Indonesian Journal of Biotechnology

VOLUME 30(4), 2025, 210-216 | RESEARCH ARTICLE

Enzyme and hormone activities related to phosphorus uptake limitation in oil palm (*Elaeis guineensis* Jacq.)

Sigit Dwi Maryanto[1,2,*], Randi Abdur Rohman[2], Roberdi[2], Tri Rini Nuringtyas[3], Purnomo[3], Diah Rachmawati[3], Eka Tarwaca Susila Putra[4], Condro Utomo[2], Tony Liwang[2], Budi Setiadi Daryono[3,*]

[1]Doctoral Program, Department of Biology, Faculty of Biology, Universitas Gadjah Mada, Jl. Teknika Selatan, Sekip Utara, Sleman 55281, Yogyakarta, Indonesia
[2]Biotechnology Department, Plant Production and Biotechnology Division, PT SMART Tbk, Jl. Raya Cijayanti, Babakan Madang, Bogor 16810, West Java, Indonesia
[3]Faculty of Biology, Universitas Gadjah Mada, Jl. Teknika Selatan, Sekip Utara, Sleman 55281, Yogyakarta, Indonesia
[4]Faculty of Agriculture, Universitas Gadjah Mada, Jl. Flora, Bulaksumur, Yogyakarta 55281, Indonesia
*Corresponding author: sigit.dwi.m@mail.ugm.ac.id; bs_daryono@mail.ugm.ac.id

SUBMITTED 31 July 2025 **REVISED** 16 October 2025 **ACCEPTED** 16 October 2025

ABSTRACT Phosphorus (P) is an essential element for oil palm growth and development. Acid phosphatase (Apase) and Pti-interacting serine/threonine kinase are two enzymes which enzymes confirmed to be related to P-uptake in oil palm, therefore their activities in oil palm treated with P-limitation need to be quantified. Acid phosphatase is believed to be induced by P-deprivation. Conversely, the Pto-interaction (Pti) serine/threonine kinase activity is associated with abiotic stress. The aim of this study was to quantify of activities of two selected enzymes and phytohormone content in oil palm-clones in the P-limitation condition. Two oil palms genotypes were treated with three P dosages i.e. 0% (v/v), 4.67% (v/v), and 14.02% (v/v) represented as starvation, deficiency, and optimum condition, respectively. The activity of these two enzymes was quantified in mitochondria and cytoplasm using spectrophotometry and modified dot-blot methods, while abscisic acid, indole acetic acid and gibberellic acid content was quantified using ultra performance liquid chromatography (UPLC). The result showed that the Apase activity in P-optimum was higher than starvation and deficiency in leaf and root tissues in both genotypes, whereas Pti serine/threonine kinase activity was higher in prolific than non-prolific genotypes in P-deficient dosage. Furthermore, abscisic acid content was higher in prolific than non-prolific genotypes in starvation and deficient, whereas other hormone contents were similar. Association study showed that prolific was separated with non-prolific ones at different doses of P. Finally, the prolific genotype is more adaptable with P deficiency.

KEYWORDS Abscisic acid; Acid phosphatase; Pti-interacting serine/threonine kinase; Oil palm; P-limitation

1. Introduction

The oil palm (*Elaeis guineensis* Jacq.) is a perennial crop that fulfill most of global vegetable oil demand (Corley and Tinker 2016). The optimal mineral nutrition, which encompasses absorption, utilization, and supply of the essential nutrients, should be provided to manage a high yield (Martin et al. 2022). Oil palm requires a substantial quantity of regular phosphorus (P) fertilizer input to maintain an optimal oil yield. It is the second most restrictive macronutrient for crop productivity, following nitrogen (Muhammad et al. 2021). P is a vital element of nucleic acids, which are crucial for the preservation and conveyance of genetic information and structural component of a diverse array of molecular compounds, which are essential for the regulation of physiological processes in plant cells (Kumar et al. 2021).

The oil palm plantation is estimated to be roughly 30–40 percent of land have low P availability and are dependent on P fertilizer (Martin et al. 2022). Consequently, in order to ensure the P sustainability in oil palm plantation, it is imperative to expand of understanding of the mechanisms that could enhance of the oil palm ability to assimilate phosphorus (Viegas et al. 2023). The symptoms of phosphorus deficiency in oil palms are including stunted palms with short fronds, palm trunk a pronounced a pyramid shape with a reduced number of flowers and bunches (Behera et al. 2021). Indonesia's palm oil production could be significantly declined by P deficiency conditions, if not seriously mitigated.

Oil palm applies a variety of adaptation strategies in response to P limitation, including substantial alteration of root growth and architecture. Increased number and length of root filaments and oil palm lateral roots grown in

Copyright © 2025 THE AUTHOR(S). This article is distributed under a Creative Commons Attribution-ShareAlike 4.0 International license.

P starvation was reported (Kong et al. 2021). Furthermore, plants cultivated under a P-deficient environment are optimizing their P utilization by secreting of APase, RNase, and organic acids into the rhizosphere, which could increase the P soil availability (Thuynsma et al. 2016). P stress induces the expression of APase, which is responsible for the mobilization of immobile phosphate in the soil or within plant cells (Bhadouria et al. 2017).

Two genes namely *EgPap3* and *EgPti1* were identified involved in P regulation in oil palm (Maryanto et al. 2021). Purple acid phosphatases (PAPs) are the most numerous subclasses of plant acid phosphatases (APases) (EC 3.1.3.2) (Srivastava et al. 2020). During the development stage, PAPs are involved in numerous biological functions, including the accumulation of P, modulation of ascorbate biosynthesis, development of flowers, biosynthesis of cell walls, regulation of seed germination, and production of reactive oxygen (Deng et al. 2020). The utilization of phosphate (Pi) is associated with the PAP, which is suggested to be induced by phosphorus deprivation. Plants use and recycle phosphorus in large part due to increased acid phosphatase activity (Gao et al. 2017).

The serine/threonine protein kinase Pto can phosphorylate a diverse group of proteins known as a Pto interaction (Pti) protein. The Pto protein is a key component of the plant's immune system. These proteins are participated in the maturation of plants and the response to stress (Huangfu et al. 2021). The expression of *Pti* in cucumber leaves was induced by salicylic acid, abscisic acid, and methyl jasmonate. Plants responses to biotic and abiotic stresses were positively regulated by the *Pti* gene. Although a *Pti* has not been previously reported to participate in P-limitation in plant, it plays a diverse function in abiotic stress responses. Therefore, its activity in oil palm seedlings grown in P limitation would be quantified.

Further investigation was applied to these two genes including genomic and transcriptomic approaches. The expression of these genes was upregulated on oil palm seedlings treated with P deficient dosage using RT-qPCR analysis. Single nucleotide polymorphism (SNP) was also identified on both genes which used for molecular marker development.

SNP is molecular markers defined by the modification of a single nucleotide within a DNA sequence (Grzegorczyk et al. 2021). SNP markers of *EgPap3* and *EgPti1* could differentiate of high-uptake efficiency and low-uptake efficiency oil palm genotypes. The SNP markers then was used for genotyping of mother palms using kompetitive-allele specific PCR (KASP). Furthermore, two DxP ramets (clones) represented prolific and non-prolific genotype were selected for this research (Maryanto et al. 2019).

P availability is closely linked to APase and Pti serine/threonine kinase enzymes activity. To date, there has been no report on APase and Pti serine/threonine kinase activities and hormone concentration associated with P-limitation in different oil palm genotype. Thus, the research aimed was to determine of APase and Pti serine/threonine kinase activities and hormone contents in oil palm seedlings grown in P limitation. It is expected that these two enzymes could be used as a biomarker for oil palm response to P limitations. Furthermore, the study would also benefit for the development of oil palm genotype with improved P-uptake efficiency by providing a more comprehensive understanding of the critical regulator mechanism involved in P-limitation responses.

2. Materials and Methods

2.1. Planting materials

The planting materials used were two DxP ramets (clones), consisted of prolific genotype represented a high P-uptake efficiency (Genotype-A) and non-prolific genotype represented a low P-uptake efficiency (Genotype-B). The ramets P uptake was categorized based on their Tenera DxP mother palms allele using mass genotyping of SNP on *EgPap3* and *EgPti1*.

2.2. Fertilization trials

Oil palm ramets exhibiting consistent plant height about 15 cm were carefully selected and cultivated in a hydroponic system. A hydroponic nutrient solution was made following the Hoagland method with several modifications (Hoagland and Arnon 1950). The pH of the culture solution was maintained at 5.5 by supplementing with 0.1 N of NaOH or 0.1 N of HCl, and was monitored weekly. In total 200 L media was renewed for every 14 days to maintain sufficient nutrient delivery, and an air pump was utilized for continuous aeration.

According to the previous research findings regarding the impact of P fertilizer treatment on the growth of oil palm in hydroponic system, three P concentrations were applied i.e. 0% (v/v) represented starvation (P1), 4.67% (v/v) represented deficiency (P2), and 14.02% (v/v) represented optimum (P3) (Maryanto et al. 2021).

2.3. APase assay

The APase enzyme activity was quantified after the root and leaf samples were pulverized using liquid nitrogen. The grounded sample was mixed with 1 mL of buffer extract kit, (Sigma-Aldrich, Missouri, USA) and vortexed for 10 min. The supernatant was isolated using centrifugation at 10,000 g and 4 °C for 10 min. A pure enzyme was prepared from the supernatant. An 80 µL of crude enzyme was transferred into each well of the plate, then 20 µL of working reagent was added. The solution was mixed slowly by tapping the plate followed by an incubation at ambient temperature for 30 min. The absorbance of the solution was quantified at 620 nm with an Epoch spectrophotometer.

2.4. Pti serine/threonine kinase assay

The Pti was measured using a modified dot-blot method developed by Cheng and collaborators (Cheng et al. 2019). The primary antibody used was anti-Pti, synthesized via a

third-party (GenScript) based on the Pto-interacting protein 1 sequence accession number A0A6I9QE65. The protein extraction process was commenced by adding of protein extract buffer to the powdery sample. The solution was homogenized by vortexing for 10 min. The supernatant was isolated using centrifugation at 12,000 g and 4 °C for 15 min. Crude protein was extracted from the supernatant. The total protein concentration of crude protein was assessed with the Bradford (1976) technique, following Rohman et al. (2022). A grid on the nitrocellulose membrane is drawn to indicate the protein region to blot. A total of 2 µL of samples were pipetted and placed on the indicated spot at the grid's center. The membrane was permitted to dry before being submerged in a blocking solution for an hour. A primary antibody solution was used to incubate the membrane at room temperature for 30 min. The membrane was then rinsed three times with the wash solution for 5 min each and followed by incubation in the secondary antibody-conjugated HRP solution for 30 min at ambient temperature. Subsequent to rinsing, the membrane was incubated with an enhanced chemiluminescence (ECL) solution for one minute prior to visualization using UV-Tech. The quantity of pixels generated on the membrane was quantified using ImageJ software (Rohman et al. 2022).

2.5. Hormones assay

The hormone content was quantified from the root and leaf samples. The extraction method for hormone analysis was adapted from Kelen et al. (2004) utilizing Ultra Performance Liquid Chromatography (UPLC). Ten grams of fresh tissue was ground with liquid nitrogen and homogenized with 80% of methanol (v/v) before being macerated over night at 4 °C. The extract was filtered with a Whatman filter no. 41, and the methanol was evaporated using vacuum. The pH of the aqueous phase was adjusted to 8.5 by the addition of 0.1 M of phosphate buffer solution, which had been partitioned three times with ethyl acetate. Following the removal of the ethyl acetate phase, the pH of the aqueous phase was then adjusted to 2.5 using 1 N of HCl. Diethyl ether was used to partition the solution three times before passing through anhydrous sodium sulphate. Subsequently, the desiccated residue containing the hormone was dissolved in 2 mL of methanol and preserved in a vial at 4 °C. The diethyl ether phase was evaporated using a vacuum. The samples were separated using UPLC with C18 as the solid phase and acetonitrile-phosphate buffer as the mobile phase. Abscisic acid, gibberellic acid, and indole-3-acetic acid were used as a standard (Sigma-Aldrich, Missouri, USA) (Rohman et al. 2022).

2.6. Data analysis

The Minitab® 20 statistical software applications were employed to data analysis for all measuring parameters. The Analysis of Variance (ANOVA) and Duncan's Multiple Range Test (DMRT) at $\alpha = 0.05$ were employed to determine the differences between parameters. Association of phenotype and genotype was analyzed using Principal Component Analysis (PCA) with Pearson correlation test.

3. Results and Discussion

3.1. Results

The enzyme activities were varied. The result showed that APase activity in P optimum dosage was higher than starvation and deficient environments in leaf and root tissues of both tested genotypes, whereas Pti serine/threonine kinase activity was higher in deficient dosage in prolific genotype (Figure 1a–d). Furthermore the activity of Pti was higher in prolific than non prolific genotype in all P dosages.

The hormone contents were varied in the ramets (clones). It was measured from root and leaf samples which P-dosage variation namely, abscisic acid (ABA), indole acetic acid (IAA), gibberellic acid (GA). The ABA content in prolific was higher than non-prolific genotypes of P-dosages variation, whereas the IAA and GA hormones showed unclear pattern between prolific and non-prolific genotypes (Figure 2a–c).

The PCA is a statistical technique used to ascertain the correlation among samples based on all evaluated attributes directly. The clustering among samples and the relationship among parameters were determined using the score plot and the biplot, respectively (Figure 3). In this research, the score plots were generated in two clusters according to the genotypes in the root and leaf tissues. The black dot group was associated with prolific, while the red dot group was linked to non-prolific genotype. According to the score plot, a genotype exhibited a variation in phosphorus assimilation, particularly in phosphorus intake. All examined parameters had a positive correlation, as seen by their uniform direction in the biplot. Pti serine/threonine kinase had a robust association with abscisic acid (ABA) across all tissues, but APase shown no correlation with hormonal activity.

3.2. Discussion

Planting materials used in this research were selected according to SNP markers that are linked to phosphorus uptake efficiency (Maryanto et al. 2021). SNP markers have been employed for progeny selection in various plant species, including rice cultivars exhibiting high nutritional efficiency (Jewel et al. 2019) and wheat high P uptake efficiency cultivars (Soumya et al. 2021). The nucleotide polymorphism of *EgPap3* and *EgPti1* were associated with phosphorus uptake in oil palm. The palms with prolific allele had high P content in their leaves and assumed as efficient genotype, while the low P content in leaves was identified in palms with non-prolific allele and was assumed as non-efficient P uptake. Furthermore, the SNP markers of *EgPap3* and *EgPti1* could be used to differentiate of high P-uptake efficiency and low P-uptake efficiency genotype (data unpublished).

Classification of oil palm ramets (clones) are also

supported by particular morphological traits and expression profiles of *EgPap3* and *EgPti1*. Several specific traits observed including morphological, physiological, and molecular characters, were distinct among P starvation, P deficient and P optimum dosage. The *EgPap3* and *EgPti1* were up-regulated at P-starvation and

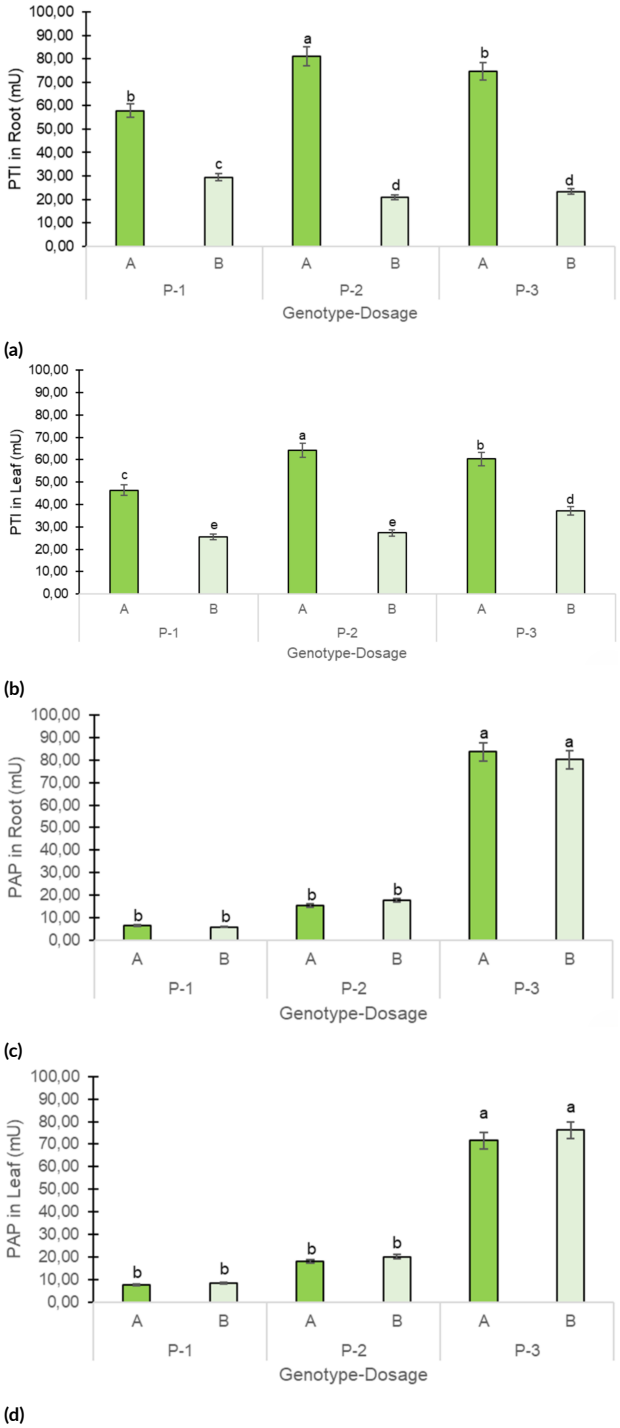


FIGURE 1 Enzyme activity of Pti serine/threonine kinase in root (1a) and leaf (1b). APase activity in root (1c), and leaf (1d). Note: A is prolific and B is non-prolific genotype; P1: P-starvation, P2: P-deficient, P3: P-optimum. The same letter on the top of the bar chart shows no statistical difference, according to Duncan's multiple range test ($p < 0.05$).

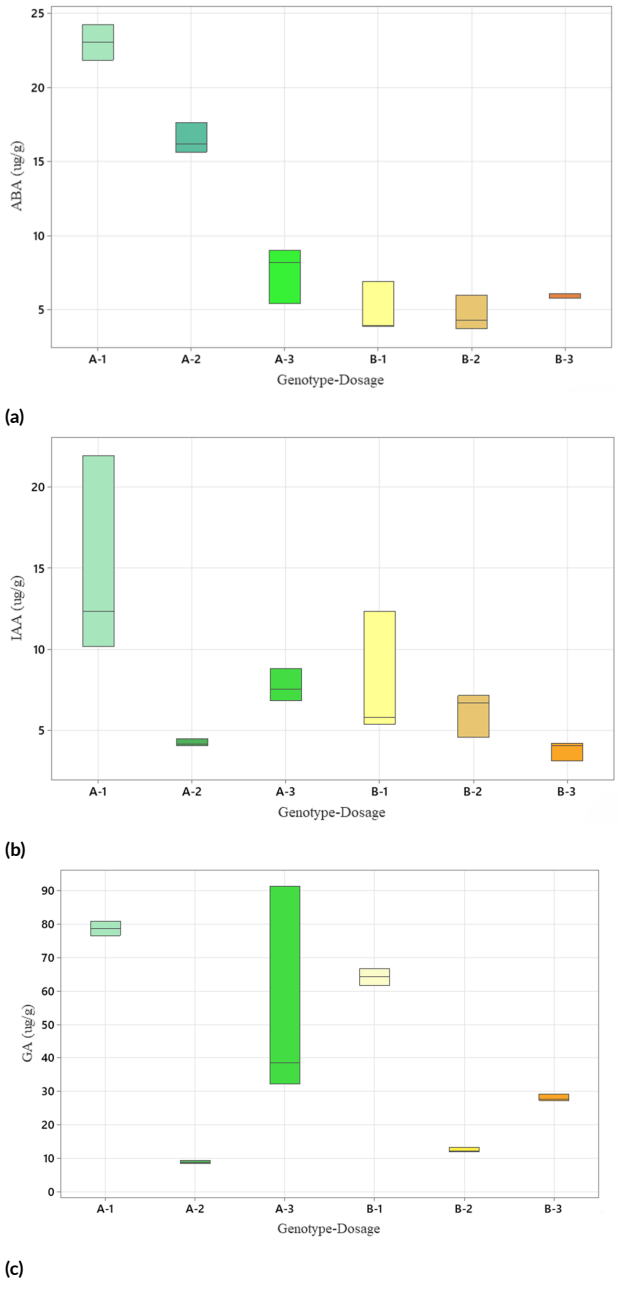


FIGURE 2 Total hormone contents were measured in P-dosage variation, A: abscisic acid (ABA), B: indole acetic acid (IAA), C: gibberellic acid (GA). Note: A is prolific and B is non-prolific genotypes; P1: P-starvation, P2: P-deficient, P3: P-optimum.

P-deficient that supported by genotype-phenotype association data which showed that prolific were separated with non-prolific genotype at different P doses (data unpublished).

Plants react to P limitation through defined molecular, biochemical, morphological, and physiological responses. The enzyme and hormone identified in this investigation were examined in oil palm root and leaf of oil palms. These two organs have significant differences in the metabolic processes. Leaf is organ for the primary photosynthetic process while the primary nutrient assimilation process is taking place in the root. Acid phosphatase

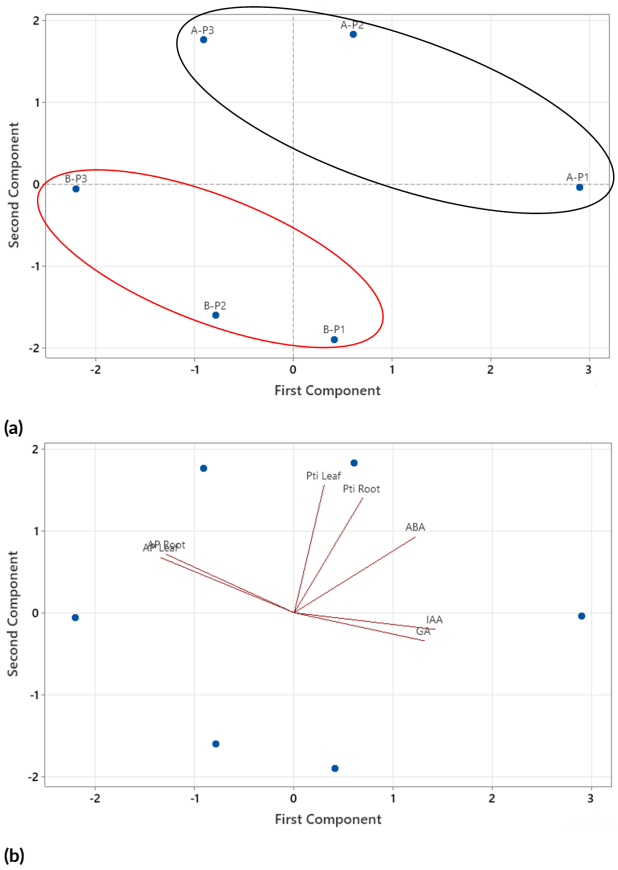


FIGURE 3 Genotype-phenotype association, (a) PCA analysis; (b) biplot analysis. Notes: A-P1: prolific-starvation; A-P2: prolific-deficient; A-P3: prolific-optimum; B-P1: non-prolific-starvation; B-P2: non-prolific-deficient; B-P3: non-prolific-optimum.

(APase) enzyme plays a crucial role in the assimilation of P, which in the soil is often present in organic forms that cannot be directly absorbed by plants. APase is secreted by roots into the surrounding environment. APase catalyzes the hydrolysis of organic phosphorus compounds, breaking them down into inorganic phosphates that can be absorbed by the roots and used by plants. The hydroponic media might be not present or very low content of inorganic forms in P-starvation and P-deficiency condition affected low activities of APase in root and leaves. Furthermore, APase activity in crops grown in P deficiency are involved in several mechanisms such as attaining and utilization of phosphorus, recycle organic phosphorus in the rhizosphere during crop development, regulate plant growth under phosphorus limitation conditions and enhance phosphorus use efficiency in crop. The *GmPAP17* that regulated of APase was upregulated in soybean grown in low phosphorus condition. Paps genes were reported enhances root growth, P use efficiency, and changes of acid phosphatase activity (Zhu et al. 2020).

The APase is also a key enzyme that improve plants adapt to low P conditions through facilitates P movement in the transition from senescing to non-senescing foliage, eliminating P from organophosphate compounds in the rhizosphere, converting ATP to inorganic phosphorus in the growth medium, and enhancing of P accessibility to plants (Gao et al. 2017). In this research, Apase activity was significantly decreased in P-starvation and the P-deficient at prolific and non-prolific genotypes (Figure 1). The Apase activity was observed low in P-starvation and P-deficiency condition in root and leaf organs. This might be a response to P-limited conditions through the use large quantities of APase for several actions including P movement in the transition from senescing to non-senescing foliage, elimination of P from organophosphate, and ATP into inorganic P conversion.

The Pti are primarily a group of protein kinases that can interact with and be phosphorylated by Pto. The Pti are essential regulators of stress response, disease resistance, and plant development. The homologs of Pti in soybean, cucumber, and maize were previously reported to be implicated in drought, low temperature, and salt stress, respectively. In maize, the *ZmPti1* gene was associated in salt and low-temperature stresses via an ABA-independent pathway (Sun et al. 2022). Pti serine/threonine kinase has diverse abiotic stress response include P limitation. The Pti expression in cucumber leaf with low temperatures stress was induced by abscisic acid. Several protein kinases are induced by abiotic stress, and these stress responses are linked to ABA signalling (Saijo and Loo 2020).

In this study, the activity of Pti serine/threonine kinase in prolific genotype was higher and significantly different with non-prolific genotype in P-deficient dosages. Pti serine/threonine kinase activity was induced by abscisic acid (Sun et al. 2022). Abscisic acid content of prolific genotype was higher than non-prolific genotype in P starvation and deficient dosage, whereas the other hormone content was similar. ABA would be induced during root development in P limitation conditions. The different responses between primary and lateral roots might be correlated with lateral root-specific ABA signaling in response to P-limitation. This hormone specificity may serve as a general mechanism for plants to manage their distinct growth responses between primary and lateral roots (Tian et al. 2014). The primary roots of prolific genotype were higher than non-prolific genotype in P-starvation and P-deficient (not published). Increasing of primary roots were influenced by P-limited condition which induces of Pti expression that correlated with ABA activities. Hence, ABA exhibited a robust correlation with Pti serine/threonine kinase in all tissues, while APase was not correlated with hormone activities.

4. Conclusions

Association study showed that prolific genotype was separated with non-prolific genotypes at different doses of phosphorus. Abscisic acid (ABA) exhibited a robust correlation with Pti serine/threonine kinase in all tissues, while APase had not correlation with hormone activities. Two enzymes can be used as biomarkers for oil palm related to P deficiency, while ABA content has correlation

with P stress. The prolific progeny is more adaptable to P deficiency compared with non-prolific progeny based on enzyme activities and ABA content. Further testing with more samples is needed to validate these results.

Acknowledgments

The authors are grateful to the management of PT Sinar Mas Agro Resources & Technology (SMART) Tbk. and Palm Oil Fund Management Agency, Ministry of Finance, Republic of Indonesia for their support in completing this study. We also thanks to Wulan Artutiningsih, Olivia S. Purba, Tengku Imam Saputra, Widyartini Made Sudania, Zulfikar A. Tanjung for their support and Allif Reinaldy, Redy W. Permana, Nur Afifah T., Elsanda N., Ranny Hanifah, and Yusuf Rezaludin for technical assistance in laboratory and greenhouse activities.

Authors' contributions

SDM conceived and designed. SDM, RAR performed the experiments, and statistic analyzed the data. SDM, RAR, RBD wrote the paper. RBD, BSD, TRN, PRM, DR, ETS, CU, TL reviewed and supervised of the research. All authors have read and approved the final manuscript.

Competing interests

The authors declare no conflict of interest.

References

Behera SK, Suresh K, Shukla AK, Kamireddy M, Mathur RK, Majumdar K. 2021. Soil and leaf potassium, calcium and magnesium in oil palm (*Elaeis guineensis* Jacq.) plantations grown on three different soils of India: status, stoichiometry and relations. Ind. Crops Prod. 168:1–9. doi:10.1016/j.indcrop.2021.113589.

Bhadouria J, Singh AP, Mehra P, Verma L, Srivastawa R, Parida SK, Giri J. 2017. Identification of purple acid phosphatases in chickpea and potential roles of *CaPap7* in seed phytate accumulation. Sci. Rep. 7(1):1–12. doi:10.1038/s41598-017-11490-9.

Bradford MM. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein–dye binding. Anal. Biochem. 72:248–254. doi:10.1016/0003-2697(76)90527-3.

Cheng LT, Zeng YJ, Chu CY, Wang HY. 2019. Development of a quick dot blot assay for the titering of bovine ephemeral fever virus. BMC Vet. Res. 15:313. doi:10.1186/s12917-019-2059-6.

Corley RHV, Tinker PB. 2016. The oil palm. West African Agriculture. Cambridge: Cambridge Univ. Press. doi:10.1017/cbo9781316530122.010.

Deng S, Lu L, Li J, Du Z, Liu T, Li W, Xu F, Shi L, Shou H, Wang C. 2020. Purple acid phosphatase 10c encodes a major acid phosphatase that regulates plant growth under phosphate-deficient conditions in rice. J. Exp. Bot. 71(14):4321–4332. doi:10.1093/jxb/eraa179.

Gao W, Lu L, Qiu W, Wang C, Shou H. 2017. *OsPap26* encodes a major purple acid phosphatase and regulates phosphate remobilization in rice. Plant Cell Physiol. 58(5):885–892. doi:10.1093/pcp/pcx041.

Grzegorczyk J, Gurgul A, Ockowicz M. 2021. Single nucleotide polymorphism discovery and genetic differentiation analysis of geese bred in Poland using genotyping-by-sequencing. Genes 12:1074–1086. doi:10.3390/genes12071074.

Hoagland DR, Arnon DI. 1950. The water-culture method for growing plants without soil. California Agricultural Experiment Station, Circular 347. Berkeley: University of California, College of Agriculture.

Huangfu Y, Pan J, Li Z, Wang Q, Mastouri F, Li Y, Yang S, Liu M, Dai S, Liu W. 2021. Genome-wide identification of *PTI1* family in *Setaria italica* and salinity-responsive functional analysis of *SiPTI1–5*. BMC Plant Biol. 21(1):1–17. doi:10.1186/s12870-021-03077-4.

Jewel ZA, Ali J, Mahender A, Hernandez J, Pang Y, Li Z. 2019. Identification of quantitative trait loci associated with nutrient use efficiency traits using SNP markers in rice. Int. J. Mol. Sci. 20(4). doi:10.3390/ijms20040900.

Kelen M, Demiralay EC, Sen S, Alsancak GO. 2004. Separation of abscisic acid, indole-3-acetic acid and gibberellic acid by reversed phase liquid chromatography. Turk. J. Chem. 28(5):603–610.

Kong SL, Abdullah SNA, Ho CL, Musa MH, Yeap WC. 2021. Comparative transcriptome analysis reveals transcriptional responses to phosphorus starvation in oil palm root. BMC Genomic Data 22(1):1–15. doi:10.1186/s12863-021-00962-7.

Kumar S, Kumar S, Mohapatra T. 2021. Interaction between macro- and micro-nutrients in plants. Front. Plant Sci. 12:665583. doi:10.3389/fpls.2021.665583.

Martin JJ, Yarra R, Wei L, Cao H. 2022. Oil palm breeding in the modern era: challenges and opportunities. Plants 11(11):1395. doi:10.3390/plants11111395.

Maryanto SD, Kusnandar AS, Sudania WM, Tanjung ZA, Saputra TI. 2019. Technical annual report: screening single nucleotide polymorphism (SNP) markers related to phosphorus uptake efficiency. Internal report, Plant Production and Biotechnology, Bogor, Indonesia.

Maryanto SD, Tanjung ZA, Roberdi, Sudania WM, Pujianto, Hairinsyah, Utomo C, Liwang T. 2021. Involvement of purple acid phosphatase gene into nitrogen uptake of oil palm. Biodiversitas 22(3):1385–1390. doi:10.13057/biodiv/d220340.

Muhammad II, Abdullah SNA, Saud HM, Shaharuddin NA, Isa NM. 2021. Dynamic responses of oil palm leaf and root metabolome to phosphorus deficiency. Metabolites 11:217. doi:10.3390/metabo11040217.

Rohman RA, Maryanto SD, Sudania WM, Utomo C,

Liwang T. 2022. Nitrogen uptake efficiency induced fumarate hydratase activity in oil palm seedlings. J. Proteins Proteomics 13(2):117–124. doi:10.1007/s42485-022-00087-0.

Saijo Y, Loo EP. 2020. Plant immunity in signal integration between biotic and abiotic stress responses. New Phytol. 225(1):87–104. doi:10.1111/nph.15989.

Soumya PR, Burridge AJ, Singh N, Batra R, Pandey R, Kalia S, Rai V, Edwards KJ. 2021. Population structure and genome-wide association studies in bread wheat for phosphorus efficiency traits. Sci. Rep. 11(1). doi:10.1038/s41598-021-87182-2.

Srivastava R, Akash, Parida AP, Chauhan PK, Kumar R. 2020. Identification, structure analysis and transcript profiling of purple acid phosphatases under phosphate deficiency in tomato. Int. J. Biol. Macromol. 165:2253–2266. doi:10.1016/j.ijbiomac.2020.10.080.

Sun M, Qiu L, Liu Y, Zhang H, Zhang Y, Qin Y, Mao Y, Zhou M, Du X, Qin Z, Dai S. 2022. Pto interaction proteins: critical regulators in plant development and stress response. Front. Plant Sci. 13. doi:10.3389/fpls.2022.774229.

Thuynsma R, Kleinert A, Kossmann J, Valentine AJ, Hills PN. 2016. Effects of limiting phosphate on photosynthesis and growth of *Lotus japonicus*. S. Afr. J. Bot. 104:244–248. doi:10.1016/j.sajb.2016.03.001.

Tian H, De Smet I, Ding Z. 2014. Shaping a root system: regulating lateral versus primary root growth. Trends Plant Sci. 19(7):426–431. doi:10.1016/j.tplants.2014.01.007.

Viegas IJM, Santos LD, Costa MG, Oliveira Ferreira EV, Silva Barata H, Silva DAS. 2023. Production of oil palm under phosphorus, potassium and magnesium fertilization. Rev. Ceres 70(2):112–123. doi:10.1590/0034-737X202370020013.

Zhu S, Chen M, Liang C, Xue Y, Lin S, Tian J. 2020. Characterization of purple acid phosphatase family and functional analysis of *GmPAP7a/7b* in soybean. Front. Plant Sci. 11. doi:10.3389/fpls.2020.00661.