palm and other species, where gas exchange capacity directly influences shoot growth under suboptimal conditions (Saleem et al., 2019). SRR also showed a strong negative correlation with root dry weight (RDW; $r = -0.66$; $p < 0.01$), suggesting that SRR was more sensitive to RDW than CDW under waterlogging conditions. In general, these results underscore a coordinated response comprising stomatal regulation, aerenchyma development, and biomass allocation in oil palm facing waterlogging stress.

Principal component analysis (PCA) biplot was used to reduce data dimensionality and explore multivariate relationships among selected variables under varying water table depths (Fig 9). In this analysis, the first two principal components (Dim1 and Dim2) explained 69.1% (56.2% and 12.9%, respectively), with vector orientation indicating the degree and direction of variable correlations. These dimensions were sufficient to distinguish waterlogging treatments into several distinct clusters corresponding to water table levels.

The 0 cm water table depth group, located predominantly in the negative direction of Dim1, was separated from the other groups and strongly associated with variables such as aerenchyma formation (AF0, AF15, and AF30), number of pneumatophores (PN), and internal CO2 concentration (Ci) in the leaves. These results strengthen the report by da Ponte et al. (2019) and Nuanlaong et al. (2021), which states that aerenchyma and pneumatophore formation are key survival traits in oil palm exposed to hypoxic soil(da Ponte et al., 2019; Nuanlaong et al., 2021). In contrast, the 30 cm water table depth group clustered on the positive side of Dim1 were closely associated with variables such as morphological performance (PH, NL, SD, and LL), photosynthesis parameters (A, E, and gsw), stomatal aperture width (SAWm, SAWmd, and SAWn), PSO, and LWC. The 45 cm group clustered is more dominant in positive Dim1 and intersects more with the 30 cm water table depth group. The associations suggest that crops under moderate or deeper water tables maintained more favorable physiological performance and shoot biomass accumulation. The 15 cm water table depth group occupied an intermediate space in the biplot, overlapping slightly with the 0 cm and 30 cm water table depth groups, reflecting transitional physiological and anatomical responses under moderate waterlogging. Biomass allocation (CDW, RDW, and TDW) can be an indicator of oil palm plants experiencing moderate waterlogging stress. SRR vectors pointed closer to the origin, showing weaker discriminatory power of these traits in explaining group variation. In general, the PCA biplot confirms that oil palm has clear multivariate differentiation under varying waterlogging intensities, with severe waterlogging (0 cm) associated with strong anatomical adaptation but suppressed physiological traits. A moderate water table depth (30 cm below the soil surface) supports more balanced physiological and growth performance.



	NL	SD	LL	E	A	Ci	gsw	LG	LWC	SAWm	SAWmd	SAWn	PSO	Sde	AF0	AF15	AF30	PN	CDW	RDW	TDW	SRR
TDW																						-0.08 ns
RDW																					0.78 ***	-0.66 **
CDW																				0.58 *	0.97 ***	0.17 ns
PN																			-0.52 *	-0.20 ns	-0.47 ns	-0.10 ns
AF30																		0.87 ***	-0.60 *	-0.34 ns	-0.58 *	-0.03 ns
AF15																	0.92 ***	0.69 **	-0.49 ns	-0.36 ns	-0.49 ns	0.06 ns
AF0																0.88 ***	0.98 ***	0.88 ***	-0.56 *	-0.26 ns	-0.52 *	-0.09 ns
Sde															0.14 ns	-0.05 ns	0.03 ns	0.11 ns	0.40 ns	0.39 ns	0.44 ns	-0.03 ns
PSO														0.25 ns	-0.74 **	-0.78 ***	-0.83 ***	-0.78 ***	0.56 *	0.41 ns	0.57 *	-0.05 ns
SAWn													0.34 ns	-0.13 ns	-0.59 *	-0.36 ns	-0.53 *	-0.61 *	0.66 **	0.38 ns	0.63 **	0.01 ns
SAWmc												0.55 *	0.71 **	-0.21 ns	-0.82 ***	-0.78 ***	-0.83 ***	-0.73 **	0.54 *	0.45 ns	0.57 *	-0.07 ns
SAWm											0.81 ***	0.72 **	0.78 ***	0.02 ns	-0.78 ***	-0.74 **	-0.79 ***	-0.79 ***	0.57 *	0.57 *	0.63 **	-0.26 ns
LWC										0.52 *	0.58 *	0.17 ns	0.42 ns	-0.41 ns	-0.49 ns	-0.48 ns	-0.45 ns	-0.37 ns	-0.12 ns	-0.03 ns	-0.10 ns	-0.05 ns
LG									0.63 **	0.64 **	0.69 **	0.63 **	0.56 *	-0.18 ns	-0.76 ***	-0.66 **	-0.73 **	-0.63 **	0.47 ns	0.13 ns	0.41 ns	0.23 ns
gsw								0.62 *	0.37 ns	0.83 ***	0.54 *	0.62 *	0.76 ***	0.21 ns	-0.69 **	-0.65 **	-0.70 **	-0.67 **	0.69 **	0.49 ns	0.69 **	-0.06 ns
Ci							-0.51 *	-0.67 **	-0.11 ns	-0.58 *	-0.58 *	-0.67 **	-0.45 ns	0.16 ns	0.70 **	0.60 *	0.70 **	0.61 *	-0.56 *	-0.25 ns	-0.52 *	-0.10 ns
A						-0.50 *	0.73 **	0.52 *	0.14 ns	0.67 **	0.61 *	0.71 **	0.48 ns	0.02 ns	-0.65 **	-0.60 *	-0.65 **	-0.55 *	0.76 ***	0.51 *	0.76 ***	-0.04 ns
E					0.83 ***	-0.47 ns	0.92 ***	0.55 *	0.21 ns	0.80 ***	0.52 *	0.79 ***	0.61 *	0.18 ns	-0.58 *	-0.46 ns	-0.58 *	-0.64 **	0.77 ***	0.52 *	0.76 ***	-0.03 ns
LL				0.56 *	0.50 *	-0.41 ns	0.67 **	0.59 *	0.53 *	0.68 **	0.69 **	0.33 ns	0.72 **	-0.12 ns	-0.81 ***	-0.70 **	-0.81 ***	-0.82 ***	0.41 ns	0.26 ns	0.40 ns	0.03 ns
SD			0.55 *	0.69 **	0.73 **	-0.52 *	0.63 **	0.47 ns	0.03 ns	0.57 *	0.49 ns	0.65 **	0.53 *	0.17 ns	-0.74 **	-0.49 ns	-0.71 **	-0.72 **	0.71 **	0.37 ns	0.67 **	0.07 ns
NL		0.81 ***	0.49 ns	0.63 **	0.72 **	-0.63 **	0.59 *	0.65 **	0.22 ns	0.65 **	0.73 **	0.68 **	0.66 **	0.09 ns	-0.81 ***	-0.66 **	-0.81 ***	-0.71 **	0.79 ***	0.28 ns	0.70 **	0.29 ns
PH	0.59 *	0.35 ns	0.55 *	0.34 ns	0.26 ns	-0.73 **	0.39 ns	0.53 *	0.24 ns	0.57 *	0.63 **	0.47 ns	0.58 *	-0.19 ns	-0.66 **	-0.55 *	-0.68 **	-0.75 ***	0.42 ns	-0.01 ns	0.32 ns	0.32 ns

ns p >= 0.05; * p < 0.05; ** p < 0.01; and *** p < 0.001

Fig 8. Pearson's correlation coefficient r matrix of observed variables. PH= plant height, NL= number of leaves, SD= stem diameter, LL= leaflet length, E= transpiration rate, A= photosynthesis rate, Ci= internal CO2 concentration, gsw= stomatal conductance, LG= leaf greenness index, LWC= leaf water content, SAWm= stomatal aperture width at 8:00-9:00 h, SAWmd= stomatal aperture width at 11.30-12.30 h, SAWn= stomatal aperture width at 15:00-16:00 h, PSO= percentage stomatal open, Sde= stomatal density, AF0= aerenchyma formation at 0-15 cm soil depth, AF15= aerenchyma formation at 15-30 cm soil depth, AF30= aerenchyma formation at >30 cm soil depth, PN= number of pneumathopore, CDW= canopy dry weight, RDW= root dry weight, TDW= total dry weight, and SRR = shoot-root ratio.

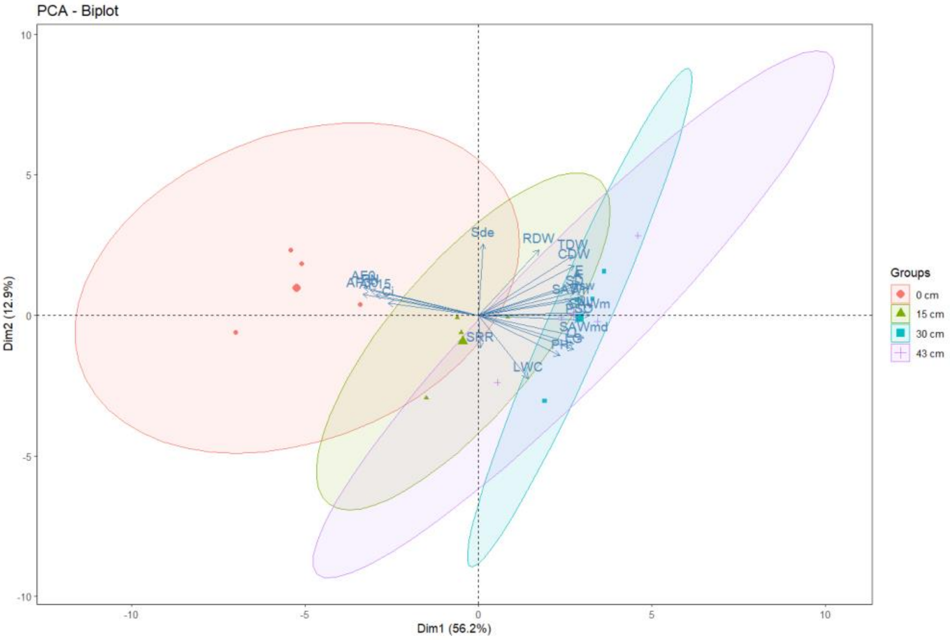


Fig 9. PCA biplot of waterlogging level and selected observed variables. Dim1 and Dim2 represented PC1 and PC2. PH= plant height, NL= number of leaves, SD= stem diameter, LL= leaflet length, E= transpiration rate, A= photosynthesis rate, Ci= internal CO2 concentration, gsw= stomatal conductance, LG= leaf greenness index, LWC= leaf water content, SAWm= stomatal aperture width at 8:00-9:00 h, SAWmd= stomatal aperture width at 11.30-12.30 h, SAWn= stomatal aperture width at 15:00-16:00 h, PSO= percentage stomatal open, Sde= stomatal density, AF0= aerenchyma formation at 0-15 cm soil depth, AF15= aerenchyma formation at 15-30 cm soil depth, AF30= aerenchyma formation at >30 cm soil depth, PN= number of pneumathopore, CDW= canopy dry weight, RDW= root dry weight, TDW= total dry weight, and SRR = shoot-root ratio.

Materials and Methods

Experimental site and plant materials

This study was conducted at the Cikabayan Experimental Station of IPB University, Bogor Regency, Indonesia. The oil palm seedlings used were twelve-month-old (cv. Tenera) with uniform vigor and morphology (plant height 138.68 ± 14.02 cm, number of leaves 12.89 ± 0.24, and stem diameter 83.18 ± 4.35 mm). Each seedling was transplanted into a 100-litre planter bag (50 cm × 50 cm) filled with mineral soil and was allowed to grow until it reached a height of 45 cm. At this point, 250 g of rock phosphate was applied as a basal fertilizer to supply phosphorus, and the seedlings were acclimated for an additional 30 days. The acclimated seedlings were arranged in open field conditions at 180 cm spacing and placed inside experimental ponds lined with A20 pond liner to allow precise control of water table depths. To support plant nutrition, as described by Fuady and Satriawan (2020), urea fertilizer was applied 1, 3, and 5 months after transplanting at doses of 100 g, 250 g, and 250 g per plant. Potassium chloride (KCl) was applied at 100 g and 250 g per plant, respectively, 3 and 5 months after transplanting.

Waterlogging treatment

The experiment followed a randomized complete block design (RCBD) with a single factor and four replications. Waterlogging treatment consisted of four water table depths measured from the soil surface, including 43 cm (control), 30 cm (shallow waterlogging), 15 cm (moderate waterlogging), and 0 cm (severe waterlogging) as shown in Fig 10. These water levels were maintained constantly throughout the study for six months (26 weeks) to simulate long-term waterlogging conditions. The treatments were imposed in lined experimental ponds, where permanent markings were made on the pond walls using waterproof paint to indicate each waterlogging level. The water level was checked and corrected daily to compensate for evaporation. Each experimental unit consisted of four plants.

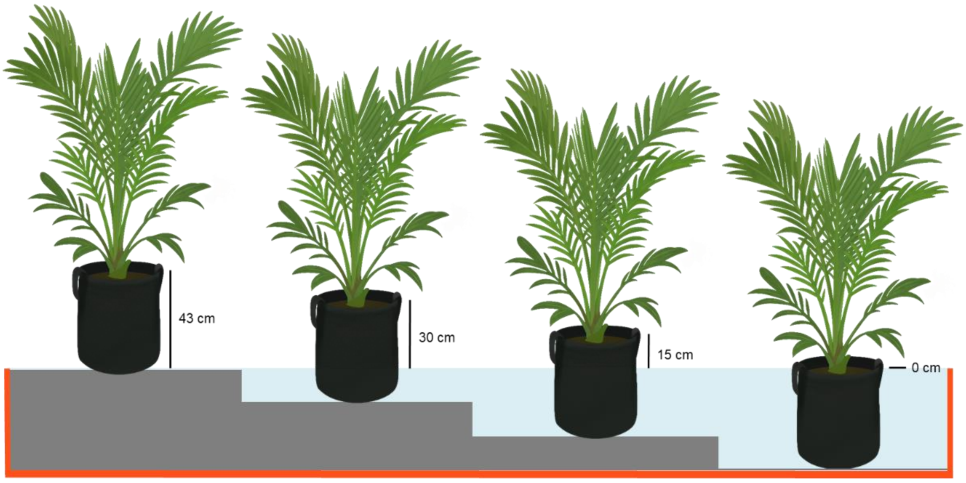


Fig 10. Four levels of waterlogging treatment in the experiment.

Observation variables

Observations were carried out on several groups of plant traits, including morphological, physiological, anatomical, and biomass-related variables. Morphological measurements included plant height, number of leaves, stem diameter, and leaflet length, which were measured using a measuring tape and digital caliper. Photosynthesis parameters were measured with the LI-6800 Portable Photosynthesis System (LI-COR Environmental, USA) at 9:00-11:00 h, as carried out by Montoya et al. (2024). Leaf greenness index was measured using a SPAD 502 chlorophyll meter (Konica-Minolta, Japan). Similarly, LWC was determined using an MB25 moisture analyzer (OHAUS Corporation, USA). Leaflet anatomy observations were performed using a COXEM E40 scanning electron microscope (SEM) (COXEM Co., Ltd., Republic of Korea) operated at 15 kV and magnification x1.000 for capturing micrographs. Sample preparation followed the method described by Shi et al. (2023), in which leaflet sections were fixed in 2.5% glutaraldehyde. After fixation, the samples were rinsed several times with distilled water to remove any residual glutaraldehyde, then dehydrated through a graded ethanol series at concentrations of 30%, 70%, 80%, and 90%. The dehydrated samples were then dried using a critical point dryer and coated with gold prior to imaging. Abaxial stomatal density and aperture width were assessed using an Olympus CX23 binocular microscope at 400x magnification at three times (8:00–9:00 h, 11:30–12:30 h, and 15:00–16:00 h). All measurements related to leaf physiology, including photosynthesis, SPAD, LWC, and anatomical observations, were conducted on the same leaf, specifically the third fully expanded leaf counted from the uppermost opened leaf. Root traits such as the number of pneumatophores and the formation of aerenchyma were also examined. Observations of aerenchyma were carried out at depths of 0-15 cm, 15-30 cm, and >30 cm below the soil surface. Aerenchyma was observed in root cross-sections stained with toluidine blue O under an Olympus CX23 binocular microscope at 40x magnification. The percentage of aerenchyma formation was quantified using ImageJ software (National Institutes of Health, USA). Dry weights of shoot and root biomass were quantified, along with the shoot-root ratio and total biomass. SRR was calculated as the ratio of CDW to RDW, while TDW was obtained by summing CDW and RDW.

Data analysis

The assumption of data normality was examined by the Shapiro-Wilk test and homogeneity of variances by Levene's test. After ANOVA ($p \leq 0.05$), differences between means were examined by post hoc Tukey Honestly Difference (HSD) test ($p \leq 0.05$). Pearson's correlation analysis and PCA were performed on all observed variables. All statistical analyses and visualizations were performed using RStudio software (RStudio Inc., Boston, MA, USA).

Conclusion

In conclusion, oil palm responded to waterlogging stress through distinct morphophysiological, anatomical, and biomass allocation strategies. Control and shallow waterlogging supported better vegetative growth, higher leaf greenness index, greater LWC, and wider stomatal apertures, reflecting maintained physiological function. In contrast, severe waterlogging reduced growth, photosynthesis performance, and stomatal activity but induced anatomical adaptations, significantly increasing aerenchyma formation and pneumatophore development. At 15 cm of waterlogging below the soil surface, crops showed significant declines in growth and physiological performance, along with the initial activation of anatomical adaptations. Biomass allocation shifted under stress, with reduced CDW and TDW, while RDW and SRR remained relatively stable. Anatomical adaptations, particularly the formation of aerenchyma and pneumatophores, are recognized as key factors enhancing oil palm tolerance to severe waterlogging stress. These results show that oil palm uses integrated strategies to tolerate waterlogging. In addition, maintaining shallow water table depths is essential to support growth and adaptive function under waterlogged conditions. This can be achieved by constructing mound beds before planting in low-lying areas and managing drainage channels to remove excess water (Shampazuraini et al., 2018; Suwardi et al., 2022; Nadaraj et al., 2024), thereby improving aeration and reducing water saturation in the soil.

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