



Review

Phosphorus deficiency tolerance in sorghum

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ABSTRACT

Sorghum is a globally important commodity for food, feed, and fuel, and is known to have a high tolerance to heat, drought, and other abiotic stresses, and have a large genetic variation for grain yield under low-P conditions. Agricultural land in Indonesia is dominated by acid soils with limited P availability, of a total of 144.5 million ha, around 107.3 million ha are acid soils. Information regarding the tolerance of sorghum to P deficiency conditions is still very limited. The review aimed to discuss the adaptation strategy of sorghum to P deficiency. Studies showed that sorghum has a moderate adaptation to Al³⁺ stress with low P. Under various P levels, the performance of sorghum was also very diverse following the wide genetic diversity. From evaluations of several varieties and inbred lines with high tolerance to P deficiency that has been obtained, sorghum tolerance strategies to low P conditions are: (1) increase root size (length, diameter, and volume), and root proteoid on several genotypes, (2) increase secretion of oxalic acid, particularly in tolerant genotypes, the secretion of which are higher when Al³⁺ is present, (3) higher P-use efficiency (PUE), eventhough the specific absorption ratio (SAR) was lower than the sensitive ones. The high PUE is thought to contribute to higher grain weight compared to sensitive genotypes under P starvation condition, and (4) higher stay green percentage, which has a high correlation to grain weight/plant. Such strategies should be considered in precision breeding program of sorghum to P deficiency.

Keywords: adaptation strategy; oxalic acid; P-use efficiency; sorghum genotypes; sorghum low P; stay green

Edited by:

Maya Melati

Received:

27 March 2023

Accepted:

29 April 2023

Published online:

29 April 2023

Citation:

Sopandie, D.,
Trikoesoemaningtyas, &
Wirnas, D. (2023).
Phosphorus deficiency
tolerance in sorghum.
*Indonesian Journal of
Agronomy*, 51(1), 121-
133

INTRODUCTION

Phosphorus (as phosphate, PO₄³⁻) is an integral component of important compounds of plant cells, including as sugar-phosphate intermediates in respiration and photosynthesis, and as phospholipids that make up plant membranes. It is also a component of nucleotides used in plant energy metabolism (such as ATP) and in DNA and RNA (Taiz et al., 2015). Inorganic orthophosphate (Pi) is the main source of P for plants. However, Pi can be easily fixed with aluminum and iron in acid soils and with calcium in alkaline soils. In acid soils, the available Pi content is too low to meet the needs of plant growth, and excessive amounts of P fertilization must be applied, which can cause environmental pollution.

The supply of P, as one of the three most widely used plant fertilizers (N, P, and K), is constrained by limited P reserves worldwide (Cordell & White, 2013). More than 30% of global agricultural land is deficient in P, mainly due to the fixation of P as a phosphate anion tightly bound to the surface of soil clay minerals (Lopez-Arredondo et al., 2014), also due to bonds with Al³⁺, Fe⁺³ on acid soils in the tropics (Marschner, 2012). When P fertilizer is applied to the soil, the percentage of P absorbed by plants is generally lower

than 20% and most of the applied P is fixed by the soil as Al-P and Fe-P compounds with low solubility in acid soils and Ca- and Mg- compounds P in alkaline soil.

Agricultural land in Indonesia is dominated by acid soils with limited P availability, of a total of 144.5 million ha of land, around 107.3 million ha are acid soils (ultisols). Under this condition, development of crops that are more adapted to low P environments is a sustainable and economical approach in agricultural production.

Tolerance to P deficiency in plants can be achieved by mechanisms underlying both P acquisition and P internal utilization efficiency. To adapt to persistent P deficiency, plants have developed several strategies, including: (i) altering root morphology, (ii) secreting organic acids or sugar and phosphatases, (iii) establishing symbiotic relationships with arbuscular mycorrhizal fungi or microbe, and (iv) increased expression of inorganic P transporters or increasing *phosphorus acquisition efficiency* (PAE) and *phosphorus use efficiency* (PUE) (Hiradate et al., 2007; Lazali & Drevon, 2021; Mo et al., 2022).

Sorghum is known to have a high tolerance to heat, drought, and other abiotic stresses (Gladman et al., 2022), which have a large genetic variation for grain yield under low-P conditions (Leiser et al., 2015). Several inbreed lines have been developed from parent varieties such as Numbu (tolerant), ZH-30-29-07 (tolerant), B-69 (sensitive), and B-75 (sensitive) (Wirnas et al., 2018). Sorghum is moderately tolerant to Al³⁺ stress under low P condition, in which the variation in genetic diversity was narrow, but when the availability of P became highly variable, the genetic diversity become very wide (Sopandie et al., 2014). Nevertheless, there are few reports related to P nutrition and the mechanism of tolerance to P starvation in sorghum. In this review, we discuss the adaptation strategy of sorghum to P deficiency by discussing some results of our studies which are supported by several references derived from other plants in order to support precision breeding program.

RESULTS AND DISCUSSION

Plant responses to P deficiency

Phosphorus (P) is an essential element determining plants' growth and productivity. Due to soil fixation of P, its availability in soil is rarely sufficient for optimum growth and development of plants. In plants, P exists as sugar phosphate, nucleic acid, nucleo pairs, coenzymes, phospholipids, inositol phosphate (phytic acid), and plays an indispensable role in energy storage and structural integrity as much as N, K, Ca, Mg, and S. The function of phosphorus as a component of macromolecular structures is most prominent in nucleic acids, which, as components of DNA, are the carriers of genetic information and, as units of RNA, are the structures responsible for the translation of the genetic information. In both DNA and RNA, phosphate forms a bridge between ribonucleoside units to form macromolecules (Marschner, 2012).

To support sufficient growth, plant in general requires P at the level of 2 g kg⁻¹ biomass (Taiz et al., 2015). The P requirements for optimal growth are in the range of 3 to 5 mg g⁻¹ DW during the vegetative growth stage, but some plants that have evolved on very poor P soils contain less P in their leaves (Lambers et al., 2010). Common symptoms of phosphorus deficiency in plants are stunted growth at young age and dark green coloration of the leaves, and further deficiency may cause malformed and contain small spots of dead tissue called necrotic spots (Taiz et al., 2015). Marschner (2012) mentioned that in P-deficient plants, reduction in leaf expansion as well as leaf number is the most obvious effect. The average length of the cell division zone was reduced in P-deficient maize leaves, and cell production and cell division rates were reduced. Leaf expansion is strongly related to epidermal cell expansion, and this process can be impaired in P-deficient plants. In contrast to the severe inhibition of leaf expansion under P deficiency, protein and chlorophyll concentrations per unit leaf area are less affected. Low P stress significantly inhibited shoot and root growth, photosynthesis, tissue P content, and root P concentration in both tolerant and sensitive genotypes of maize, in which the tolerant

genotype to P stress showed a less reduction of these traits compared to the sensitive ones (Liang et al., 2022). Phosphorus deficiency in soil inhibits N₂ fixation (Lazali and Drevon, 2021), as shown by the decrease in legume production, due to strong impact of phosphorus deficiency on the growth and survival of both rhizobia and host plant. Moreover, P deficiency results in enhancement of reactive oxygen species (ROS), which leads to oxidative damage to plant cells. To overcome the effect of reactive oxygen species, plants have developed the mechanisms like production of antioxidants (Reddy et al., 2022). Recent works also showed that P deficiency affects electron transport to photosystem I (PSI) in sorghum, but the underlying mechanisms are unknown (Carstensen et al., 2018).

Alteration of root architecture in sorghum and other plants

Most plant morphology changes in response to the deficiency of a particular nutrient. In common natural soils, P is accessible to plants, but it is usually present as organic P in upper soil horizons and decreases with soil depth (Lazali & Drevon, 2021). Some plant species respond to P deficiency by altering their root architectures. Phosphorus deficiency results in increased length and density of root hairs and in increased lateral root formation and elongation (Hiradate et al., 2007). Soybean plants grown under low-P condition showed a reduction in the growth of the primary root with the induction of lateral roots and root hairs (Zhu et al., 2020). Several works have revealed the response of plants to low P by altering root morphology and their root properties (Hiradate et al., 2007; Niu et al., 2013; Hufnagel et al., 2014; Muller et al., 2015; Huang et al., 2019; Wu et al., 2019; Barros et al., 2020; Tang et al., 2020; Gladman et al., 2022; Chen et al., 2022; Mo et al., 2022).

Our studies used the tolerant and sensitive sorghum genotypes and their progeny inbred lines which were grown in the field (Agustina et al., 2010), nutrient culture (Lestari et al., 2017), and pots (Mandasari et al., 2020) with several P levels shows interesting results in root characters (Table 1, 2, and 3). In the presence of high Al³⁺ in the soil (exchangeable Al³⁺ 2.73 cmol 100 g⁻¹, pH 4.3-4.5) (Table 1), the sensitive genotypes B-75 was greatly stressed when no supplement Ca²⁺ and P were added, in which root length was severely inhibited. The tolerant genotype, Numbu, had relatively the same root length as when P availability was enhanced (low P or sufficient P). As long as P (low P or sufficient P) was provided, the two genotypes of sorghum had almost the same root length whether Ca²⁺ was added or not. Similar results were shown by the increased root diameter under enhanced P conditions (Table 1). The experiments using nutrient cultures showed similar responses (Table 2), where the presence of P is needed for the growth of sorghum roots. Root elongation was more inhibited by low P than by Al³⁺ stress. Numbu as the tolerant genotype showed greater tolerance than UPCA-SI which was sensitive to Al stress and low P (Lestari et al., 2017).

Table 1. Effect of liming and P deficiency on root length and root diameter of two sorghum genotypes grown on ultisol soil (exchangeable Al³⁺ 2.73 cmol 100 g⁻¹; pH 4.3-4.5).

Treatments	Root length (cm)		Root diameter (cm)	
	Numbu (T)	B-75 (S)	Numbu (T)	B-75 (S)
(-Ca2+) + (-P) (control)	52.20a	12.87b	8.85cd	5.10d
(-Ca2+)+ low P	64.50a	60.33a	16.50a	12.67abc
(-Ca2+) + Sufficient P	66.33a	69.40a	14.33abc	15.00ab
(+Ca2+) +(- P)	60.00a	55.87a	12.67abc	9.50bcd
(+Ca2+) + low P	68.33a	63.00a	17.67a	13.67abc
(+Ca2+) + Sufficient P	68.33a	66.33a	17.33a	14.83abc

Note: Numbers followed by the same letter in the same column are not significantly different in the DMRT test at $\alpha = 5\%$; T = tolerant; S = sensitive (Source: Agustina et al., 2010)

Table 2. Effect of various treatments of Al and P on root length of two genotypes of sorghum grown in nutrient culture.

Al and P treatments		Root length (cm)	
AlCl ₃ (μM)	KH ₂ PO ₄ (mM)	Numbu (T)	UPCA-S1 (S)
0	0.00	19.60bcd	15.36ab
0	0.01	19.00cd	16.33ab
0	0.10	22.70abc	17.23a
0	1.00	24.50a	18.10a
74	0.00	16.36d	10.60ab
74	0.01	18.28cd	12.43ab
74	0.10	23.67ab	17.67a
74	1.00	18.67cd	16.85a

Note: Numbers followed by the same letters in the same column are not significantly different based on DMRT $\alpha = 5\%$. (Source: Lestari et al., 2017)

Table 3 showed root length, root volume, and number of proteoid roots (root cluster) of sorghum inbred lines grown on latosol (oxisols) soil media with sufficient and low P in pots (Mandasari et al., 2020). Most of tolerant inbred lines responded to P starvation by lengthening the roots and increasing root volume. Some tolerant inbred lines were able to increase the number of proteoid roots. In contrast, root length of sensitive inbred lines and the sensitive parent B-69 was greatly inhibited by low P conditions, as well as root volume and the number of proteoid roots (Table 3). Gladman et al. (2022) showed that during limiting P condition, sorghum RSA (root architecture structure) was renovated to increase root length and surface area, likely enhancing its ability to acquire P. Hubnagel et al. (2014) mentioned that the rice protein kinase, *PHOSPHORUS-STARVATION TOLERANCE1* (*OsPSTOL1*) has shown to enhance P acquisition and grain yield in rice under P deficiency. Their study indicated that multiple *SbPSTOL1* genes have a more general role in the root system, not only enhancing root morphology traits but also changing root architecture, which leads to grain yield gain under low-P availability in the soil.

Niu et al. (2013) postulated the role of root architecture in alleviating P stress. Plants adapt their root architecture to low P conditions by inhibiting primary root growth, promoting lateral root growth, enhancing root hair development and cluster root formation, all of which promote P uptake by plants. The mechanism of activation of root architectural changes in response to P deficiency depends on changes in local P concentration, and transport or sensitivity to growth regulators such as sugars, auxins, ethylene, cytokinins, nitric oxide (NO), reactive oxygen species (ROS) and ABA. In the process, many genes are activated, which in turn trigger changes in molecular, physiological and cellular processes. Consequently, the root architecture is modified, enabling the plant to adapt effectively to a low P environment. Moreover, morphological changes of roots under P starvation are actually an outcome of complex interactions between P and other nutrients, such as N, Fe and Ca. Wu et al. (2019) pointed out that to overcome low P stress, remodeling of root morphology and architecture in plants must be accompanied by modification of root cell walls, in which cell wall proteins (CWP) play an important role in forming the cell wall, transmitting signals, and protecting cells from environmental stresses. Zhang et al. (2019) conducted a transcriptome analysis to reveal candidate genes related to phosphorus starvation tolerance in 29 genotypes of sorghum. Their study revealed that internal P content in shoots correlated with P tolerance. Gene ontology (GO) enrichment analysis showed that candidate genes were associated with oxidoreductase activity. In addition, further studies have shown that malate affects primary root length and shoot number in sorghum that is experiencing low P stress. Plant hormones (auxin, ethylene, jasmonic acid, salicylic acid and abscisic acid) signal transduction-related genes and many transcription factors were found to be involved in low P tolerance in sorghum (Zhang et al., 2019).

Table 3. Root length, root volume, and number of proteoid roots of sorghum inbred lines grown on soil media with sufficient and low P in pots.

Recombinant inbred lines/varieties	Root length (cm)		Root volume (mL)		Number of proteoid roots	
	Sufficient P	Low P	Sufficient P	Low P	Sufficient P	Low P
B-69/N 104-7 (T)	31.67	56.00acd	8.73	9.50a	3.33	2.7a
B-69/N114-7 (T)	44.00	41.33a	7.60	9.30a	3.00	2.7a
B-69/N 151-8 (T)	44.33	46.50a	8.23	9.93a	3.67	3.7ad
B-69/N115-9 (T)	41.00	52.33a	10.36	9.90a	3.00	2.3a
B-69/N 286-6 (T)	47.83	61.87abcd	10.07	12.87ad	2.67	4.0ad
B-69/N 170-9 (T)	42.00	48.00a	10.40	9.23a	3.67	3.7acd
B-69/N 177-4 (S)	44.00	27.67bcd	10.90	3.10bc	2.33	1.0b
B-69/N 48-4 (S)	57.00	26.33bcd	10.47	3.47bc	3.33	0.3bcd
B-69/N 67-9 (S)	48.50	24.83bcd	14.37	2.93bc	3.00	0.0bcd
B-69/N110-6 (S)	45.00	32.00b	11.13	3.50bc	2.67	0.0bcd
B-69 (SP)	43.67	23.67	11.17	3.10	3.67	0.3
Numbu (TP)	44.00	47.33	11.10	10.20	3.00	2.7
WHP (NV)	38.67	41.00	11.17	11.23	3.33	1.7
Kawali (NV)	55.33	40.67	14.13	6.07	3.33	1.7
P-value	0.5770	0.0000	0.1942	0.0000	0.9603	0.0000
CV (%)	25.81	18.21	27.93	32.40	34.19	32.08
LSD	-	12.56	-	4.09	-	1.05

Note: a = significantly different according to the LSD test at the 5% level with comparison B-69; b = significantly different according to the LSD test at the 5% level with the Numbu comparison; c = significantly different according to the LSD test at the 5% level with the WHP comparison; and d = significantly different according to the LSD test at the 5% level with Kawali's comparison; +P = P enough; -P = low P; T = tolerant, S = sensitive; TP= tolerant parent; SP = sensitive parent; NV = national variety (Source: Mandasari et al., 2020)

Modification of plant root architecture to overcome P deficiency requires adaptation of metabolites as shown by several studies (Muller et al., 2015; Huang et al., 2019). According to Muller et al. (2015), white lupin (*Lupinus albus* L.) highly adapts to soils that have low P by diminishing the levels of fructose, glucose, and sucrose in shoots after 14 days of P deficiency. Phosphorylated metabolites such as glucose-6-phosphate, fructose-6-phosphate, myo-inositol-phosphate and glycerol-3-phosphate were reduced in both shoots and roots; on the contrary, organic acids, amino acids, and several products of the shikimate pathway showed increased levels in P-deficient roots and shoots at 22 days old. Huang et al. (2019) showed that P deficiency induces lateral root growth in the seedling phase of *Fraxinus mandshurica*, which is related to potential molecular mechanisms. P deficiency significantly reduced levels of IAA, brassinolide, and ethylene, and increased levels of GA₃, cytokinins, ABA, and phosphatase in lateral roots of *F. mandshurica* seedlings when compared to seedlings supplied with sufficient P.

Roots secretion of organic acids, sugar and phosphatases

Several plant species secrete organic acids such as citric and malic in response to P deficiency. Organic acids can release P from Al-, Fe-, and Ca-P sources with low solubility (Hiradate et al., 2007; Lazali & Drevon, 2021). The most typical plant, *Lupinus albus* releases large amounts of organic acid anions from specialized root structures under phosphorus deficiency, so-called cluster or proteoid roots, to mobilize and acquire sparingly soluble phosphates from a restricted soil volume. The mechanisms underlying this release and its regulation are, however, poorly understood (Hiradate et al., 2007; Zhou et al., 2019). The phenomenon of organic acid secretion as a strategy for plants to release P from low-solubility in soil has been well-documented in several crops (Niu et al., 2013; Mora-Macias et al., 2017; Lazali & Drevon, 2018; Lestari et al., 2017; Maruyama et

al., 2019; Rakotoson et al., 2020, Zhu et al., 2020; Zhu et al., 2021; Mo et al., 2022), but there were not so many reports dealing with this matter in sorghum.

Our study on sorghum grown in nutrient solution with Al³⁺ stress and low P treatment showed oxalic acid secretion (Table 4) from roots of both genotypes of sorghum (tolerant Numbu and sensitive UPCA-S1), where UPCA-S1 secreted more oxalic acid than Numbu. This study showed that oxalate acid secretion increased in response to Al³⁺ stress, but was decreased by P addition (Lestari et al., 2017). P-deficiency-induced secretion of organic acids is also reported in soybean (Liang et al., 2013; malate), white lupin (Cheng et al., 2014; citrate, malate, succinate; Zhou et al., 2020; malate; Zhou et al., 2021, isoflavonoid), barley (Wang et al., 2015; citrate, malate, succinate), *Arabidopsis thaliana* (Mora-Macías et al., 2017; malate), sorghum (Lestari et al., 2017; oxalate), *Brassica napus* (Wang et al., 2015, 2016; citrate, malate, succinate), wheat (Wang et al., 2017; citrate, malate, succinate), oat (Wang et al., 2018; citrate, malate), and tropical grasses (Almeida et al., 2020; citrate, isocitrate, malate). It is very rare to obtain information regarding this matter on sorghum.

Table 4. Oxalic acid secretion from roots of two genotypes sorghum grown on Al and P treatments.

Al and P treatments		Oxalic acid secretion (ppm)	
AlCl ₃ (μM)	KH ₂ PO ₄ (mM)	Numbu (T)	UPCA-S1 (S)
0	0.00	33.72bc	58.65ab
0	0.01	0.10d	48.29abc
74	0.00	41.84abc	71.50a
74	0.01	22.35cd	56.73ab

Note: Numbers followed by the same letters in the same column are not significantly different based on DMRT $\alpha = 5\%$. (Source: Lestari et al., 2017)

Hiradate et al. (2007) postulated that the secretion of citrate is supposed to be mediated by an anion transporter. The main channel, an inwardly rectifying anion conductance (IRAC), showed higher selectivity for citrate than for Cl. Moreover, they explained that the secretion of organic acids is accompanied by acidification of rhizosphere, which may lead to increased solubility of low-solubility Ca-P compounds in soils. Zhu et al. (2021) mentioned that the synthesis of malate and its secretion in legume roots due to low P also has a negative impact on nodule growth, causing nodule size in roots to decrease. In legume nodules, malate is generally considered to provide carbon for both nodule bacteroid respiration and skeletons for NH₄⁺ assimilation. Maruyama et al. (2019) pointed out that *AtALMT3* is involved in malate efflux induced by P deficiency in *Arabidopsis thaliana* root hairs. They suggested that *AtALMT3* localized in root hair membranes is involved in malate efflux in response to P deficiency. In addition to organic acid secretion, Zhu et al. (2020) revealed another strategy, P-efficient genotype soybean L13 activated sugar metabolism in roots and released H⁺ into the root hair zone to acidify the rhizosphere to resist P deficiency. P deficiency induced an increase in aspartic acid concentrations in root, the increase being substantially greater in the P-efficient genotype.

Regarding P deficiency-induced phosphatase secretion, Hiradate et al. (2007) explained that some soil organic P derived from plant residues and soil organisms can be utilized by several plant species such as white lupine which secrete acid phosphatase (S-APases). The role of S-APases is to hydrolyze organic P compounds in the rhizosphere and supply inorganic P to plants. Moreover, Lazali and Devron (2021) pointed out that apart from inorganic complexes, P is also present in the form of organic complexes which include inositol phosphates, phosphate sugars, nucleotides, phosphoproteins, phosphonates, and phospholipids both in cells and in decaying biomass in the soil. An excellent example is shown in rice, where this organic complex is broken down with the help of phosphatase and phytase enzymes (Mehra et al., 2017; Pandey et al., 2017). Lazali and Devron (2021) further explained that phosphatases are nonspecific and divided into

two categories: acid or basic phosphatases. Acid phosphatases (APases) are widely distributed in all organisms and are primarily involved in organic P mineralization. There are two types of Pi starvation-induced APases; the first is intracellular APase, which is likely involved in the remobilization and recycling of Pi from intracellular P monoesters and older tissue anhydrides to more photosynthetically active tissues, whereas the second, extracellular or secreted APase, is believed to scavenge Pi from organophosphate compounds in the external environment. So far there has been no report on this matter in sorghum plants.

Enhanced expression of P transporters, PAE and PUE

Plants have strategies for obtaining more P and using it more efficiently in cells. The results of studies on this subject have been well documented in several crops (Hiradate et al., 2007; Rose & Wissuwa, 2013; Hufnagel et al., 2014; Malhotra et al., 2018; Dixon et al., 2020; Mo et al., 2022; Jha et al., 2023). Based on several references, Hiradate et al. (2007) stated that the concentration of dissolved Pi in the soil solution is very low, ranging from 0.1 to 10 mM, therefore Pi is principally supplied to plant roots by diffusion rather than mass flow. On the other hand, the concentration of Pi in root cells is much higher (Lazali & Drevon, 2021). Therefore, Pi must be actively transported against the concentration gradient from the external solution to the root cells. The uptake of Pi across the PM has been demonstrated to be transporter-mediated (Hiradate et al., 2007). The kinetics of P uptake shows the presence of: (1) high-affinity transporters that are active at low P concentrations, and (2) low-affinity transporters that are active at high P concentrations. The low P in the soil solution indicates that the high-affinity transporter is more active than the low-affinity transporter. Increased expression of genes from the *Pht 1* group that encodes a proton-Pi cotransporter in potato plant roots grown in P deficiency conditions. P absorption through transporters is mediated by H⁺-Pi cotransport which gets energy from H⁺-ATPase. In P-deficient conditions, some plant species will adapt by increasing proton pumping activity by increasing H⁺-ATPase activity in the plasma membrane. Increased H⁺-ATPase activity will be followed by an increase in P uptake kinetics as observed in lupin (*Lupinus alba*) in P deficiency condition.

According to Lazali and Drevon (2021), phosphate transporters are classified into four families: *Pht1*, *Pht2*, *Pht3*, and *Pht4*, which are located in the plasma membrane, plastidial membrane, mitochondrial membrane, and Golgi compartment, respectively. Among Pi transporters, the *Pht1* family is the most intensively studied in plants. *Pht1*, localized in the plasma membrane, is directly related to Pi uptake from soil and Pi translocation in the plant. In plants, two P uptake systems have been identified: one with high affinity, which is regulated by Pi availability and activated mainly under P deficiency, with Km 3–7 μM; and the other is a low-affinity system expressed constitutively with Km 50–300 μM as revealed by Tian et al. (2017). Moreover, Tian et al. (2017) mentioned that P deficiency rapidly induces the expression of genes encoding Pi transporters leading to increased transcription and protein synthesis, assembly of proteins in the outer layer plasma membrane of root cells, and increased Pi uptake. In soybean, 15 *Pht1* paralogs have been identified by bioinformatics and experiments (Lazali & Drevon, 2021).

There is increasing evidence that fertilizers alone cannot sustain crop yields for an extended period, indicating the need to develop superior sorghum genotypes for Pi acquisition and Pi-use efficiency. Dixon et al. (2020) stated that plants can overcome low P by increasing *P-use efficiency (PUE)*. High PUE requires high P uptake by roots and increased P uptake in processes that result in healthy growth. PUE can be described as the sum of *P-acquisition efficiency (PAE)* (ability to acquire P from the soil) and *P-utilization efficiency (PUE)* (ability to use P internally to produce better growth). Our study has shown differences in PUE between tolerant and sensitive sorghum inbred lines under P deficiency (Mandasari, 2021; Mandasari et al., 2020), where deficient P-tolerant inbred lines showed relatively higher PUE values under low P stress conditions (Table 5). On the other hand, the value of SAR under low P of the sensitive sorghum inbred lines was much higher than the tolerant ones. SAR represents the shoot content divided by the weight of

the new roots. The greater SAR of the deficient P-sensitive sorghum inbred lines indicated that they were absorbing more P per unit of new-root dry weight, for each unit of shoot dry weight, which reflects higher PAE. So even though the acquisition of P is quite large (PAE) occurred in sensitive genotypes of sorghum inbred lines, the PUE was very low, which is predicted to have contributed to the low grain weight/plant of the sensitive inbred lines (Table 6; Mandasari, 2021). There was a high correlation between PUE values and stay green for the two sorghum genotypes. Our study shows that the correlation between stay green and grain weight/plant was very significant ($r=0.91^{**}$). The character of stay green, therefore, is important as a tool for sorghum selection to develop low-P tolerant and high-yielding sorghum varieties.

Table 5. Tissue P content, total uptake, P-utilization efficiency (PUE) and specific absorption rate (SAR) of tolerant and sensitive sorghum inbred lines grown under low P and sufficient P.

Sorghum inbred lines	P content (%)		Total uptake (mg/plant)		SAR (mg/g/hr)		PUE (mg ² TDW/ mg P)	
	Sufficient	Low	Sufficient	Low	Sufficient	Low	Sufficient	Low
B-69/N 104-7 (T)	0.25	0.24b	77.06	44.05	3.55	2.66b	121.24b	78.02b
B-69/N 28-6-6 (T)	0.21	0.23b	87.72	69.24	3.13	3.82b	206.72ab	119.27a
B-69/N 177-4 (S)	0.16	0.25b	67.94	46.54	2.34	4.02b	265.42a	76.44b
B-69/N 110-6 (S)	0.24	0.39a	93.75	64.36	3.48	6.88a	176.58ab	40.56c

Note: Number followed by the same letters are not significantly different at LSD 5% probability, T=tolerant, S=sensitive (Mandasari, 2021)

Table 6. Stay green, grain filling rate, and grain weight/panicle of tolerant and sensitive sorghum inbred lines grown at sufficient and low P conditions of soil media using latosol soil.

Sorghum lines	Stay green (%)		Grain filling rate (g/day)		Grain weight/panicle (g)	
	Sufficient P	Low P	Sufficient P	Low P	Sufficient P	Low P
B-69/N 104-7 (T)	57.00a	55.67a	3.99a	3.60abc	99.95a	98.41a
B-69/N 28-6-6 (T)	50.67ab	44.00b	3.17bc	3.03c	87.45a	89.79a
B-69/N 177-4 (S)	58.66a	30.33c	3.64abc	1.73d	80.02a	53.03b
B-69/N 110-6 (S)	54.33a	27.67c	3.83ab	1.54d	85.66a	50.84bc

Note: Number followed by the same letters are not significantly different at LSD 5% probability, T=tolerant, S=sensitive (Source: Mandasari, 2021)

Establishing symbiotic relationships with mycorrhizal fungi or microbes

Several studies have revealed the symbiotic mechanism between plants and mycorrhizae and/or soil microbes as a strategy to cope with P deficiency stress (Hiradate et al., 2007; Niu et al., 2013; Kariman et al. 2014; Mattos et al., 2020; Liang et al., 2022). Phosphorus is mainly absorbed and utilized by plant roots through phosphate transport protein carriers. However, most of the P in the soil is in the form of insoluble organic P, which is also characterized by high adsorption and low mobility, so P often becomes scarce in the soil (Liang et al., 2022). According to Kariman et al. (2014), several plant species have mechanisms to increase P extraction from the soil. Root symbiotics with arbuscular mycorrhizae (AM), ectomycorrhizae (ECM) and cluster root formation (proteoid) are one of the P acquisition strategies to make them available to plants.

Watts-William et al. (2022) pointed out that sorghum can be highly colonized by AM fungi, and the plant-fungal association can lead to improvements in biomass and nutrient uptake. High-throughput phenotyping allows us to non-destructively interrogate the 'hidden' effects of AM fungi on sorghum growth and phenology. The study revealed that AM colonization affected early stages of growth, flowering time, harvest indices, grain yield and nutrition. Generally, the effects of AM colonization on sorghum grain yield and nutrition were positive. In a low soil P system, AM fungal colonization increased the yield of six diverse grain sorghum genotypes (relative to a non-colonized control). Apart from mycorrhiza, sorghum has the ability to absorb insoluble P in the soil through association

with other microorganisms as shown by Mattos et al. (2020) who used PSB (phosphate solubilizing bacteria). Their study revealed that the inoculation response depended on the sorghum genotype, P source and microbial strain. The use of PSB as a bioinoculant, in combination with rock phosphate, is a promising alternative for reducing the use of synthetic fertilizers, contributing to sustainable sorghum production.

Lazali and Drevon (2021) pointed out that microorganisms play an important role in the acquisition and transfer of nutrients in soil. For P, soil microorganisms are involved in a range of processes that affect P transformation and thus influence the subsequent availability of P to plant roots. In particular, microorganisms can solubilize and mineralize P from inorganic and organic pools of total soil P. Microorganisms directly affect the ability of plants to acquire P from soil through a number of structural or process-mediated mechanisms. These include, (i) an increase in the surface area of roots by either an extension of existing root systems or by enhancement of root branching and root hair development, (ii) by displacement of sorption equilibria that results in increased net transfer of phosphate ions into soil solution or an increase in the mobility of organic forms of P and (iii) through stimulation of metabolic processes that are effective in directly solubilizing and mineralizing P from poorly available forms of inorganic and organic P.

Future strategies

The development of low P tolerant sorghum in Indonesia has not been fully implemented, since sorghum is not classified as a major crop. However, due to its high adaptability to various abiotic stresses in the tropics, sorghum must be considered as an important crop, which is able to grow and produce normally on acidic soils with low P such as in Indonesia. Proper breeding efforts are the key to the success of developing sorghum tolerant to low P in acid soils. Information on several important characters involved in tolerance to low P is very useful in breeding efforts (Table 7). Table 7 shows that root characters such as root length, root diameter, root volume and root proteoids are important characters for selection of low P tolerant sorghum. Another character, which is easy to observe in the field, is the percentage of stay green. This character is a promising character for obtaining genotypes of P tolerant sorghum with high grain production. Breeding efforts by developing cultivars that are more efficient in obtaining soil P (PUE) are very important, increasing the PUE of plant cultivars will complement the PAE properties.

Table 7. Summary of sorghum adaptation strategies to P deficiency stress.

Adaptation strategies	Sensitive genotypes	Tolerant genotypes
Alteration of root morphology	Severe inhibition of root length, root diameter, root volume and number of proteoid roots	Able to sustain root growth, increase root length, root diameter, root volume, and several genotypes were able to increase the number of proteoid roots
Secretion of organic acids	Secrete higher amounts of oxalic acid, but the percentage of increase was low	Secrete lower amounts of oxalic acid, with higher increase in percentage from normal condition to low P
Degree of phosphorus acquisition efficiency (PAE) and phosphorus use efficiency (PUE)	Higher specific absorption rate (SAR) with much lower PUE under low P	Lower SAR, with much higher PUE under low P
Percent of stay green	Much lower stay green percentage under low P	Much higher stay green percentage under low P

Speeding up breeding program through precision method assisted by biotechnology approach is prospective. Phosphorus acquisition efficiency is the major component of P efficiency for sorghum cultivated under low-P availability in the soil. The low-P tolerance of sorghum is probably manifested through regulation of root growth, Pi acquisition and cellular Pi homeostasis as well as Pi signaling pathway. Identification of the genes involved

in increasing P uptake and its utilization is urgently needed. The identified genes can be potentially used to design a breeding strategy for developing P-efficient sorghum cultivars to grow on acid soils in the tropics, especially in Indonesian cases. Attempts should be made to improve P-acquisition ability by manipulating genes involved in P-deficiency responses. Several genes are known to be involved in increasing P uptake in plants such as *Pht1*. *CS* gene is involved in organic acid synthesis, it has been reported to be useful in enhancing P acquisition in some plants. From the agronomic point of view, the use of PSB as a bioinoculant combined with rock phosphate application is a method that needs to be tried as a promising method for increasing sustainable sorghum production in Indonesia.

CONCLUSIONS

Information regarding the tolerance of sorghum to P deficiency conditions is still very limited. Our studies so far show that sorghum has a moderate adaptation to Al^{3+} stress with low P. At various P levels, the performance of sorghum was also very diverse with wide genetic diversity. Sorghum is very responsive to differences in P availability, more than its response to Al^{3+} stress. Several varieties and inbred lines of sorghum that have high tolerance to P deficiency have been obtained, both in high Al^{3+} conditions and without Al^{3+} . These genotypes have the potential to be developed further in breeding programs. The results of our study on several genotypes of sorghum showed that sorghum has tolerance to low P conditions through several strategies, namely: (1) increasing root length, root diameter, root volume, and several genotypes were able to increase the number of proteoid roots, (2) increasing secretion of oxalic acid, especially in tolerant genotypes, the secretion of which be higher when Al^{3+} is present, and (3) tolerant genotypes have much higher PUE (P-use efficiency) than sensitive genotypes, even though the SAR (specific absorption ratio) is lower than the sensitive genotype. High PUE is thought to contribute to higher grain weight/plant compared to sensitive genotypes under P starvation conditions, and (4) genotypes tolerant have a higher stay green percentage, which has a high correlation to grain weight/plant ($r=0.91^{**}$).

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