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Drought-Induced Morphophysiological and Metabolite Changes in Oil Palm Seedlings from Jambi, Indonesia

Evan Vria Andesmora[1], Hamim[2], Sulistijorini[2], Mafrikhul Muttaqin[2], Triadiati[2*]

[1]Graduate School of Plant Biology Study Program, IPB University, Darmaga Campus, Bogor 16680, Indonesia
[2]Departement of Biology, Faculty Mathematics and Natural Sciences, IPB University, Darmaga Campus, Bogor 16680, Indonesia

ABSTRACT

Oil palm requires sufficient water for optimal growth. However, oil palm plantations in Indonesia face the challenge of global climate change, which causes increased temperatures and unpredictable rainy seasons. The research aimed to analyze oil palm accessions from Jambi that are tolerant to drought based on plant morphophysiological characteristics and metabolite profile. The experiment was conducted in the greenhouse using a factorial randomized block design. Five oil palm accessions were evaluated in this study, i.e., Muara Jambi (MJ), Tebo (TB), Tanjung Jabung Barat (TJB), Merangin (MR), and Simalungun (SM). Seedlings were planted in pots containing 20 kg of soil and acclimatized for 14 days before treatment. Drought treatments were carried out for two, four, and six weeks. Observations were made on growth, physiological, and metabolite changes at the end of each drought period. The study showed that the SM accession exhibited a higher photosynthetic rate and fresh and dry biomass than the other accessions. However, the content of proline and MDA increased significantly in oil palm throughout the drought periods. Metabolomic profiling revealed a significant increase in 13 metabolites under drought stress, i.e., citramalate, L-tyrosine, ferulate, and 3-4-dihydroxybenzoate were the four most prevalent metabolites in the leaf. The root produced more L-proline, aspartate, aconitate, kaempferol-3-o-pentoside, oxoadipate, citrate, L-phenylalanine, maltose, phenylacetic acid, and citramalate. These metabolites have roles in plant metabolic pathways such as valine, leucine, and isoleucine biosynthesis, phenylpropanoid biosynthesis, arginine and proline metabolism, citrate cycle (TCA cycle), lysine biosynthesis, phenylalanine metabolism, and starch and sucrose metabolism.

1. Introduction

Oil palm (*Elaeis guineensis* Jacq.) is a significant plantation commodity in Indonesia. Indonesia is the world's largest palm oil producer, contributing about 55% of global production. The Indonesian palm oil industry significantly contributes to the national economy by exporting processed products such as biodiesel, which supports economic growth (Singagerda *et al.* 2018). The area of oil palm plantations in Indonesia continues to increase annually, from 14.86 million hectares in 2020 to 15.08 million hectares in 2021 (Directorate General of Plantations 2020). The export value of Indonesian palm oil also increased by 16.9% (BPS-Statistics Indonesia 2020).

Oil palm requires sufficient water for optimal growth. However, oil palm plantations in Indonesia face the challenge of global climate change, which causes increased temperatures and unpredictable rainfall patterns. Irregular rainfall and prolonged dry seasons can cause drought, while the rainy season can cause waterlogging. Drought reduces the water supply needed for the growth and development of oil palm, resulting in slowed growth, leaf drying, and decreased yields, negatively impacting palm oil production. Water is the main limiting factor for plant growth and production

* Corresponding Author
   E-mail Address: triadiati@apps.ipb.ac.id

(Kapoor *et al.* 2020) and Filho *et al.* (2021) findings show that water deficit or drought causes a decrease in net assimilation rate and stomatal conductance in oil palm.

The impact of drought is also seen in other plants. In rice, there is a decrease in plant height and grain yield (Salgotra & Chauhan 2023). In maize, there is a decrease in the fresh weight of leaves and roots, as well as the dry weight of plants (Ayub *et al.* 2021). There is a decrease in the photosynthesis rate in rice (Piveta *et al.* 2021) and an increase in proline content (Kumar *et al.* 2023). In maize, the photosynthesis rate decreases (Cai *et al.* 2020), while in coffee, photosynthesis is disrupted with a decrease in stomatal conductance and transpiration (Arunyanark *et al.* 2022).

Drought also causes an increase in lipid peroxides, with malondialdehyde (MDA) as an indicator of oxidative stress levels. MDA content increases in oil palm, causing water deficit (Filho *et al.* 2021). Additionally, drought can increase metabolites such as allantoin, L-proline, L-arginine, L-histidine, L-isoleucine, and tryptophan in plants (Khan *et al.* 2019). Changes in plant metabolism due to stress include disruptions in photosynthesis pathways, the tricarboxylic acid (TCA) cycle, glycolysis, amino acid metabolism, and hormone synthesis (Guo *et al.* 2020). On the other hand, research on drought-tolerant oil palm, especially from Jambi, has yet to be conducted. Therefore, this study aims to analyze oil palm accessions from Jambi that are tolerant to drought based on plant morphophysiological characteristics.

2. Materials and Methods

2.1. Research Design
The research was conducted in the Greenhouse and Plant Physiology and Genetics Laboratory of the Biology Department. Plant metabolites were analyzed in the Advanced Research Laboratory of IPB University. This study used a factorial randomized block design. The first factor was the accession, consisting of Muara Jambi (MJ), Tebo (TB), Tanjung Jabung Barat (TJB), Merangin (MR), and Simalungun (SM). The second factor was drought treatment and control with observation times at two, four, and six weeks. Each combination of accession and drought treatment was repeated three times. Oil palm seedlings were planted in 30 cm × 30 cm pots containing 20 kg of soil and then transferred to the greenhouse for acclimatization for 14 days before treatment. At the end of the acclimatization period, seedlings were subjected to drought treatment for the predetermined duration, namely two, four, and six weeks.

2.2. Plant Growth Measurement
Plant growth measurements included the fresh and dry weight (roots, shoots, and total) of oil palm seedlings subjected to drought treatment and control plants. The fresh plant weight was weighed and then dried in an oven at 60°C to obtain the plant dry weight.

2.3. Plant Physiology Measurements
Photosynthesis rate (A_{max}), transpiration rate (E), and stomatal conductance (g) were measured using Licor-6400XT on mature leaves at two, four, and six weeks. Chlorophyll and carotenoid content of leaves were extracted with 80% acetone p.a and measured with a spectrophotometer at 470, 646, and 663 nm (Lichtenthaler 1987). Proline content of leaves was analyzed based on the method Bates (1973) described using extraction with 3% sulfosalicylic acid solution. Lipid peroxidation level was analyzed by measuring malondialdehyde (MDA) content based on the method described by Zhu *et al.* (2023) using extraction with 5% TCA.

2.4. Plant Metabolite Profile Analysis
Metabolite analysis of oil palm leaf and root was conducted based on the method described by Jeszka-Skowron *et al.* (2014) and analysis using UHPLC Vanquish Tandem Q Exactive Plus Orbitrap HRMS ThermoScientific.

2.5. Data Analysis
Observation data were tested using ANOVA at α = 5% and further tested with DMRT using IBM SPSS Statistics 20 software. Metabolomic analysis was conducted using MZmine and MetaboAnalyst 6.0 websites. Metabolite group identification was done using MoNA and PubChem websites, and metabolic pathway identification was done through the KEGG website.

3. Results

3.1. Plant Growth
The interaction between the accession treatment and drought duration did not affect plant growth regarding the fresh and dry weight of the tested oil palm seedlings. However, it was significantly influenced by

accession and duration factors separately (p<0.05). The SM accession had the highest fresh and dry weight of roots and shoots, including total fresh and dry weight and significantly differed from the other four oil palm accessions. The total dry weight of MR and TB was not significantly different, but MJ and TJB were significantly different. The root-to-shoot ratio in all accessions was not significantly different (Table 1).

The fresh and dry weights of roots and shoots under drought treatment were lower than the control. The fresh weight of roots under drought treatment for two, four, and six weeks decreased and showed a significant difference between the two- and four-week drought treatments compared to the six-week treatment (p<0.05) (Table 2).

The shoot's fresh weight, total fresh weight, roots dry weight, shoots, and total dry weight under drought treatments of two, four, and six weeks did not show significant differences (p>0.05). The root-to-shoot ratio under the four-week drought treatment significantly differed from the two- and six-week treatments (p<0.05).

3.2. Photosynthesis Rate (A_{max}), Transpiration (E), Stomatal Conductance (g), Chlorophyll and Carotenoid Content

The photosynthesis rate of oil palm was not influenced by the interaction between treatments (p>0.05), but it was significantly influenced by accession and drought factors separately (p<0.05). The SM accession had a photosynthesis rate not different from the MR accession (p>0.05). However, the photosynthesis rate of these two accessions was significantly different from the other three accessions (p<0.05) (Table 3). The photosynthesis rate of oil palm during two weeks of drought treatment significantly differed from the four and six-week duration (p<0.05).

The transpiration rate and stomatal conductance were not affected by the interaction between accession and drought duration (p>0.05), but were affected by drought duration alone (p<0.05). The transpiration rate under the two-week drought treatment was significantly different (p<0.05) from the four- and six-week treatments. Stomatal conductance under the two- and four-week drought treatments significantly differed from the six-week drought treatment (p<0.05). Stomatal conductance under drought treatment was lower than the control (Table 4).

Chlorophyll and carotenoid content were not affected by the interaction between treatments (p>0.05) but were influenced by accession and drought duration (p<0.05). The highest chlorophyll content was found in the SM accession and was not significantly different from MR, MJ, and TB but was significantly different from the TJB accession. Chlorophyll and carotenoid content under drought treatment were lower than the control (Table 4).

Table 1. The average fresh weight, dry weight, and root-to-shoot ratio of five different oil palm seedlings accessions from Jambi, Indonesia

Accessions	Root fresh weight (g)	Shoot fresh weight (g)	Total fresh weight (g)	Root dry weight (g)	Shoot dry weight (g)	Total dry weight (g)	Root-to-shoot ratio
SM	17.32±2.62ᵃ	55.70±7.04ᵃ	73.02±9.51ᵃ	5.71±0.58ᵃ	15.08±1.57ᵃ	20.79±2.06ᵃ	0.38±0.03ᵃ
MR	9.37±1.05ᵇ	27.62±2.17ᵇ	36.99±3.10ᵇ	3.06±0.31ᵇ	7.10±0.54ᵇᶜ	10.16±0.81ᵇᶜ	0.43±0.03ᵃ
MJ	8.21±0.80ᵇ	25.81±1.58ᵇ	34.02±2.24ᵇ	2.36±0.17ᵇ	5.92±0.41ᶜ	8.28±0.51ᶜ	0.40±0.05ᵃ
TJB	9.82±2.62ᵇ	28.03±4.28ᵇ	37.85±6.70ᵇ	3.27±0.53ᵇ	8.11±1.00ᵇ	11.38±1.47ᵇ	0.40±0.03ᵃ
TB	7.02±0.99ᵇ	19.62±1.87ᵇ	26.64±2.75ᵇ	3.12±0.37ᵇ	7.53±0.87ᵇᶜ	10.65±1.12ᵇᶜ	0.41±0.04ᵃ

Number of replications (n = 18) ±SE, data followed by the same letter in the column indicates no significant difference (Duncan test, p>0.05). SM = Simalungun, MR = Merangin, MJ = Muaro Jambi, TJB = Tanjung Jabung Barat, TB = Tebo

Table 2. The average of fresh weight, dry weight, and root-to-shoot ratio of oil palm seedlings grown as control plants and under drought treatment with different durations

Treatments	Root fresh weight (g)	Shoot fresh weight (g)	Total fresh weight (g)	Root dry weight (g)	Shoot dry weight (g)	Total dry weight (g)	Root-to-shoot ratio
2-w control	9.45±1.96ᵇ	27.62±3.11ᵇ	37.07±3.86ᵇ	3.58±0.47ᵇᶜ	8.79±1.07ᵇᶜ	12.37±1.46ᵇᶜ	0.41±0.03ᵃ
2-w drought	7.39±1.71ᵇ	24.56±2.45ᵇ	31.95±3.29ᵇ	2.77±0.38ᶜ	6.25±0.65ᵈ	9.02±0.96ᶜ	0.44±0.03ᵃ
4-w control	15.34±1.80ᵃ	38.30±6.37ᵃ	53.64±9.12+	4.37±0.43ᵃᵇ	9.91±1.04ᵇ	14.28±1.41ᵇ	0.44±0.03ᵃ
4-w drought	6.63±1.54ᵇ	27.07±3.33ᵇ	33.70±3.96ᵇ	2.67±0.37ᶜ	7.15±0.88ᶜᵈ	9.82±1.16ᶜ	0.37±0.03ᵇ
6-w control	16.95±2.03ᵃ	46.29±7.98ᵃ	63.24±10.81ᵃ	4.94±0.71ᵃ	13.75±1.75ᵃ	18.69±2.34ᵃ	0.36±0.04ᵇ
6-w drought	6.33±1.52ᶜ	24.28±4.72ᵇ	30.61±5.88ᵇ	2.69±0.58ᶜ	6.64±1.41ᶜᵈ	9.33±1.96ᶜ	0.41±0.06ᵃ

Number of replications (n = 15) ± SE, data followed by the same letter in the column indicates no significant difference (Duncan test, p>0.05). w = weeks

Table 3. The average of photosynthetic rate, transpiration, stomatal conductance (PAR 1000), chlorophyll, and carotenoid content of five oil palm seedlings from Jambi, Indonesia

Accessions	Photosynthesis Rate (μmol CO_2 m^{-2} s^{-1})	Transpiration (mmol H_2O m^{-2} s^{-1})	Stomatal conductance (mmol H_2O m^{-2} s^{-1})	Chlorophyll (mg. g^{-1} fw)	Carotenoid (mg. g^{-1} fw)
SM	30.44±0.52[a]	1.85±0.10[a]	1080±0.20[a]	38.99±1.85[a]	10.26±0.37[a]
MR	29.65±0.61[ab]	1.87±0.06[a]	1180±0.21[a]	38.26±2.31[ab]	10.18±0.45[a]
MJ	28.50±0.67[b]	1.86±0.06[a]	1180±0.21[a]	35.80±8.44[ab]	9.80±0.35[a]
TJB	28.81±0.63[b]	1.76±0.06[a]	970±0.18[a]	33.55±1.97[b]	8.76±0.35[b]
TB	28.91±0.56[b]	1.72±0.07[a]	1050±0.17[a]	38.33±2.05[ab]	9.89±0.34[a]

Number of replications (n = 18) ±SE, data followed by the same letter in the column indicates no significant difference (Duncan test, p>0.05). SM = Simalungun, MR = Merangin, MJ = Muaro Jambi, TJB = Tanjung Jabung Barat, TB = Tebo.

Table 4. The average of photosynthetic rate, transpiration, stomatal conductance (PAR 1000), chlorophyll content, and carotenoid content of oil palm seedlings grown as control plants and under drought treatment with different durations

Treatments	Photosynthesis Rate (μmol H_2O m^{-2} s^{-1})	Transpiration (mmol H_2O m^{-2} s^{-1})	Stomatal conductance (mmol H_2O m^{-2} s^{-1})	Chlorophyll (mg. g^{-1} fw)	Carotenoid (mg. g^{-1} fw)
2-w control	27.52±0.50[c]	1.82±0.07[abc]	1890±0.20[a]	39.22±1.96[b]	9.95±0.53[a]
2-w drought	26.97±0.63[c]	1.66±0.08[c]	1460±0.18[b]	31.26±1.71[c]	8.68±0.31[b]
4-w control	29.72±0.48[b]	1.90±0.07[ab]	1400±0.16[b]	38.36±1.80[b]	10.71±0.37[a]
4-w drought	29.11±0.58[b]	1.81±0.06[abc]	1290±0.13[b]	30.04±1.54[c]	8.67±0.34[b]
6-w control	31.83±0.43[a]	1.98±0.05[a]	260±0.01[c]	46.29±2.03[a]	10.45±0.41[a]
6-w drought	30.42±0.52[ab]	1.69±0.06[bc]	240±0.02[c]	36.73±1.52[b]	10.22±0.34[a]

Number of replications (n = 15) ± SE, data followed by the same letter in the column indicates no significant difference (Duncan test, p>0.05), w = weeks

3.3. Proline and MDA Content

Proline and MDA content were not influenced by the interaction between accession and drought (p>0.05), but they were influenced by drought treatment (p<0.05) (Figure 1). Proline content significantly differed (p<0.05) and increased from two weeks to six weeks of drought treatment. Additionally, proline and MDA content in the control was lower than in the drought treatment.

3.4. Oil Palm Metabolite Profile Under Drought Stress

Drought treatment in oil palm caused significant changes in various metabolites in leaves and roots. Metabolite analysis showed apparent clustering between leaves and roots, where several metabolites were most important in classifying the drought-stressed oil palm metabolite groups with the control group (Figure 2). The results of metabolite identification in oil palm revealed that four metabolites in leaf organs increased significantly: citramalate, l-tyrosine, ferulate, and 3-4-dihydroxybenzoate. These metabolites originate from phenol, hydroxycarboxylic acid, and amino acids, involved in valine, leucine, and isoleucine biosynthesis, phenylpropanoid biosynthesis, ubiquinone and other terpenoid-quinone biosynthesis, and benzoate degradation (Figure 3). In the root organs, 9 metabolites showed a significant increase: l-proline, aspartate, aconitate, kaemferol-3-o-pentoside, oxoadipate, citrate, l-phenylalanine, maltose, phenylacetic acid, and citramalate. These metabolites belong primarily to amino acids, carbohydrates, carboxylic acid, flavonoids, and tricarboxylic acids, involved in at least six plant metabolic pathways (Figure 3).

4. Discussion

Drought is one of the most significant environmental stresses limiting plant growth, distribution, and production. Drought disrupts plant physiological processes, which causes a reduction of growth, including in oil palm. Among the five accessions, Simalungun (SM) produced the highest fresh and dry weight in this study (Table 1). In addition, drought has impacted the growth of oil palm plants more than the control, where drought-stricken plants have lower growth than control plants. The decrease in fresh and dry weight occurred in week 4 and continued until week 6 (Table 2); this was also supported by photosynthetic rates, which decreased significantly in week 6 (Table 4). Decreased growth is a common and earlier symptom in all plants subjected to drought stress with varying reduction parameters,
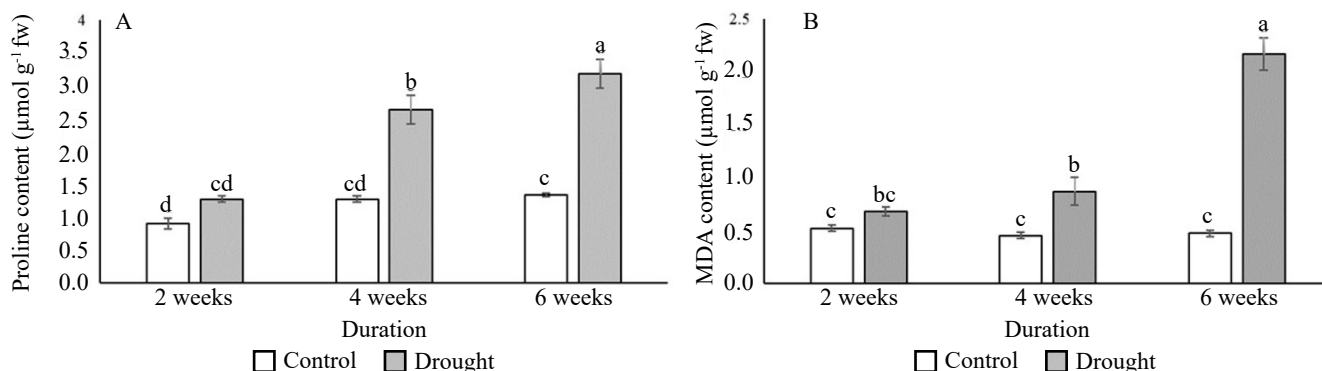
Figure 1. Proline (A) and MDA content (B) of oil palm seedlings under drought treatment for different durations. Values are means ± SE, with the number of replications (n = 15). Bars followed by the same letter indicate no significant difference (Duncan test, p>0.05); w = weeks
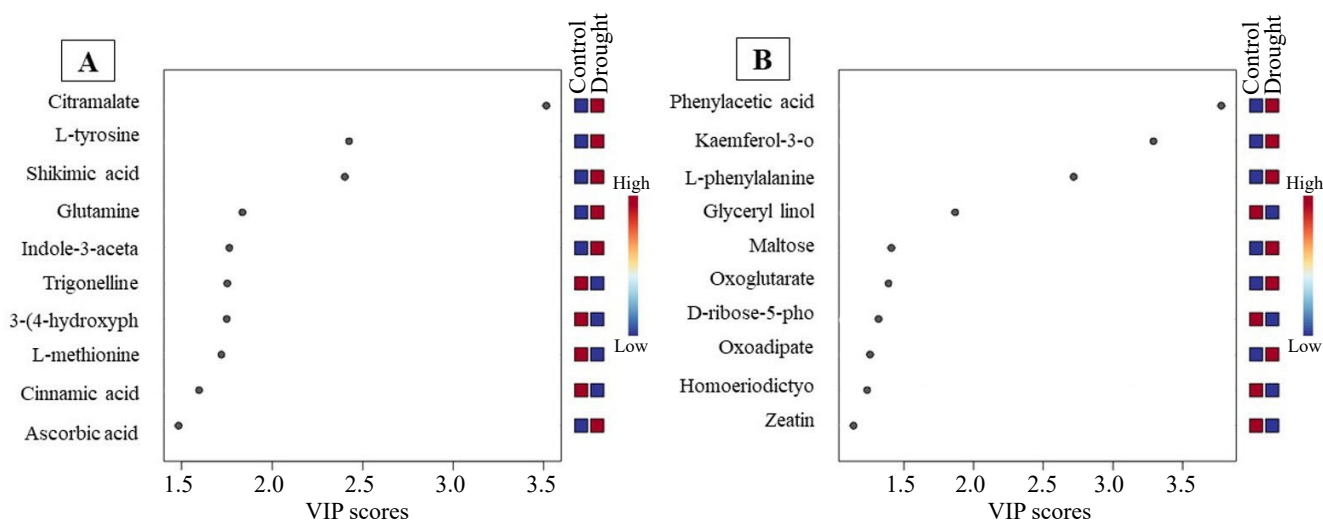

Figure 2. Metabolites significantly influence the grouping of oil palm metabolites under drought stress in the SM accession, as expressed in the leaves (A) and roots (B) (based on Partial Least Squares Discriminant Analysis/PLS-DA)

depending on genotypes and drought intensity. For example, Mukamuhirwa *et al.* (2019) found that drought reduced growth and development in rice, including plant height, flowering time, tiller number, harvest time, and grain number. Similarly, due to drought, maize also significantly decreased the fresh and dry weight of shoots and roots (Ayub *et al.* 2021). Higher fresh and dry weights during drought treatment suggest that SM seedlings could efficiently utilize resources for growth, which correlates with higher photosynthetic rates than other accessions.

In oil palm, biomass reduction in response to drought is primarily associated with decreased shoot biomass due to reduced leaf area and number during the 14-day drought (Ikhajiagbe *et al.* 2022). In addition, oil palms may avoid dehydration and maintain turgidity by reducing transpiration rates through stomata closure (Table 4). Reduced stomatal aperture is among the important mechanisms used to tolerate water stress, as seen in *Rose*

damascena in response to drought (Al-Yasi *et al.* 2020). In this study, the photosynthetic rate of SM accession was higher and significantly different from the other three accessions (Table 3). This indicates the SM accession's ability to utilize limited resources during drought. On the other hand, drought treatment in this experiment did not cause the photosynthesis rates of droughted plants to be different from the control (Table 4), probably because during photosynthesis measurement, the plants were still under mild drought conditions. During that time, the plants still had only 4-5 leaves while growing media 20 kg of soil, and therefore, for six weeks, the plants were still in the moderate stress phase. This study's results differ from those of Filho *et al.* (2021) found that water deficit causes a decrease in net assimilation rate and stomatal conductance in 17-month-old oil palms that were given a 28-day drought stress. In addition, a decrease in the photosynthetic rates was also reported in several
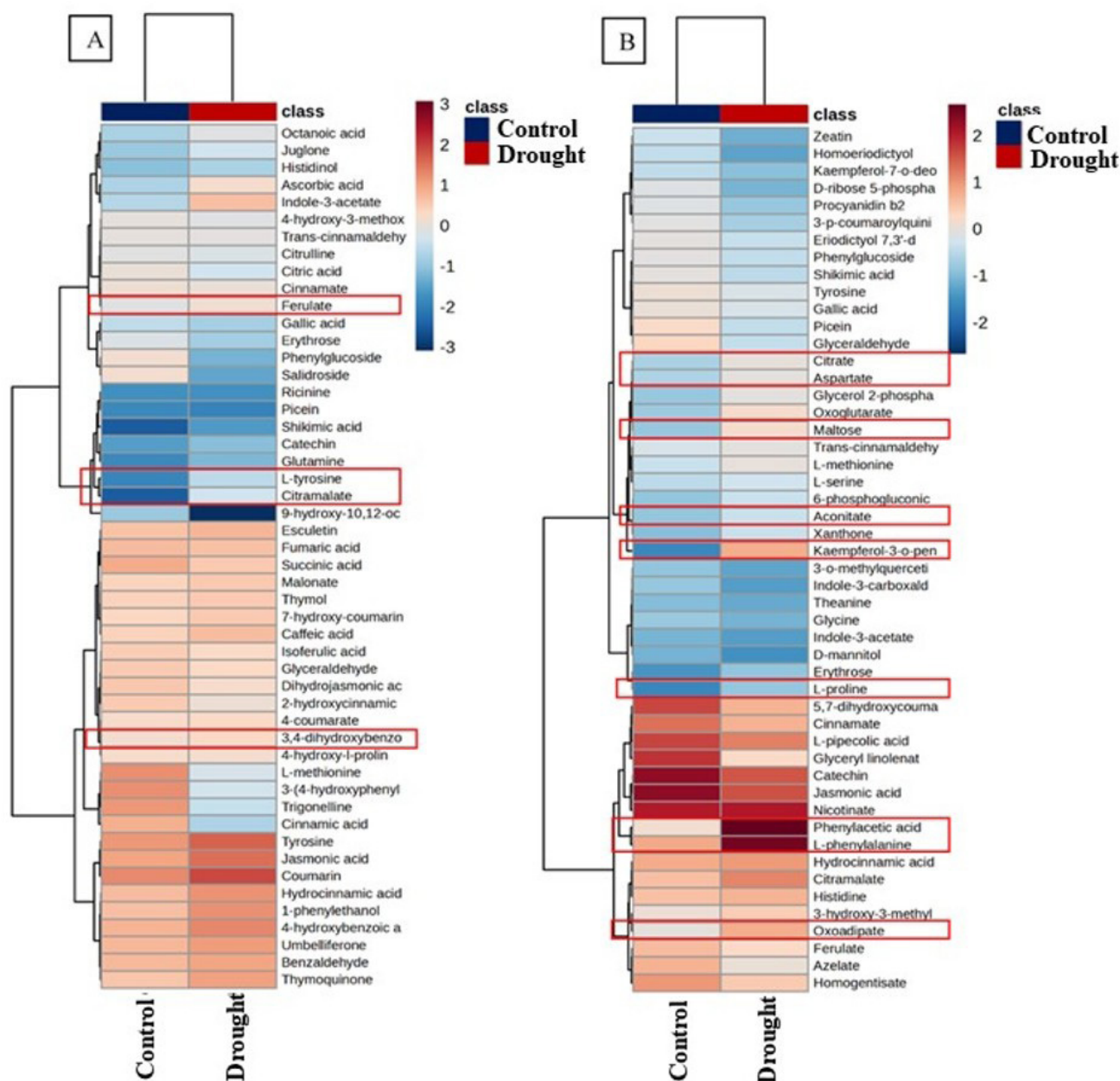
Figure 3 Heatmap of metabolite profiles in the SM accession of oil palm seedlings, displaying leaves (A) and roots (B) (The red box indicates a significant increase as determined by the t-test α = 5%)

crops related to drought stress, including in corn plants reported by (Cai *et al.* 2020) and rice (Piveta *et al.* 2021). Photosynthesis rates in drought-stressed oil palms showed a decreasing trend compared to the control at the same duration (Table 4).

In drought-stressed oil palm plants (six weeks drought), photosynthetic rates remained high despite decreased stomatal conductance. This may be due to effective adaptation mechanisms of the accessions, such as increased water use efficiency through osmotic adjustment

mechanism and proline accumulation (Figure 1), allowing the plant to produce more biomass per unit of water used. Plants may also increase the activity of enzymes involved in photosynthesis, maximizing the use of internal CO_2 when stomata are closed (Gago *et al.* 2020). Additionally, increased glucose from photosynthesis becomes the raw material for proline synthesis. Glucose is broken down into pyruvate in the Krebs cycle and converted into α-ketoglutarate to form glutamate. This process is facilitated by the enzymes Δ1-pyrroline-5-carboxylate

synthetase (P5CS) and Δ1-pyrroline-5-carboxylate reductase (P5CR), which convert glutamate into proline (Meena *et al.* 2019). The proline content of oil palm in this study showed an increase in drought treatment. This result aligns with Bayona-Rodríguez & Romero (2024) study that proline content increased in oil palm after 60 days of drought. This indicates that oil palm responds to drought by biosynthesizing proline. Proline is an osmolyte that accumulates during drought to maintain osmotic balance and provide protection. Additionally, proline accumulates in cells to support and enhance water absorption through osmosis, keeping the turgor pressure necessary for cells (Borghi *et al.* 2019).

This process indicates that oil palm adapts well to drought conditions through mechanisms that enhance photosynthesis efficiency and osmoregulation metabolism. In this study, Malondialdehyde (MDA) content in drought-stressed oil palms was consistently higher than in control plants across all drought durations, as presented in Figure 1. This finding aligns with several studies indicating that MDA content increases during drought, as observed in rice (Urmi *et al.* 2023) and Alnus glutinosa (Zhu *et al.* 2023). The elevated MDA levels in this study suggest that oil palms experience higher oxidative stress under drought conditions. To cope with drought, plants employ various strategies, including regulating lipid metabolism to mitigate the impact of drought stress through reactive oxygen species (ROS) production. ROS can induce lipid damage in membranes as a result of lipid peroxidation. The results from the study by Bayona-Rodríguez & Romero (2024) show that oil palms subjected to drought stress increased MDA content indicating cellular damage from lipid oxidation, which often occurs during drought conditions.

The SM accession was selected for metabolite profile analysis based on the highest total dry weight among other accessions. They exhibit complex physiological adaptations to drought conditions, as evidenced by changes in several metabolites shown in Figure 3. These compounds contribute to osmotic adjustment, helping to maintain cell turgor pressure and protect proteins and cell membranes from damage caused by drought stress. This accumulation of osmolyte not only supports internal osmotic balance but also enhances water use efficiency. Osmolyte helps plants reduce excessive transpiration rates under limited water conditions (Zhang *et al.* 2022). With improved osmotic adjustment, SM seedlings can better maintain cell hydration and stability, ultimately contributing to more significant biomass accumulation. Proline, which increases significantly under drought stress,

acts as an osmoprotectant, enabling plants to sustain internal osmotic pressure and preserve cell turgor (Yipu *et al.* 2024).

Previous research has shown that drought stress increases the accumulation of metabolites such as allantoin, L-proline, L-arginine, L-histidine, L-isoleucine, and tryptophan in *Cicer arietinum* (Khan *et al.* 2019). This suggests that these metabolites play a critical role in plant adaptation to drought, maintaining physiological functions, and enhancing tolerance to drought stress. Organic acids, such as citramalate in leaves, aconitate, oxoadipate, and citrate in roots, also increase their accumulation in oil palm seedlings under drought stress, as shown in Figure 3. The increase in citramalate reflects an optimized use of available carbon for energy production, supporting plant's short-term energy needs, particularly under drought conditions (Borghi *et al.* 2019).

Carboxylic acid plays a crucial role in plant responses to drought stress. This study showed significant increases in metabolites such as phenylacetic acid found in roots, as shown in Figure 3B. Ackah *et al.* (2021) reported that carboxylic acid groups and their derivatives, amino acids, peptides, and analogs are key components in drought stress responses in mulberry plants. Additionally, amino acids such as β-alanine, isoleucine, leucine, lysine, and tyrosine, as well as organic acids like 3-hydroxy propanoic acid, gluconic acid, and glycolic acid, have been found to accumulate in response to drought conditions (Kang *et al.* 2019).

Changes in metabolite profiles reflect plant adaptation mechanisms to drought conditions, involving adjustments to energy metabolism, osmoprotection, and cellular defense against oxidative damage (Fàbregas and Fernie 2019). The increase in phenylalanine in the roots suggests that SM seedlings can boost the production of phenolic compounds, which function as defense mechanisms. The phenylpropanoid pathway, with L-phenylalanine as a precursor, is crucial for synthesizing lignin and antioxidant compounds, enhancing the plants' physical and physiological resilience during drought (Pérez-Llorca & Muller 2024). These changes highlight complex adaptive mechanisms in oil palm, enabling physiological and biochemical functions to be maintained under drought conditions.

Increased levels of maltose and glyceraldehyde, shown in Figure 3, also indicate an adjustment in carbohydrate metabolism. Maltose acts as an energy reserve, supporting cell structure, while glyceraldehyde participates in glycolysis, a pathway that provides energy from glucose. This glycolysis process is crucial for supplying energy

during drought stress, particularly to sustain the basic metabolism of roots and leaves. This finding aligns with studies on quinoa plants (*Chenopodium quinoa* Willd.) (Wang *et al.* 2024) and peanuts (*Arachis hypogaea* L.) (Gundaraniya *et al.* 2020), which demonstrated that such metabolic regulation helps plants maintain essential metabolic activity to support growth, especially in roots and leaves under drought conditions.

Plants have sophisticated metabolic reactions, with patterns in leaves and roots that help them adjust to dry conditions. On the one hand, the leaves exhibit increased metabolites, including cinnamate, citramalate, gallic acid, indole-3-acetate, jasmonic acid, shikimic acid, and tyrosine. Cinnamate, gallic acid, and shikimic acid are involved in phenylpropanoid pathways, which boost antioxidant capacity and protect leaf cells from oxidative stress caused by prolonged sun exposure and water loss. According to Naikoo *et al.* (2019), phenolic metabolites can act as effective antioxidants in shielding plant tissues from oxidative damage during drought.

Plants take a slightly different approach at the root by showing increased citramalate and L-methionine while other metabolites, such as cinnamate, ferulate, gallic acid, and jasmonic acid, decrease. Increased citramalate in the roots has the same function as in leaves, namely as an osmotic agent to maintain tissue water balance. Meanwhile, the increase in L-methionine in the roots is likely related to ethylene synthesis. This hormone promotes structural adaptations such as lateral root growth or root hairs, which can improve the ability to absorb water in dry conditions (Le Deunff *et al.* 2016).

Several fascinating similarities and contrasts exist between drought responses in leaves and roots. The increase in jasmonic acid and indole-3-acetate in the leaves represents hormonal modulation aimed at water retention via stomatal closure and leaf surface area regulation. Jasmonic acid is important in reducing the rate of transpiration in this way (Rehman *et al.* 2023), whereas indole-3-acetate (IAA) can impact development patterns to diminish portions of the leaf that are directly exposed to the environment (Solanki and Shukla 2023). Meanwhile, at the root, the drop in jasmonic acid suggests that when faced with drought, plants may prioritize structural adaptation over hormonal regulation (Huang *et al.* 2023).

The decrease in levels of phenolic metabolites such as cinnamate, ferulate, and gallic acid in the roots may reflect a shift in priorities in which roots prioritize structural mechanisms and water absorption over antioxidant protection. Conversely, leaves more exposed to light and environmental stress need more oxidative protection, so the increase in these metabolites in leaves seems to support these specific needs. This adaptation mechanism is supported by other studies showing that metabolite distribution can differ between organs to optimize adaptive responses to environmental stresses (Yang *et al.* 2018). In a drought-stressed involving five oil palm seedling accessions, SM accession adapts to drought stress better than other accessions through morphological and physiological supporting parameters. In addition, the oil palm showed an increase in proline production in response to drought stress. In addition, the MDA content in oil palm in drought conditions also increased. Analysis of metabolite profiles in oil palm seedlings exposed to six weeks of drought stress revealed that citramalate, L-tyrosine, ferulate, and 3-4-dihydroxybenzoate were the four most prevalent metabolites in the leaf. These metabolites are involved in the synthesis of valine, leucine, and isoleucine, as well as phenylpropanoid, ubiquinone, and other terpenoid quinones. The root produced more L-proline, aspartate, aconitate, kaempferol-3-o-pentoside, oxoadipate, citrate, L-phenylalanine, maltose, phenylacetic acid, and citramalate. These metabolites, primarily amino acids, carbohydrates, carboxylic acids, flavonoids, and tricarboxylic acids, have roles in at least six plant metabolic pathways.

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