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*Research Article*

# A metabolomics approach to identify fertilizer-efficient oil palm (*Elaeis guineensis* Jacq.) genotypes for marginal land cultivation

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**ABSTRACT**

The cultivation of oil palm on marginal lands is constrained by poor soil fertility, resulting in a strong dependence on expensive fertilizers. Developing genotypes with high nutrient use efficiency is therefore essential for sustainable production. This study employed a metabolomics approach to assess the performance of twelve oil palm genotypes (BGA100–BGA111) under fertilized and non-fertilized conditions. By integrating biomass allocation and metabolite profiling, genotype BGA103 was identified as displaying strong adaptive responses. Under nutrient-deficient conditions, BGA103 maintained a favorable shoot-to-root ratio and a relatively stable metabolite profile, suggesting efficient nutrient utilization. Genotypes BGA102, BGA107, and BGA109 also exhibited adaptive potential, though to a lesser extent. Several metabolic pathways, including steroid and fatty acid biosynthesis, were significantly influenced by fertilization, while metabolites such as tocopherol and neophytadiene emerged as promising indicators of nutrient status. These findings provide a biochemical basis for selecting and breeding oil palm varieties suited for low-input cultivation on marginal lands, contributing to more cost-effective and environmentally sustainable production systems.

***Keywords*:** Marginal lands; metabolomics; oil palm genotypes; nutrient-deficient; sustainable Agriculture

## Introduction

As the world's largest palm oil producer, Indonesia's economy heavily relies on the oil palm (*Elaeis guineensis* Jacq.) industry, which supplies global food, cosmetic, and bio-energy markets(MPOB,2020).To meet rising global demand and maintain economic competitiveness, enhancing plantation productivity and efficiency is a national priority. However, this ambition faces a significant obstacle: the increasing use of marginal lands for cultivation. These lands, characterized by low soil fertility, demand intensive fertilization to achieve viable yields, creating substantial economic and environmental pressures. With fertilizer costs accounting for upto 60% of total operational expenses, strategies to reduce this dependency are urgently needed for the industry's long-term sustainability (Khatiwada *et al*., 2018; Zuhdi *et al*., 2021).

In response to various challenges faced in the field, several innovations and technologies have been introduced in the palm oil industry (Murphy *et al*., 2021).The primary aim is to increase productivity and maximize the utilization of available resources. However,



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beyond merely increasing the yields, sustainability efforts are also a major focus. This is reflected in the policies implemented, which aim not only to reduce negative environmental impacts but also to enhance social welfare in the vicinity of oil palm plantations (Abubakar *et al*., 2023).

One of the main challenges faced by oil palm plantation companies in Indonesia is the management of marginal lands (Fairhurst and Griffiths, 2014). Marginal lands, often characterized by low or poor soil fertility, pose a significant constraint to increase productivity and efficiency in plantations (Ahmadzai *et al*., 2022). Sub-optimal soil characteristics on marginal lands, such as limited nutrient availability and poor soil structure, hinder the growth of oil palm plants. These plants require optimal soil conditions for healthy growth, including sufficient nutrient availability and adequate soil structure for optimal root growth (Paramananthan, 2013). In practice, managing marginal lands requires additional efforts, especially in terms of intensive fertilizer application to achieve optimal growth of oil palm plants (Hidayat *et al*., 2023). Intensive application of fertilizers is necessary to compensate for the low nutrient availability in marginal soils and ensure that plants receive the necessary nutrients for optimal growth (Fairhurst and Griffiths, 2014).

The high cost of fertilizer application in the Indonesian oil palm industry is a significant economic aspect that demands serious attention. Fertilization, as a crucial stage in crop management, not only requires significant financial investment but also affects the overall profitability of companies. According to recent research, the cost of fertilization can account for 30-60% of the total operational costs of oil palm plantation companies (Saleh *et al.*,2018; USDA, 2021).This significant cost percentage indicates that fertilization has substantial economic impacts and considerably drains the financial resources of companies (Goh *et al*., 2016). Therefore, fertilizer strategies tailored to the specific needs of plants and soil conditions become essential in optimizing operational cost efficiency.

In efforts to address the challenge of high fertilization costs, companies in the oil palm plantation sector have begun directing their efforts towards developing oil palm varieties resistant to low nutrient conditions. These varieties, known as "stay green," stand out for their ability to continue growing and producing well even under limited nutrient conditions. The concept of "stay green" refers to plants that maintain green leaves and actively perform photosynthesis for as long as possible, even under nutrient stress conditions (Kamal *et al*., 2019). Research has shown that "stay green" genotypes have better adaptations to environments with low nutrient resources (Jaegglia *et al*., 2017; Zhang *et al*., 2019). These plants tend to be more efficient in utilizing available nutrients and have internal mechanisms to cope with nutrient deficiencies. The"stay green"concept reflects the physiological and genetic adaptations of plants to unfavorable environmental conditions. The mechanisms involved in this adaptation include hormonal regulation, carbohydrate metabolism, and plant stress responses. Thus, the use of "stay green" varieties can reduce dependence on intensive fertilization, which in turn can lower overall production costs (Christopher *et al*., 2016; Antonietta *et al*., 2016; Riache *et al*., 2023).To enhance the sustainability of the Indonesian oil palm industry, reducing the significant financial burden of fertilization is critical. This research focuses on identifying nutrient-efficient "stay-green" oil palm varieties as a potential solution.Weevaluated10genotypes under both fertilized and non-fertilized conditions using a metabolomics approach. This approach allows for a holistic characterization of metabolic compounds and path ways involved in plant adaptation to low-nutrien stress(Kumar *et al*., 2017; Roychowdhury *et al*., 2023; Baker *et al*., 2023). While the "stay-green" concept is promising, its underlying biochemical

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Journal of Plantation Crops, 2025, 53 (1):10-21

mechanisms in oil palm remain poorly understood. Our study's novelty is the application of non-targeted metabolomics to dissect this metabolic reprogramming. This moves beyond traditional methods by providing a biochemical fingerprint of resilience, which can significantly accelerate the development of elite, cost-effective oil palm cultivars.

## Materials and methods

### Plant material and growth conditions

This study was conducted at the main nursery of Bumitama GunajayaAgro, located in the Pundu Region, Central Kalimantan, Indonesia. The site is characterized by Ultisol soil, which is typically acidic and low in nutrient content, representing marginal land conditions common in oil palm cultivation areas. Irrigation was maintained through a semi-manual system to ensure adequate but non-saturated soil moisture throughout the study period. The twelve genotypes used in this study (BGA100–BGA111) are part of Bumitama Gunajaya Agro's proprietary collection, derived from selected Dura × Pisifera crosses known for their varying responses to environmental conditions. Seedlings were individually planted in poly bags and maintained under standard nursery conditions for 36 weeks before evaluation**.**

### Experimental design and treatments

The experiment followed a nested design with three replications. The main treatment factor consisted of two fertilization levels: fertilized and non-fertilized. The nested factor within each fertilization level was the twelve oil palm genotypes. Each experimental unit (genotype within a treatment level) consisted of ten plants, ensuring robust data collection. Fertilized plants received NPK 12-12-12 at a rate of 50 g per plant and Kieserite at 25 g per plant, following standard nursery practices. The non-fertilized group received no nutrient supplementation during the experimental period.

### Biomass measurement and sample collection

After 36 weeks of treatment, plant samples were harvested for analysis. The plants were carefully separated into roots and shoots. To determine the dry weight(DW),the root and shoot samples were dried in an oven at 60°C for 36 hours until a constant weight was achieved. The shoot-to-root dry weight ratio was subsequently calculated. For metabolomic analysis, 10 grams of fully expanded leaves were collected from each treatment unit.

### Metabolite extraction and GC-MS analysis

Metabolite extraction followed the protocol described by Adrian *et al*. (2024) with minor modifications. Leaf samples were collected from three biological replicates per treatment, oven-dried, and finely ground. Approximately 100 mg of powdered tissue was macerated in absolute methanol for five days to extract semi-polar metabolites. To enhance extraction efficiency, the mixture was subjected to ultrasonication for 60 minutes at 60 °C. The resulting crude extracts were filtered and prepared for analysis. Profiling was performed using a Gas Chromatography–Mass Spectrometry (GC–MS) system (Agilent Technologies 7890A/G3440A–5975C). Separation was achieved using an HP-5ms non-polar capillary column (30 m × 0.25 mm, 0.25 µm film thickness), which is suitable for a broad range of semi-volatile compounds. Instrumental parameters followed standard settings for temperature programming, ionization, and carrier gas flow as described in Halim *et al*. (2019).

### Data processing and statistical analysis

Raw GC–MS data were first inspected for peak integrity and consistency across replicates. Compounds were identified by comparing the obtained mass spectra with reference databases, including NIST, ChEBI, PubChem, and ChemSpider (Degtyarenko *et al*.,2007; Pence and Williams, 2010). Prior to statistical analysis, data were subjected to a multi-step normalization and quality control

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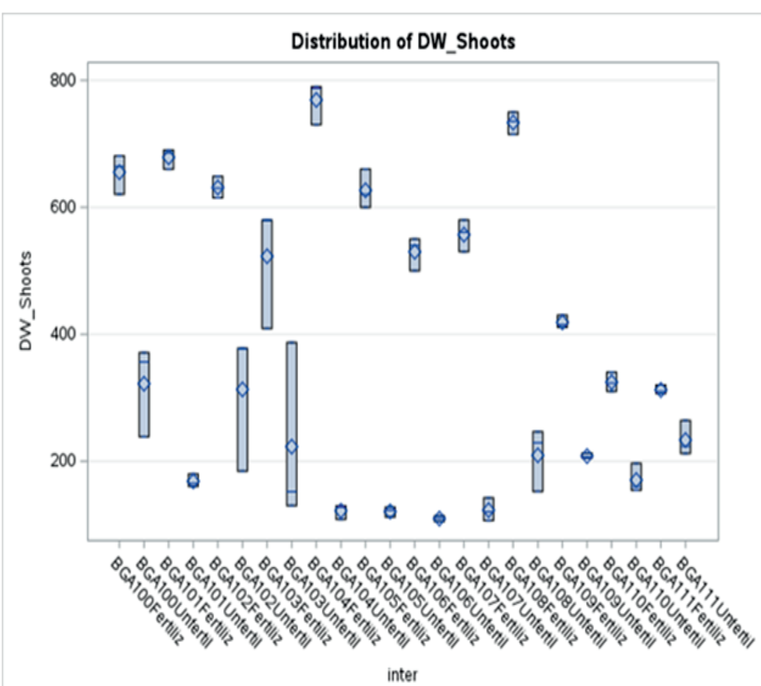
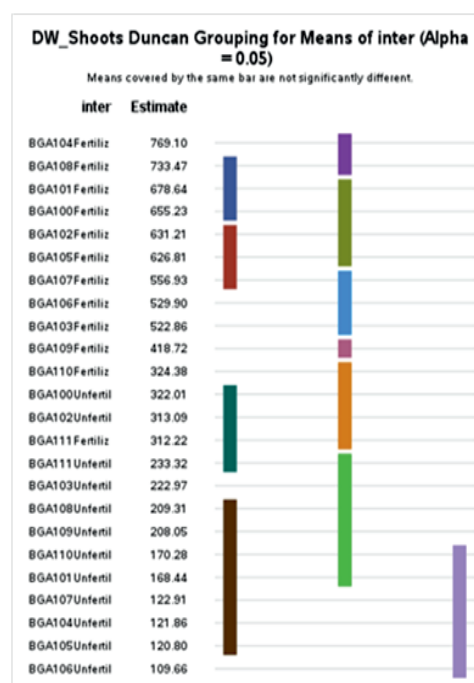
process. Peaks with signal-to-noise ratios below 10 were removed, followed by median normalization, $log_{10}$ transformation, and auto-scaling to reduce heteroscedasticity.Biomass data were analyzed using Duncan's Multiple Range Test ($\alpha$ = 0.05) to identify significant differences among treatments. Processed metabolomic data were further analyzed through multivariate approaches, including hierarchical clustering and heatmap visualization. To assess the discriminatory power of key metabolites, a Receiver Operating Characteristic (ROC) curve analysis was performed using MetaboAnalyst 5.

## Results and Discussion

### Biomass allocation: root and shoot dry weight analysis

The allocation of biomass between roots and shoots provides valuable insights into a plant's growth performance and resource-use strategy. As illustrated in the boxplot analysis (Figure 1), fertilization consistently increased both root dry weight (DW Roots) and shoot dry weight (DW Shoots). This response likely reflects the improved availability of essential macronutrients—particularly nitrogen, phosphorus, and potassium—which are vital for root proliferation, water and nutrient acquisition, and overall plant vigor (Marschner, 2012; Fageria and Moreira, 2011; De la Peña *et al*., 2023, 2024). Enhanced nutrient supply also supports greater photosynthetic capacity and shoot biomass accumulation (Taiz and Zeiger, 2020), whereas nutrient limitation can constrain growth and reduce stress tolerance (Mareri *et al*., 2022).



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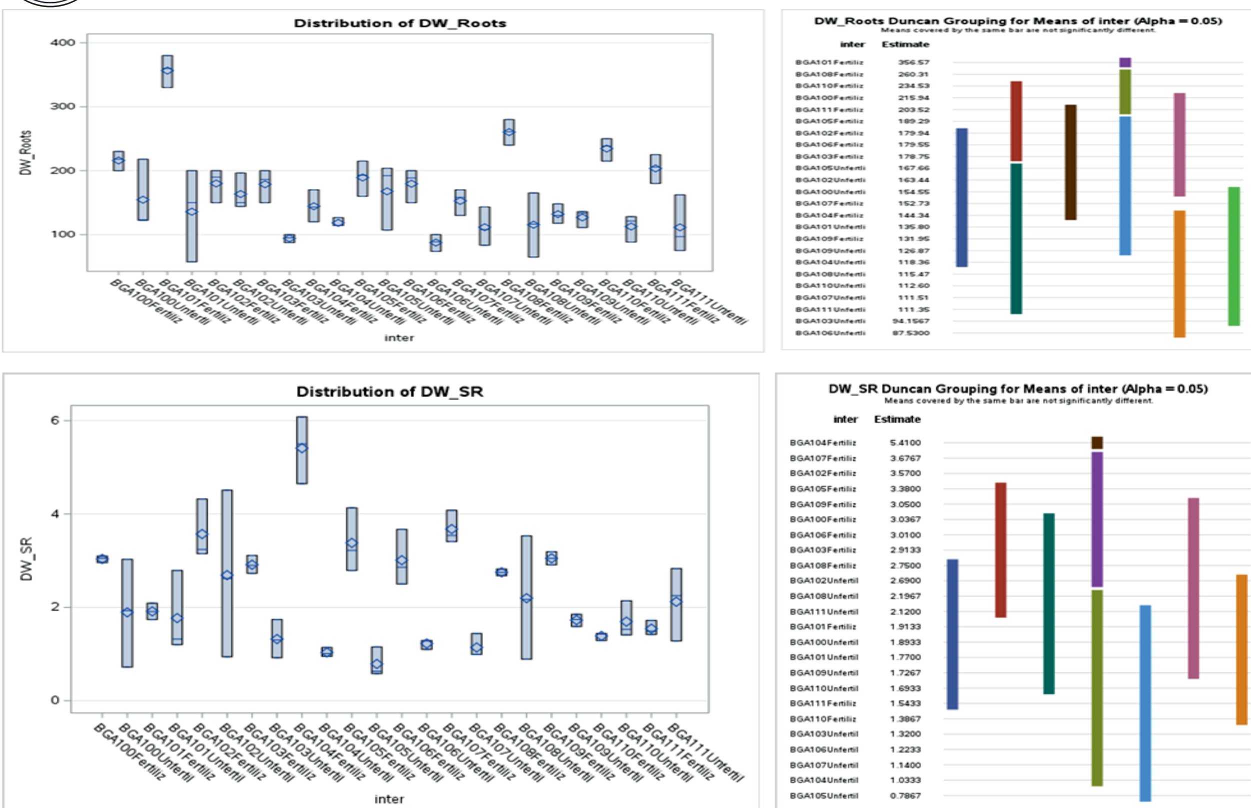


*Fig. 1. Boxplot showing biomass allocation, expressed as root and shoot dry weight. Different letters indicate significant differences according to Duncan's multiple range test.*

Significant genotypic variation was observed in biomass allocation patterns. Several genotypes, including BGA102, BGA107, BGA104, and BGA109, maintained relatively stable root dry weights across fertilization treatments, suggesting potential suitability for cultivation under reduced-input systems. In contrast, only BGA111 exhibited comparable stability in shoot dry weight. The shoot-to-root dry weight ratio (DW_SR), a key indicator of resource allocation efficiency, further distinguished the genotypes. According to Duncan's Multiple Range Test (Figure 1), BGA104 displayed the highest DW_SR (≈5.41) under fertilization, reflecting strong responsiveness to nutrient availability. However, for assessing adaptation to nutrient-limited environments, performance under unfertilized conditions is more informative. In this context, BGA103 exhibited a relatively high DW_SR (≈2.75) even without fertilizer input.

The consistent performance of BGA103 under nutrient-deficient conditions suggests a degree of physiological plasticity and efficient nutrient utilization. Such traits are commonly associated with improved root architecture and coordinated metabolic mechanisms that sustain productivity under low-nutrient stress (Li *et al.*, 2016; Ali *et al.*, 2018; Iqbal *et al.*, 2019, 2023; Lai *et al.*, 2024). While these observations indicate that BGA103 may possess adaptive features advantageous for marginal land cultivation, further evaluation across developmental stages and environments is needed to confirm its stability and potential breeding value.

### Fertilization alters the distribution and chemical composition of metabolites

A comparative analysis of metabolite profiles revealed that nutrient availability influences the metabolic strategy of oil palm. The results indicate distinct patterns in both the distribution and chemical nature of metabolites produced under fertilized and unfertilized conditions.

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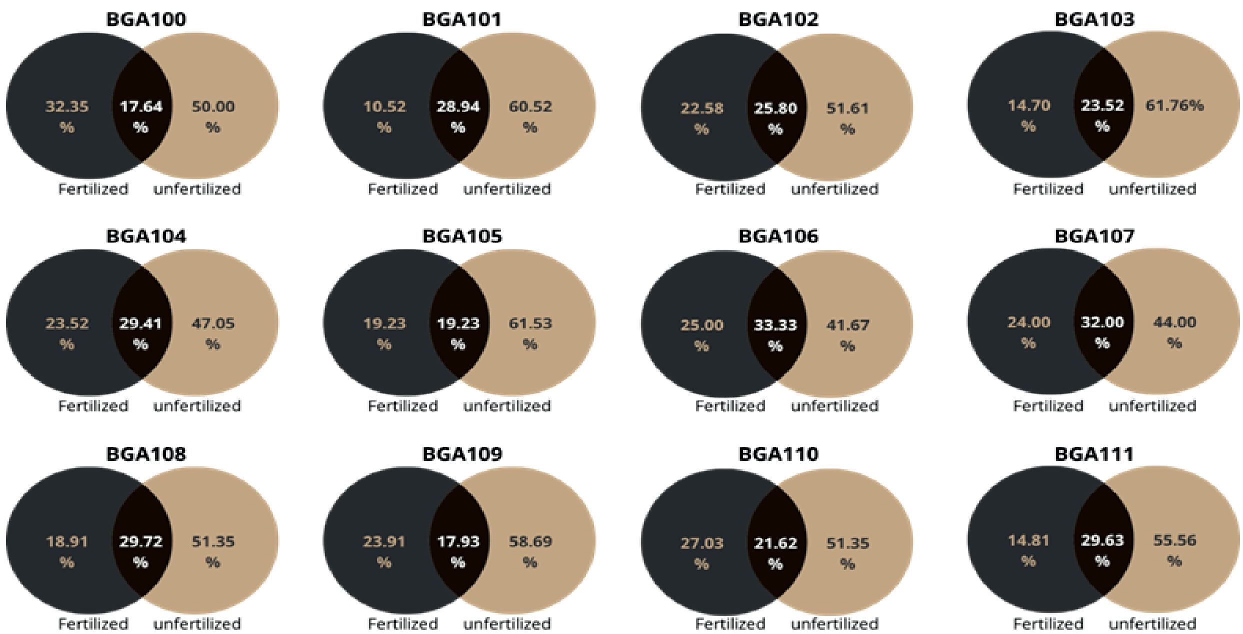


*Fig. 2. Venn diagram comparing metabolite profiles of fertilized and unfertilized treatments across 12 oil palm genotypes.*

As illustrated by the Venn diagrams in Figure 2, three major metabolite groups were identified. First, a relatively high proportion of metabolites—ranging from 44.00% to 61.76%—was detected exclusively under unfertilized conditions. This pattern suggests that nutrient limitation may induce metabolic adjustments that promote the accumulation of compounds potentially involved in stress response and resource conservation (Pandey *et al.,* 2021; Kouame *et al*., 2024). Second, a smaller yet distinct set of metabolites (10.52% to 32.35%) was found only under fertilized conditions, indicating that nutrient sufficiency can activate additional biosynthetic routes associated with growth and developmental processes (Reshi *et al*., 2023). Finally, a core group of overlapping metabolites (17.64% to 33.33%) was detected in both treatments, representing essential "housekeeping" pathways that remain active regardless of nutrient status (Cadena-Zamudio *et al*., 2023).

Further examination of chemical composition (Figure 3) provided additional insights into these metabolic trends. Under fertilized conditions, the categories *"Lipids and lipid-like molecules"* and *"Organonitrogen compounds"* were relatively more abundant, reflecting a tendency toward the production of molecules essential for cellular function, energy storage, and biosynthesis of nitrogen-based building blocks such as amino acids, proteins, and nucleotides (Zayed *et al*., 2023). In contrast, differences were also observed in *"Benzenoids"* and *"Organic acids and derivatives"*, which are commonly linked to defense metabolism, pollinator signaling, and energy balance (Picazo-Aragonés *et al*., 2020).

Overall, these findings indicate that fertilization modulates the synthesis and diversity of secondary metabolites in oil palm. Such metabolic adjustments appear to reflect a balance between growth-oriented and stress-responsive pathways, emphasizing the importance of considering genotype-specific responses when developing nutrient management strategies aimed at improving plant performance under varying soil fertility conditions.

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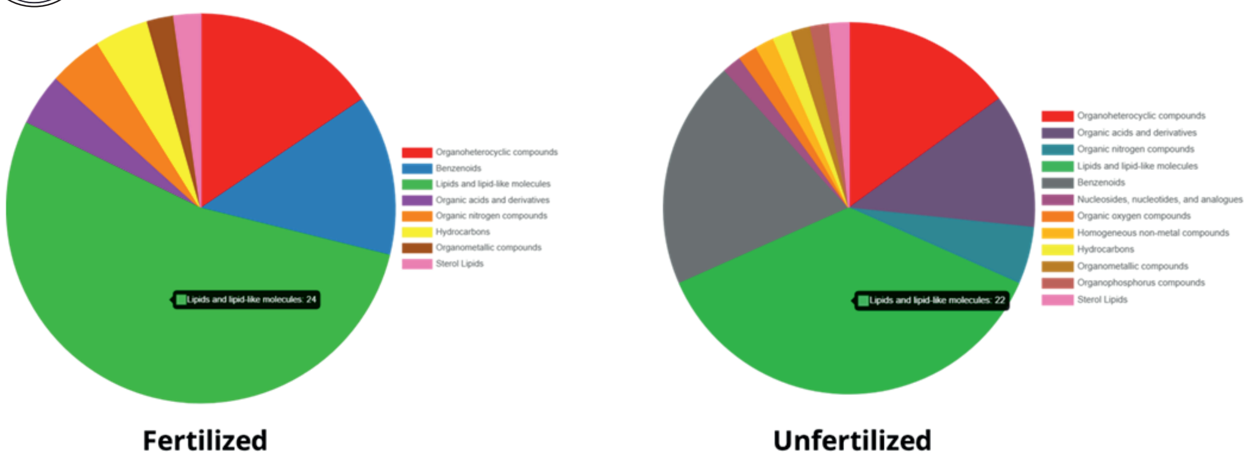
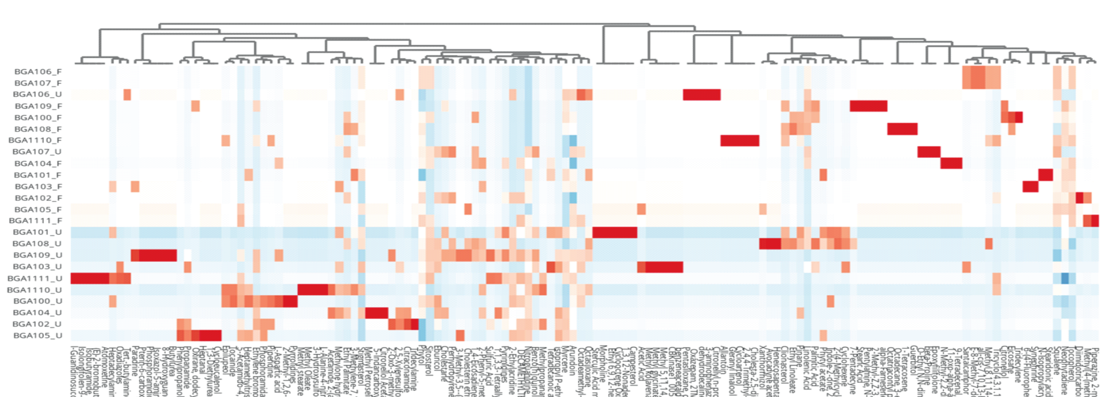



*Fig. 3. Distribution of compound types identified under fertilized and unfertilized conditions*

**Clustering of Secondary Metabolite Variations Among Different Oil Palm Genotypes Under Fertilization Treatments**

Hierarchical clustering analysis, visualized as a heatmap in Figure 4, revealed clear genotype-by-fertilization interactions influencing the secondary metabolome of oil palm. The analysis segregated the genotypes into two main groups according to their metabolic responses to nutrient availability. The first cluster comprised genotypes BGA106, BGA107, and BGA108, which showed minimal separation between fertilized and unfertilized samples. This pattern suggests that their secondary metabolite compositions were relatively stable and only slightly affected by fertilization. Such consistency highlights the dominant role of genetic background in determining metabolic homeostasis under varying nutrient conditions, aligning with previous reports that nutrient-related metabolic responses are largely genotype-dependent (Hirel *et al.,* 2007; Francis *et al.*, 2023).

In contrast, the second and larger cluster—including BGA103 and BGA102—displayed pronounced separation between fertilized and unfertilized samples. This indicates greater metabolic flexibility, where nutrient availability appears to act as a regulatory signal modulating secondary metabolism. Notably, BGA103 maintained consistent performance across treatments, suggesting a capacity for metabolic adjustment that may contribute to its superior performance under nutrient limitation. However, this observation should be interpreted cautiously as it derives from nursery-scale data (36 weeks), which may not fully represent field-level responses.



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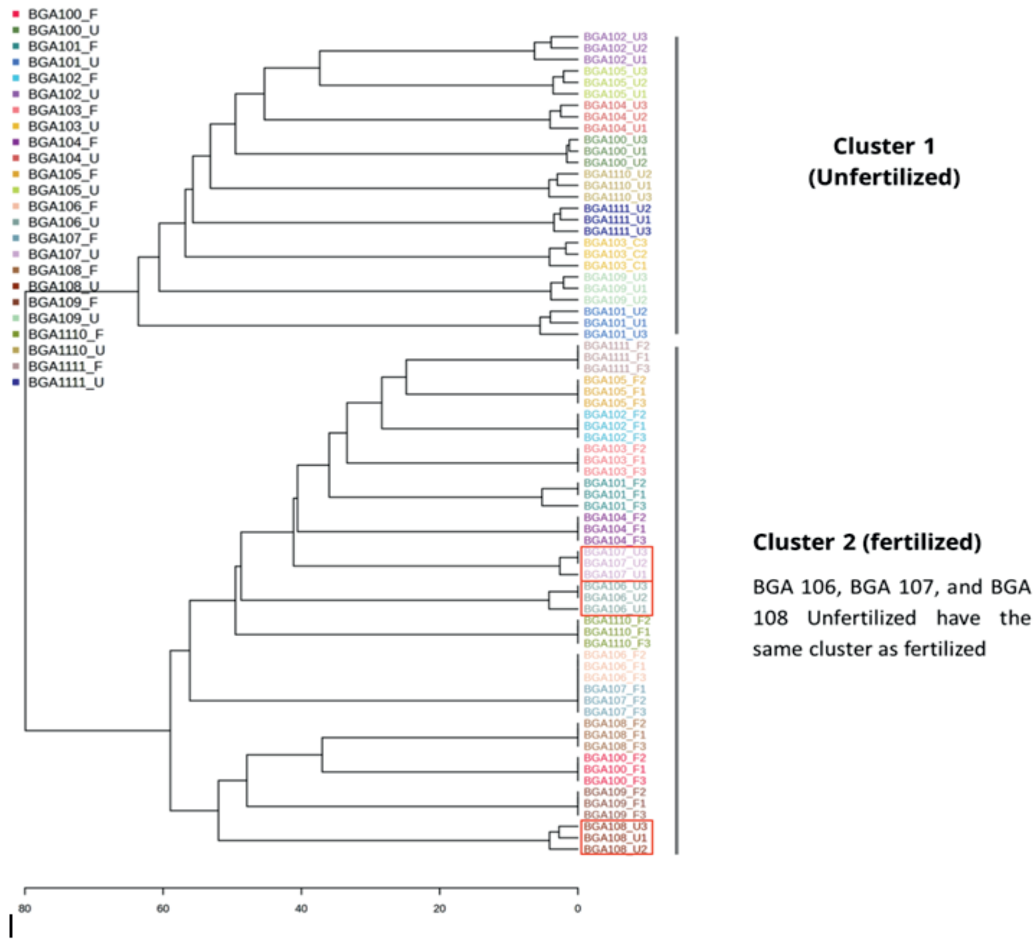


*Fig. 4. Heatmap visualization and hierarchical clustering of metabolite profiles in fertilized and unfertilized treatments across 12 oil palm genotypes.*

Additionally, the column dendrogram clustering individual metabolites revealed co-expression among groups of related compounds, implying coordinated regulation within shared biosynthetic or signaling pathways. Such clustering patterns provide valuable insight into the molecular basis of genotype-specific nutrient responses. Collectively, these findings underscore the metabolic diversity among oil palm genotypes and support the need for genotype-tailored nutrient management strategies to optimize productivity under different soil fertility regimes.

**Analyzing discriminatory biomarkers: ROC curve analysis**

To identify metabolites that effectively differentiate between fertilized and unfertilized conditions, a Receiver Operating Characteristic (ROC) curve analysis was conducted, with representative results for two key compounds shown in Figure 5. This analysis evaluated the diagnostic accuracy of each metabolite using the Area Under the Curve (AUC).

Tocopherol exhibited a high AUC value of 0.992 (95% Confidence Interval: 0.973–1.000), indicating strong discriminatory capacity between the two treatments. At a selected coordinate, 90% sensitivity (True Positive Rate) was achieved with a low 7.7% False Positive Rate (1–Specificity). The accompanying box plot confirmed this separation, showing higher and more consistent tocopherol levels in fertilized samples. These results are biologically plausible, as nutrient availability has been associated with enhanced tocopherol accumulation that contributes to

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Journal of Plantation Crops, 2025, 53 (1):10-21


stress tolerance (Ghosh *et al.*, 2022). Nonetheless, tocopherol should be regarded as a promising rather than definitive biomarker until validated across broader environmental conditions and developmental stages.

Similarly, neophytadiene demonstrated good discriminatory performance with an AUC of 0.924 (95% CI: 0.845–0.970), achieving 90% sensitivity at a 23.0% False Positive Rate. Its levels were also significantly higher under fertilized conditions, consistent with reports that fertilization can modulate the production of defense-related secondary metabolites (Adeosun *et al.*, 2017). Taken together, both metabolites appear to serve as potential biochemical indicators of nutrient status in oil palm, with tocopherol showing the most consistent response under the conditions tested.

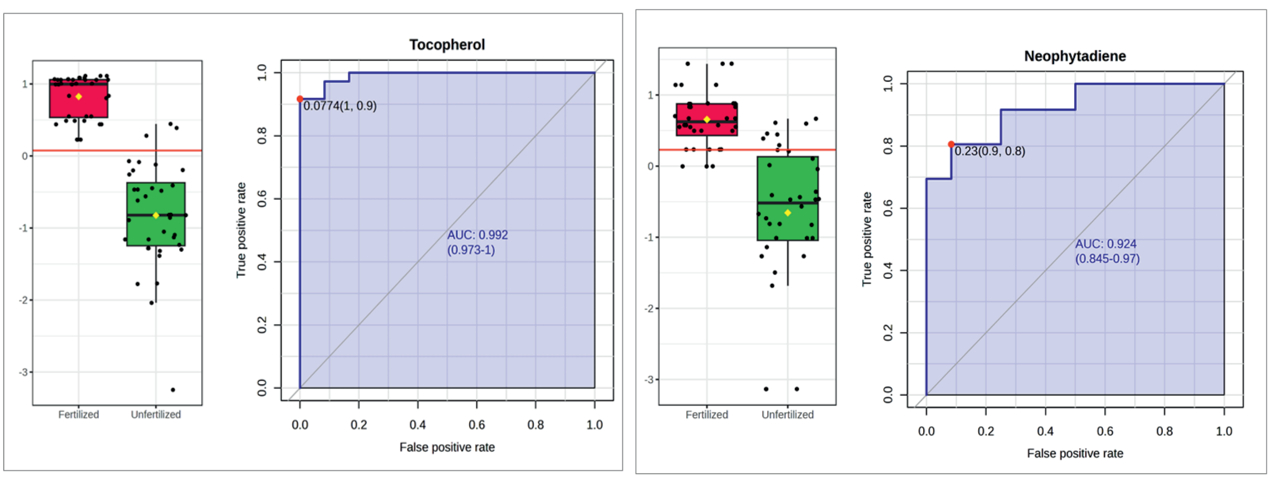


*Fig. 5. Receiver operating characteristic (ROC) analysis of tocopherol and neophytadiene as candidate biomarkers under fertilized and unfertilized conditions*

## Fertilization reprograms metabolic pathways in oil palm

Metabolic pathway analysis provided a comprehensive view of how fertilization influences cellular processes in oil palm. As visualized in Figure 6, the results suggest a potential functional shift in the plant's metabolic priorities, from predominantly "defense and maintenance" under nutrient deficiency to "growth and production" under nutrient sufficiency. Under fertilized conditions, several biosynthetic pathways associated with growth and lipid metabolism showed increased activity. The most notably up-regulated pathways included *steroid biosynthesis*, *unsaturated fatty acid biosynthesis*, and *fatty acid biosynthesis*. These trends indicate that adequate nutrient supply may enhance the operation of core metabolic routes responsible for lipid formation, membrane development, and precursor molecules for oil synthesis—the key economic product of oil palm (Alzain *et al.,* 2023).

Conversely, under nutrient-deficient conditions, pathways related to stress response and resource conservation were relatively more active. This included the up-regulation of *monobactam biosynthesis*, a pathway linked to antimicrobial compound production, suggesting a possible shift toward defensive metabolism. Adjustments in amino acid and sulfur metabolism were also observed, which may reflect strategies for maintaining essential cellular functions when nutrients are limited. Interestingly, certain core pathways such as *fatty acid biosynthesis* remained active across both nutrient regimes, implying that vital metabolic processes are maintained even under suboptimal conditions. This observation highlights the

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Journal of Plantation Crops, 2025, 53 (1):10-21

inherent capacity of oil palm seedlings to sustain essential functions despite nutritional constraints, consistent with general plant survival strategies described by Marschner (2012).Understanding these context-dependent metabolic adjustments is essential for designing fertilization strategies that balance productivity with physiological stability—maximizing yield while supporting the plant's intrinsic adaptive mechanisms.

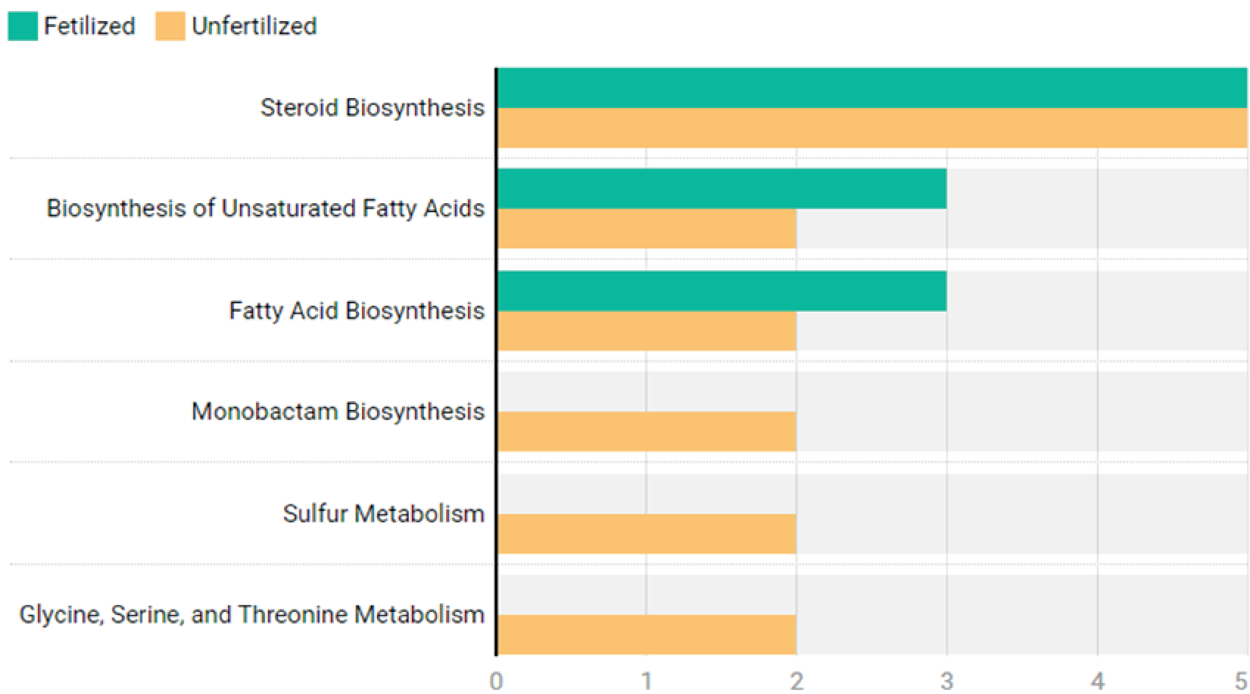


*Fig. 6. Comparative pathway analysis of metabolites under fertilized and unfertilized conditions.*

## Limitations of the Study

This study has several limitations inherent to its metabolomics-focused design. First, as the primary goal was to characterize the metabolic signatures of nutrient efficiency, the physiological assessment relied mainly on biomass allocation. It is acknowledged that future studies would be significantly strengthened by integrating our metabolic findings with a broader range of vegetative parameters (e.g., plant height, LAI) to establish a more direct link between specific metabolites and whole-plant agronomic performance. Second, this study did not include soil or tissue nutrient analysis. While our metabolomic data strongly indicates differential responses, incorporating direct nutrient measurements in future work would provide a definitive mechanistic link between nutrient uptake and the observed metabolic shifts.

## Conclusion

This study identified the oil palm genotype BGA103 as a promising candidate for cultivation under nutrient-limited conditions. This genotype exhibited *stay-green* characteristics, a favourable shoot-to-root ratio, and stable biomass accumulation even in the absence of fertilization. These traits suggest an adaptive physiological capacity supported by distinct metabolic adjustments, including the activation of defense-associated pathways under nutrient stress. Other genotypes, such as BGA102, BGA107, and BGA109, also showed adaptive tendencies, though to a lesser extent. Additionally, tocopherol (AUC = 0.992) emerged as a strong candidate biomarker for assessing plant nutritional status, demonstrating consistent differentiation between fertilized and unfertilized treatments. However, further validation across developmental stages and environmental conditions is required to confirm its reliability as a universal indicator. Collectively, these findings highlight both a promising genetic resource (BGA103) for breeding programs and a potential biochemical marker (tocopherol) to support the selection of nutrient-efficient oil palm genotypes, contributing to more sustainable and resource-efficient cultivation systems.

### Availability of data and material

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request

### Competing interests

The authors declare that they have no competing interests

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This research was conducted as part of an internal project and received full financial support from the BumitamaGunajayaAgro Company

### Authors' contributions

A.A. designed the study, wrote the manuscript. M.A. analyzed the data, wrote the manuscript.B.N., R.W., S.D.T. provided technical assistance. All authors read and approved the finalmanuscript

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## References

Abubakar, A., Kasim, S. and Ishak, M.Y. 2023. Maximizing oil palm yield: Innovative replanting strategies for sustainable productivity. *Journal of Environmental and Earth Sciences;* **5(2):** 61-75.

Adeosun, T.E., Ogunwande, I.A., Avoseh, O.N., Raji, I.P. and Lawal, O.A. 2017. Composition and anti-inflammatory activity of essential oil of *Jatropha curcas*. *Natural Product Communications;* **12**: 439-440.

Adrian, M., Wulandari, R., Sembiring, E. and Natawijaya, A. 2024. Metabolomic profiling unravels divergent adaptive responses of oil palm (*Elaeis guineensis*) seedlings to drought stress under shaded and unshaded conditions. *Biodiversitas;* **25(6):** 2404-2414.

Ahmadzai, H., Tutundjian, S., Dale, D., Brathwaite, R., Lidder, P., Selvaraju, R., Malhotra, A., Boerger, V. and Elouafi, I. 2022. *Marginal lands: potential for agricultural development, food security and poverty reduction*. FAO, Rome.

Ali, J., Jewel, Z.A., Mahender, A., Anandan, A., Hernandez, J. and Li, Z. 2018. Molecular genetics and breeding for nutrient use efficiency in rice. *International Journal of Molecular Sciences;* **19(6)**: 1762.

Alzain, M.N., Loutfy, N. and Aboelkassem, A. 2023. Effects of different kinds of fertilizers on the vegetative growth, antioxidative defense system and mineral properties of sunflower plants. *Sustainability;* **15(13):** 10072.

Antonietta, M., Acciaresi, H.A. and Guiamet, J.J. 2016. Responses to N deficiency in stay green and non-stay green Argentinean hybrids of maize. *Journal of Agronomy and Crop Science;* **202**: 231-242.

Baker, C.R., Patel-Tupper, D., Cole, B.J., Ching, L.G., Dautermann, O., Kelikian, A.C., Allison, C., Pedraza, J., Sievert, J., Bilbao, A., Lee, J.Y., Kim, Y.M., Kyle, J.E., Bloodsworth, K.J., Paurus, V., Hixson, K.K., Hutmacher, R., Dahlberg, J., Lemaux, P.G. and Niyogi, K.K. 2023. Metabolomic, photoprotective, and photosynthetic acclimatory responses to post-flowering drought in sorghum. *Plant Direct;* **7(11):** e545.

Cadena-Zamudio, J.D., Monribot-Villanueva, J.L., Pérez-Torres, C.A., Alatorre-Cobos, F., Guerrero-Analco, J.A. and Ibarra-Laclette, E. 2023. Non-targeted metabolomic analysis of *Arabidopsis thaliana* (L.) heynh: metabolic adaptive responses to stress caused by N starvation. *Metabolites;* **13(9):** 1021.

Christopher, J.T., Christopher, M.J., Borrell, A.K., Fletcher, S. and Chenu, K. 2016. Stay-green traits to improve wheat adaptation in well-watered and water-limited environments. *Journal of Experimental Botany;* **67(17):** 5159-5172.

De la Peña, M., Ruiz-Romero, R. and Romero, H.M. 2023. Nitrogen use efficiency in oil palm seedlings: unraveling the untapped potential of elevated external ammonium supply. *Plants;* **12:** 2819.

De la Peña, M., Ruiz-Romero, R., Castro-Arza, L.I. and Romero, H.M. 2024. Changes in the root architecture of oil palm seedlings in response to nitrogen starvation. *Agronomy;* **14:** 409.

Degtyarenko, K., de Matos, P., Ennis, M., Hastings, J., Zbinden, M., McNaught, A., Alcántara, R., Darsow, M., Guedj, M. and Ashburner, M. 2007. ChEBI: A database and ontology for chemical entities of biological interest. *Nucleic Acids Res;* **36:** D344-D350.

Fageria, N.K. and Moreira, A. 2011. The role of mineral nutrition on root growth of crop plants. *Advances in Agronomy;* **110**: 251-331.

Fairhurst, T.H. and Griffiths, W. 2014. No tillage, residue management and replanting. In: *Achieving sustainable cultivation of oil palm*. Burleigh Dodds Science Publishing, Cambridge, UK. pp. 1-24.

Francis, B., Aravindakumar, C.T., Brewer, P.B. and Simon, S. 2023. Plant nutrient stress adaptation: A prospect for fertilizer limited agriculture. *Environmental and Experimental Botany;* **213**: 105431.

Ghosh, U.K., Hossain, M.S., Islam, M.N. and Khan, M.A.R. 2022. Role of tocopherol in conferring abiotic stress tolerance in plants. In: *Antioxidant Defense in Plants: Molecular Basis of Regulation*. Springer Nature, Singapore. pp. 215-233.

Goh, K.J., Hardter, R. and Fairhurst, T.H. 2016. Enhancing nutrient use efficiency in oil palm cultivation: Improving fertilizer management through best management practices. *Oil Palm Industry Economic Journal;* **16(2):** 1-12.

Halim, H.R., Hapsari, D.P., Junaedi, A., Ritonga, A.W., Natawijaya, A., Poerwanto, R., Sobir, Widodo, W.D., Matra, D.D. 2019. Metabolomics dataset of underutilized Indonesian fruits; rambai (Baccaureamotleyana), nangkadak (Artocarpus nangkadak), rambutan (Nephelium lappaceum) and Sidempuansalak (Salaccasumatrana) using GCMS and LCMS.*Data in Brief.* **6(23):**103706.

Hidayat, F., Yudhistira, Y., Desika Putri Pane, R., Sapalina, F., Listia, E., Amalia, R., Muhayat, M. and Winarna, W. 2023. Biofertilizer application to enhance the oil palm growth and productivity. *Jurnal Penelitian Kelapa Sawit;* **31(2):** 96-107.

Hirel, B., Le Gouis, J., Ney, B. and Gallais, A. 2007. The challenge of improving nitrogen use efficiency in crop plants: towards a more central role for genetic variability and quantitative genetics within integrated approaches. *Journal of Experimental Botany;* **58(9):** 2369-2387.

Iqbal, A., Gui, H., Zhang, H., Wang, X., Pang, N., Dong, Q. and Song, M. 2019. Genotypic variation in cotton genotypes for phosphorus-use efficiency. *Agronomy;* **9**: 689.

Jaegglia, B.G., Mortlockb, M.Y. and Borrell, A. 2017. Bigger is not always better: Reducing leaf area helps stay-green sorghum use soil water more slowly. *Environmental and Experimental Botany;* **138**: 119-129.

Kamal, N.M., Alnor Gorafi, Y.S., Abdelrahman, M., Abdellatef, E. and Tsujimoto, H. 2019. Stay-green trait: a prospective approach for yield potential, and drought and heat stress adaptation in globally important cereals. *International Journal of Molecular Sciences;* **20(23):** 5837.

Khatiwada, D., Palmén, C. and Silveira, S. 2018. Evaluating the palm oil demand in Indonesia: production trends, yields, and emerging issues. *Biofuels;* **12(2):** 135-147.

Kouame, K.P., Agrahari, R.K., Konjengbam, N.S., Koyama, H. and Kobayashi, Y. 2024. Ability of nutrient management and molecular physiology advancements to overcome abiotic stress: A study on sub-Saharan African crops. *Agriculture;* **14:** 285.

Kumar, R., Bohra, A., Pandey, A.K., Pandey, M.K. and Kumar, A. 2017. Metabolomics for plant improvement: status and prospects. *Frontiers in Plant Science;* **8**: 1302.

Lai, Z., Zhang, H., Ding, X., Liao, Z., Zhang, C., Yu, J., Pei, S., Dou, Z., Li, Z. and Fan, J. 2024. Ridge-furrow film mulch with nitrogen fertilization improves grain yield of dryland maize by promoting root growth, plant nitrogen uptake and remobilization. *Soil and Tillage Research;* **241**: 106118.

Li, X., Zeng, R. and Liao, H. 2016. Improving crop nutrient efficiency through root architecture modifications. *Journal of Integrative Plant Biology;* **58**: 193-202.

Malaysian Palm Oil Board (MPOB). 2020. *Malaysian Palm Oil Statistics 2020*. MPOB, Kuala Lumpur, Malaysia.

Mareri, L., Parrotta, L. and Cai, G. 2022. Environmental stress and plants. *International Journal of Molecular Sciences;* **23(10):** 5416.

Marschner, H. 2012. *Marschner's Mineral Nutrition of Higher Plants*. Academic Press, California, US. pp. 100-204.

Murphy, D.J., Goggin, K. and Paterson, R.R.M. 2021. Oil palm in the 2020s and beyond: challenges and solutions. *CABI Agriculture and Bioscience;* **2**: 39.

Pandey, R., Vengavasi, K. and Hawkesford, M.J. 2021. Plant adaptation to nutrient stress. *Plant Physiology Reports;* **26**: 583-586.

Paramananthan, S. 2013. Managing marginal soils for sustainable growth of oil palms in the tropics. *Journal of Oil Palm and the Environment;* **4(1):** 1-16.

Pence, H.E. and Williams, A. 2010. ChemSpider: An online chemical information resource. *J Chem Educ;* **87(11):** 1123-1124.

Picazo-Aragonés, J., Terrab, A. and Balao, F. 2020. Plant volatile organic compounds evolution: Transcriptional regulation, epigenetics and polyploidy. *International Journal of Molecular Sciences;* **21(23):** 8956.

Reshi, Z.A., Ahmad, W., Lukatkin, A.S. and Javed, S.B. 2023. From nature to lab: A review of secondary metabolite biosynthetic pathways, environmental influences, and in vitro approaches. *Metabolites;* **13(8):** 895.

Riache, M., Djemel, A., Revilla, P., Malvar, R.A. and Mefti, M. 2023. Genetic analyses of stay green for tolerance to water stress and nitrogen deficiency in Algerian Saharan maize populations. *Euphytica;* **219**: 66.

Roychowdhury, R., Das, S.P., Gupta, A., Parihar, P., Chandrasekhar, K., Sarker, U., Kumar, A., Ramrao, D.P. and Sudhakar, C. 2023. Multi-omics pipeline and omics-integration approach to decipher plant's abiotic stress tolerance responses. *Genes;* **14(6):** 1281.

Saleh, S., Bagja, B., Suhawa, T.A. and Widyapratami, H. 2018. *Intensification by smallholder farmers is key to achieving Indonesia's palm oil targets*. World Resources Institute, Washington, United States.

Taiz, L. and Zeiger, E. 2020. *Plant Physiology and Development*. Sinauer Associates, Massachusetts, US. pp. 90-120.

United States Department of Agriculture (USDA). 2021. *Indonesia Oil Seeds and Product Annual Report*. Diakses dari: https://www.fas.usda.gov/data/indonesia-oilseeds-and-products-annual-5.

Zayed, O., Hewedy, O.A., Abdelmoteleb, A., Ali, M., Youssef, M.S., Roumia, A.F., Seymour, D. and Yuan, Z.C. 2023. Nitrogen journey in plants: From uptake to metabolism, stress response, and microbe interaction. *Biomolecules;* **13(10):** 1443.

Zhang, J., Fengler, K.A., John, L., Hemert, V., Gupta, R., Mongar, N., Sun, J., Allen, W.B. and Wang, Y. 2019. Identification and characterization of a novel stay-green QTL that increases yield in maize. *Plant Biotechnology Journal;* **17:** 2272-2285.

Zuhdi, D.A.F., Abdullah, M.F., Suliswanto, M.S.W. and Wahyudi, S.T. 2021. The competitiveness of Indonesian crude palm oil in international market. *Jurnal Ekonomi Pembangunan;* **19(1):** 111-124.