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# FROM DISCOVERY TO DEPLOYMENT: *PUP1* IN RICE PHOSPHORUS NUTRITION AND YIELD STABILITY

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## ABSTRACT

Phosphorus (P) deficiency is a major constraint to rice production especially in rainfed and nutrient depleted soils. The *Phosphorus uptake 1 (Pup1)* locus, first identified in the upland landrace Kasalath has been recognized as a key determinant of tolerance to Phosphorus starvation. While absent in most high yielding irrigated varieties, *Pup1* confers an adaptive advantage in low Phosphorus environments. The major gene within this QTL, *OsPSTOL1*, encodes a serine/threonine protein kinase that enhances early root growth thereby improving nutrient acquisition and yield stability under stress. QTL mapping across diverse populations has revealed additional loci associated with root traits Phosphorus uptake and yield under stress with some overlapping drought-responsive regions suggesting pleiotropy or close linkage. Molecular markers targeting the Kasalath *Pup1* region including K20-1, K29-1 and K46-1 have been widely used for foreground selection. Marker-assisted backcrossing (MABC) has enabled successful transfer of *Pup1* into several popular but Phosphorus sensitive cultivars such as IR64, IR74, MTU1010, ADT 43, ASD 16 and Improved Samba Mahsuri, consistently conferring yield advantages under Phosphorus limited conditions. Novel alleles reported from *Oryza glaberrima* further expand opportunities for genetic enhancement. Deployment of *Pup1* through molecular breeding represents a significant step toward input efficient and climate resilient rice. By promoting robust root architecture and superior Phosphorus use efficiency, *Pup1* reduces dependence on fertilizers and ensures stable productivity in marginal soils. Its integration into breeding pipelines aligns with global goals of food security and sustainable nutrient management.

***Keywords* :** Rice; Phosphorus; PUE, *OsPSTOL1, Kasalath*

## Introduction

Rice (*Oryza sativa* L.) has been cultivated for over five millennia and stands as one of the most significant staple crops worldwide. It plays a crucial role in global food security, especially across Asia where nearly 60% of the global population resides (Le *et al*., 2020). As a primary food source, rice contributes approximately 19–21% of the daily caloric intake per person worldwide with this figure rising to 27–28% in many developing countries (Awika 2011; IRRI 2020). Nutritionally rice provides around 12.7% of the global daily protein intake and 1.8% of dietary fat. 100-gram portion of cooked white rice contains about 130 calories, including 28.7 grams of carbohydrates (around 10%) and 2.36 grams of protein (approximately 5%) along with small amounts of fats and other nutrients (USDA 2020).

### Global perspective on rice production

Among the world's three most essential cereal crops, rice is consumed by a significant portion of the global population. It is cultivated across all inhabited continents including Asia, Africa, Europe, Australia and the Americas which highlights its global reach and its adaptation to diverse cultural practices and farming systems (Chauhan 2017). The crop is grown from 53°N to 40°S latitude and thriving in a wide range of environments ranging from high-altitude regions up to 2,600 meters above sea level to arid deserts such as those in Egypt and from wetlands to drylands (Nguyen 2002). Today, rice is grown in more than 100 countries covering an estimated 163 million hectares (mha) of land (Laborte *et al.*, 2017). Global rice production amounts to roughly 700 million tonnes (mt) of paddy yielding around 470 million tonnes of milled rice. The cultivation areas are generally classified into three main ecosystems: irrigated lowlands which accounts for about 80–95 mha: rainfed lowlands spanning 40–45 mha and rainfed upland areas comprising the remainder of global rice-growing regions (Seck, 2012).

In 2018 global paddy rice production reached 769.9 million tonnes (Mt) with China emerging as the largest producer and harvesting approximately 210 Mt followed closely by India (FAO, 2018). Asia remains the dominant rice producing region contributing nearly 90% of global output at around 640 Mt of paddy. Within South Asia countries such as Bangladesh, Bhutan, India, Nepal, Pakistan and Sri Lanka are often referred to as the "food bowl of Asia" due to their significant contribution to rice cultivation. Although China leads in total rice production globally, India cultivates the largest rice growing area with China following in second place. Southern Asia which is home to roughly a quarter of the global population accounts for 37.6% of the world’s harvested rice area and contributes 32.4% to total global rice output (Gumma *et al.*, 2017; IRRI 2020). In 2019, India’s rice production was reported at 115.60 Mt. Moreover, during 2017–2018, India was the world’s top rice exporter with Thailand ranking second (GoI, 2019).

## Rice distribution in Indian context

In India, rice is cultivated across approximately 43.5 million hectares (mha) covering all states and encompassing a wide range of ecological conditions. These range from regions below sea level such as Kuttanad in Kerala to elevations of up to 2,000 meters above mean sea level (MSL) in Jammu & Kashmir, Himachal Pradesh, the hills of Uttarakhand and the northeastern hill states (IRRI, 2020).

In terms of area under rice cultivation Uttar Pradesh ranks first with 5.87 mha followed by West Bengal with 4.28 mha and Odisha with 3.80 mha. When it comes to production Uttar Pradesh also leads, harvesting 128.3 million tonnes (mt) followed by West Bengal (117.2 mt) and Punjab (111.9 mt). Despite its vast cultivation area India’s average rice productivity remains comparatively low at 3.76 tonnes per hectare (t/ha) falling short of the global average of 4.76 t/ha. The major rice growing ecosystems in the country include irrigated rice which spans around 22 mha as well as rainfed upland and rainfed lowland ecosystems which together cover approximately 14.4 mha (Mahajan *et al.*, 2017).

Although rice productivity in India has improved by 17.9% over the last decade it still reaches only 54.6% of China’s average productivity which stands at 6.89 tonnes per hectare (t/ha). Between 1960 and 2018 India experienced a 27.5% expansion in rice cultivation area alongside a remarkable 214.4% increase in production and a 147.5% rise in productivity. These gains were largely driven by the adoption of semi-dwarf rice varieties and the development of hybrid strains. At the global level rice cultivation area grew by 34.5% during the same period with total production increasing by 230% and productivity improving by 145%. Besides high-yielding varieties, advances in cultivation practices enhanced irrigation infrastructure, and increased use of chemical fertilizers played significant roles in these improvements (Zhu *et al.*, 2010). Despite this progress rice production in India has not kept pace with the country’s rapid population growth and escalating food demand. Khush (1997) projected a 60% increase in rice production from 1996 levels by 2025 to meet the needs of the growing population. However, by 2018 only 29% of this target had been achieved.

## Role of Phosphorus in Rice Growth and Development

Phosphorus (P) along with nitrogen (N) and potassium (K) constitutes the three primary macronutrients required for food production while micronutrients are also needed in smaller but significant amounts. Among these P is considered the second most crucial for plant growth and development. Nevertheless, its concentration in soil is usually very low often between 2–10 μM (Raghothama 1999) and about 30–40% of global arable land faces acute phosphorus deficiency. The supply of P to plant roots is further constrained because its transfer through soil diffusion is inherently slow (Fitter *et al.*, 2002). In addition, P is highly immobile in soils which makes it a key limiting factor for agricultural productivity (Fageria *et al.*, 1997). Nearly 90% of the fertiliser-applied phosphorus becomes unavailable to crops as it quickly transforms into insoluble complexes due to low solubility and strong fixation in soils (Liu *et al.*, 2013). Continuous cropping worsens this scenario as soil P reserves decline both through crop removal and fixation. Such low P availability in rice-growing soils can severely impair physiological, biochemical and metabolic processes resulting in yield reduction or even crop failure. To counteract this farmer often apply excessive amounts of soluble P fertilisers. However, this non-judicious practice only accelerates fixation into unavailable forms and consequently raises the overall demand for additional P fertilisation (Achal *et al.*, 2007).

Phosphorus (P) plays multiple critical roles in plant metabolism. It is directly involved in cellular energy transfer through ATP and NADPH forming an essential part of genetic material and contributes to the synthesis of phospholipids. In addition, phosphorus is vital for maintaining membrane stability (Gonias *et al.*, 2005). Given these functions, P deficiency disrupts overall plant physiology often leading to yield loss and impaired membrane integrity. When plants experience P starvation several morphological and physiological symptoms become evident. These include reduced shoot growth, fewer tillers, slower phyllochron and decreased leaf elongation. Photosynthetic activity is also suppressed accompanied by reductions in both shoot and root biomass (Wissuwa *et al.*, 2005). Another characteristic indicator of phosphorus deficiency is the purplish discoloration of leaves caused by reduced hydration and lower leuco-anthocyanin accumulation (Atkinson, 1973). Prolonged P stress further manifests as poor tillering, stunted growth, premature leaf senescence, delayed anthesis, and significant reductions in grain yield. Under severe deficiency plants show marked stunting and reduced root mass during the vegetative phase. Moreover, dry matter partitioning between roots and shoots as well as within shoot tissues becomes imbalanced with these effects intensifying as the crop matures (Elliott *et al.*, 1997). Although nitrogen and phosphorus fertilisers are widely applied to mitigate these stresses their excessive and indiscriminate use contributes to environmental pollution (Tan *et al.*, 2013).

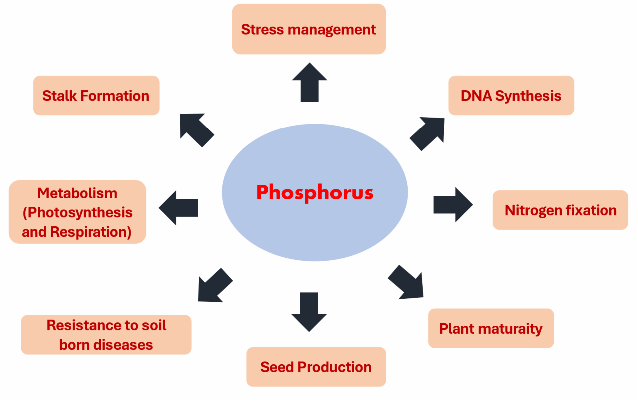

**Fig. 1 :** Major functions of Phosphorus in plant developmental physiology.

## Dynamics of Phosphorus Availability in Soils

Unlike nitrogen (N) phosphorus (P) is a non-renewable resource and thus remains the major limiting macronutrient in crop production systems. Nitrogen, in contrast can be replenished naturally through biological fixation or physical processes such as lightning (Ezawa *et al.*, 2002). In soils, P is largely confined to the surface layer (0–30 cm) and its availability declines with increasing depth (Xiao *et al.*, 2012). Several approaches exist for evaluating soil P fertility but the Olsen method is the most widely applied especially in acidic soils (Olsen *et al.*, 1954; Olsen and Sommers 1982). Using this criterion, the critical phosphorus level in lowland rice soils is defined as 10 mg/kg whereas in calcareous soils the threshold is considerably higher at 25 mg/kg (Dobermann and Fairhurst 2000). In soils, the majority of phosphorus (P) occurs in inorganic forms which can be classified into four major types: (i) labile or exchangeable P which is readily available and bound to soil particle exchange sites (ii) P complexed with iron (Fe) and aluminium (Al) oxides and hydroxides (iii) P bound to calcium compounds primarily in appetites and (iv) occluded P which is adsorbed and entrapped within the soil matrix (Adhami *et al.*, 2006). Soil organic phosphorus on the other hand is highly variable ranging from about 20% to 80% of total P. Much of this organic fraction is associated with fulvic acids while smaller amounts are linked to humic acid and humin. In general soils with higher organic matter content tend to show greater P availability (Dalai 1977).

The principal forms of organic P are phosphate esters with phosphate monoesters comprising the bulk followed by phosphate diesters such as DNA, RNA, phospholipids and teichoic acids. Less common forms include phosphonates and phosphoric acid anhydrides which play important roles in biochemical energy transfer (Turner *et al.*, 2005). The availability of phosphorus (P) to plants is strongly influenced by several soil-related factors including soil pH, the nature of the parent material and past management practices (Kanwar *et al.*, 1967). Among these P fixations is the most critical chemical process controlling its availability. The extent of fixation is largely determined by soil pH, organic matter content and the method of fertiliser placement (USDA 2012). Phosphorus fixation varies across the pH spectrum. In strongly acidic soils maximum fixation occurs between pH 3.0 and 3.5 due to iron compounds though it can persist albeit at lower intensity up to about pH 5.0 (Price 2006). Around pH 5.5 aluminium becomes the dominant fixing agent while under alkaline conditions (near pH 8.0) calcium ions are primarily responsible for fixation (Barrow 2017).

In most soils phosphorus (P) constitutes about 0.05% of the total mass but only a very small fraction roughly 0.1% is available for plant uptake (Blume *et* *al*., 2016). Soil P exists primarily in two forms organic and inorganic and their relative availability varies across soil types and is strongly influenced by soil pH (Yadav *et al*., 2012). In the arid regions of India total soil P content ranges between 560–900 kg/ha yet the amount available to plants is extremely limited only about 15–25 kg/ha. These soils also contain low levels of organic matter typically 1.5–4.2 mg/kg (Dhir 1997). The majority of phosphorus in such soils occurs in the form of calcium and aluminium phosphates (Yadav *et al*., 2012). Phosphorus fertilisers are generally supplied as di-ammonium phosphate (DAP), triple superphosphate (TSP) or rock phosphate. However, in acid soils applied P often becomes unavailable because iron and aluminium compounds rapidly fix it into insoluble forms (Maghanga *et al*., 2015).

## Phosphorus Availability in Soils: Global Patterns and Indian Scenario

Phosphorus (P) remains a critical limiting factor for agricultural productivity with more than 40% of the world's arable land affected (Dey *et al*., 2017). Globally, over 5.7 billion hectares of land are considered P deficient restricting crops from reaching their yield potential (Raghothama 2005). Current phosphorus consumption is around 50 million tonnes annually and demand is projected to rise by nearly 20 million tonnes by 2030 (Cakmak 2002). P deficiency is particularly severe in tropical regions with large areas in Asia and Africa exhibiting critically low levels. In Asian countries such as India, China and Nepal soils are reported to have relatively low phosphorus (Han *et al*., 2005; Regmi and Zoebisch 2004). In China the proportion of P-deficient soils increased dramatically from 30% in the 1930s to 74% by 1990 (Zhu and Xi 1990; Desai and Gandhi 1990). Across Africa soil P deficiencies are widespread, for instance 88% of soils in southwestern Ethiopia were found below critical levels (Nigussie *et al*., 2013) while other regions such as western Ethiopia reported low to moderate P status (Goshu *et al*., 2015). In Kenya, however, several agricultural areas-maintained soil P levels above the critical threshold (Itabari *et al*., 2013).

By contrast, European soils tend to be relatively rich in phosphorus with 70–80% of agricultural land showing high P availability (Dey *et al*., 2017). In Germany, however, soil P levels decline with depth decreasing progressively from topsoil to subsoil (Werner *et al*., 2016). In Australia phosphorus status varies by cropping system ranging from high levels in fruit orchards to moderate levels in vegetable and sugarcane fields in Queensland (Rayment *et al*., 2006). In India, the first comprehensive soil phosphorus (P) fertility map was developed and published in 1979 (Hasan 1996). National assessments indicated that 49.3% of Indian soils are low in P, 48.8% fall within the medium range and only 1.9% are categorized as high in available phosphorus. A more detailed district level survey showed that out of 500 districts 257 were classified as low in soil P, 200 as medium and just 43 as high (Muralidharudu *et al*., 2011). The critical levels of phosphorus vary not only across soil types but also among different crop varieties grown in the country (Singh and Agrawal 2007). This variability is largely attributed to differences in soil pH and phosphorus buffering capacity.

## Sources of Phosphatic Fertilisers

Globally, the sole source of phosphatic fertilisers is natural phosphate rock commonly referred to as phosphorite. These are sedimentary or igneous rocks rich in phosphate minerals predominantly apatites and in rare cases may also contain traces of radioactive minerals (Menzel 1968). The most abundant form of apatite in the earth's crust is fluoroapatite ($Ca_5(PO_4)_3F$) which serves as the principal source of phosphorus. Although phosphate rock deposits are distributed worldwide, large reserves are concentrated in only a few countries including Morocco, Western Sahara, China, Algeria, Syria, Brazil, Saudi Arabia, South Africa, Egypt, Australia, the United States, Finland and Jordan (Jasinski, 2020). Phosphate mining began in the United State and in South Carolina in 1867 and gradually expanded to other regions following the discovery of local deposits (Cathcart, 1980; van Kauwenbergh, 2010). Smaller deposits also occur in countries such as Russia, Peru, Tunisia, Israel, India and Mexico.

In India, phosphorus is mainly present in the form of apatites and rock phosphates. Apatite reserves are concentrated in West Bengal (57%), Jharkhand (30%) and Meghalaya (8%) with smaller shares in Rajasthan, Tamil Nadu, Gujarat and Andhra Pradesh. Rock phosphate deposits are mainly located in Jharkhand (36%), Rajasthan (30%), Madhya Pradesh (17%), Uttar Pradesh (9%) and Uttarakhand (7%) (GoI 2015). Almost 90% of the world's phosphate production is channelled into the manufacture of fertilisers such as single superphosphate (SSP), triple superphosphate (TSP), monoammonium phosphate (MAP) and diammonium phosphate (DAP) which are primarily used in agriculture (Khan *et al*., 2012). With the global population projected to rise sharply by 2050 fertiliser demand is expected to increase correspondingly.

Since phosphate reserves are unevenly distributed localised deposits often trigger geopolitical tensions over access to phosphatic resources particularly fertilisers. Projections indicate that at the current rate of exploitation commercially viable reserves of phosphorite in 12 major deposits worldwide could be depleted within the next 50–100 years (Cordell *et al.*, 2009). Given the accelerating depletion of phosphate rock strategies such as recovering phosphorus from animal manures and crop residues after suitable processing have been proposed to supplement future demand (Oenema *et al.*, 2012). Furthermore, global production trends suggest that phosphorus may follow a "peak curve" similar to that of oil rising to a maximum level before entering a steady decline (van Kauwenbergh, 2010).

## Phosphorus use efficiency (PUE)

Phosphorus (P) is a highly mobile nutrient within plants which is quickly assimilated into various metabolites. In soils, plants primarily absorb P as $H_2PO_4^-$ yet its natural concentration in soil solutions is extremely low averaging around 10 µM. Consequently, phosphate fertilisation becomes essential to sustain crop growth. Depending on the extent of P inputs rice cultivation systems worldwide can be broadly classified as high-input or low-input with corresponding differences in management practices. Of the applied P only a small portion is actually taken up by rice plants typically 10–15% and in exceptional cases up to 25% (Roberts and Johnston, 2015). The larger share of P is often fixed in the soil making it unavailable to the subsequent crop.

Assessing P use efficiency is challenging due to the complex dynamics of P utilisation in plants. Direct measurements using radioactive P isotopes are considered highly accurate but are impractical, costly and restricted by the short half-life of $^{32}P$. Hence, efficiency is usually estimated by comparing differential uptake between P-fertilised and unfertilised plots relative to the amount applied which typically gives values around 10–15%. However, this method overlooks the role of native soil P a key contributor to plant nutrition. Johnston *et al.* (2014) therefore caution that such estimates may substantially underestimate true P use efficiency. Over-reliance on these figures can lead to unnecessary P supplementation particularly where soils already retain adequate exchangeable P reserves. Importantly, several studies confirm that residual P from fertiliser applications remains available to succeeding crops.

Phosphorus uptake efficiency (PUpE) is strongly influenced by soil P availability which varies widely across rice-growing soils and is largely governed by soil pH and structural characteristics. Since irrigated rice accounts for nearly 56% of the global rice area most production systems experience anaerobic conditions. Flooded soils generally enhance P availability through reduction processes yet in soils rich in active Fe, P tends to be adsorbed reducing its accessibility to plants (Dobermann and Fairhurst, 2000; Inglett *et al.*, 2005). Rice plants however can utilise acid-soluble P fractions present in such environments. Soil pH plays a critical role in P dynamics: at low pH, fixation by Fe and Al ions decreases P availability, while at high pH, Ca ions are responsible for immobilisation. Consequently, P deficiency often coincides with Fe and Al toxicity in acidic soils and with salinity stress in alkaline soils. The recovery of applied P is maximised around an optimum soil pH of 5.5 (Yu *et al.*, 2013).

Due to these soil environment interactions rice genotypes exhibit considerable variation in PUpE across different locations and soil types. Improving PUpE is therefore essential for broad adaptation ensuring stable performance under both high and low P conditions. Current P use efficiency in rice averages only 25% underscoring significant scope for genetic improvement (Dobermann and Fairhurst 2000). Notably, the shift towards input-responsive semi-dwarf cultivars during the Green Revolution has inadvertently led to negative selection for PUpE in rice breeding programmes.

With the continuous depletion of natural resources, sustaining high input farming practices in the future is becoming increasingly unrealistic. Therefore, the urgent priority is to adopt strategies that ensure higher yields while simultaneously enhancing resource use efficiency, particularly phosphorus use efficiency (Heuer *et al.*, 2017). While phosphorus uptake efficiency (PUpE) remains a critical target, phosphorus utilisation efficiency (PUtE) has already shown considerable improvement in modern rice cultivars which respond positively to P application in terms of yield. The most effective plant breeding strategy would thus be one that combines and maximises both PUpE and PUtE (Römer and Schenk 1998).

## Adaptive responses of Rice for Low Phosphorus Tolerance

The spread of high-yielding cultivars has shifted rice farming towards high-input practices but in low input systems efficient P uptake and internal P use are vital to withstand deficiency stress (Rose and Wissuwa, 2012). To adapt to low P conditions, crops employ morphological, physiological, biochemical and symbiotic mechanisms, with root system modification being the most crucial (Rengel *et al.*, 2005). Improved

P uptake is crucial for conferring low P tolerance in rice. The primary adaptive response under P deficiency is extensive root growth enabling plants to explore a wider soil volume for nutrients. Consequently, stresses that restrict root development indirectly reduce PUpE, highlighting the need to consider such factors in breeding programs (Heuer *et al.*, 2017). Key architectural adaptations include enhanced meristematic activity, lateral root proliferation and profuse root hair growth that increase root surface area (Lopez-Bucio *et al.*, 2003), along with greater adventitious root number (Bates and Lynch 2001), finer root diameter (Lynch *et al.*, 2008), larger root volume (Trachsel *et al.*, 2011), higher rooting density (Walk *et al.*, 2006), and specialised structures like cluster roots (Shane *et al.*, 2005). These traits allow roots to penetrate soil laterally and vertically covering more volume and accessing immobile nutrient ions. Given the heterogeneous distribution of P, high root plasticity ensures efficient foraging (Lynch, 1995). Under P stress, plants accelerate root development diverting assimilates to roots (Hermans *et al.*, 2006) with carbohydrate accumulation increasing the root-to-shoot ratio (Cakmak *et al.*, 1994). Such adjustments require modifications in photosynthetic metabolism to enhance carbohydrate partitioning between source and sink tissues (Sanchez-Calderon *et al.*, 2006). Besides root modifications auxiliary mechanisms also contribute to improved P uptake.

Under low P conditions root exudation of organic acids, phytases, acid phosphatases (APases), and ribonucleases is a prominent mechanism enhancing P uptake (Lopez-Arredondo *et al.*, 2014). Acid exudation breaks P from complex ester linkages improving availability for absorption. In P efficient genotypes, a range of low molecular weight organic acids (LMOAs) such as aconitic, citric, malic, oxalic, succinic and others are released at the rhizosphere to mobilise P. Efflux of ribonucleases (RNS) (Bariola *et al.*, 1994) and purple APases (PAPs) (Duff *et al.*, 1994) has also been reported with PAPs releasing P from organic pools. Genes regulating root hair development and the expression of inorganic P (Pi) transporters further strengthen P acquisition (Gilroy and Jones, 2000).

Root exudates also foster microbial associations that accelerate P solubilisation. Endosymbionts like arbuscular mycorrhizae (AM) form extraradical hyphae expanding the effective root surface area and enhancing P uptake. A notable genetic adaptation in rice is the *Pup1* QTL (Wissuwa *et al.*, 1998) containing the OsPSTOL1 gene that promotes root system proliferation under P deficiency (Gamuyao *et al.*, 2012). Beyond uptake, internal P mobilisation plays a key role in utilisation. High-affinity Pi transporters and several Pht genes mediate P uptake and transport across roots (Ye *et al.*, 2015; Vinod 2015) while vacuolar regulators manage storage and remobilisation of P reserves (Pratt *et al.*, 2009). Plants also adapt by replacing P rich phospholipids in membranes with sulfolipids and galactolipids (Pant *et al.*, 2015). Since the cytoplasmic P concentration is typically higher than soil P, uptake occurs actively across the plasmalemma via specific Pi transporters expressed at different soil P levels (Epstein and Leggett 1954; Schachtman *et al.*, 1998).

Another adaptation is internal translocation of P, where remobilisation occurs from older to developing tissues (Gill and Ahmad, 2003). In tolerant genotypes greater mobilisation towards leaves compared to roots and stems has been observed (Snapp and Lynch 1996). Considering these diverse morphological, biochemical, physiological and genetic responses modern breeding programs have ample scope to exploit these mechanisms for developing P efficient rice varieties.

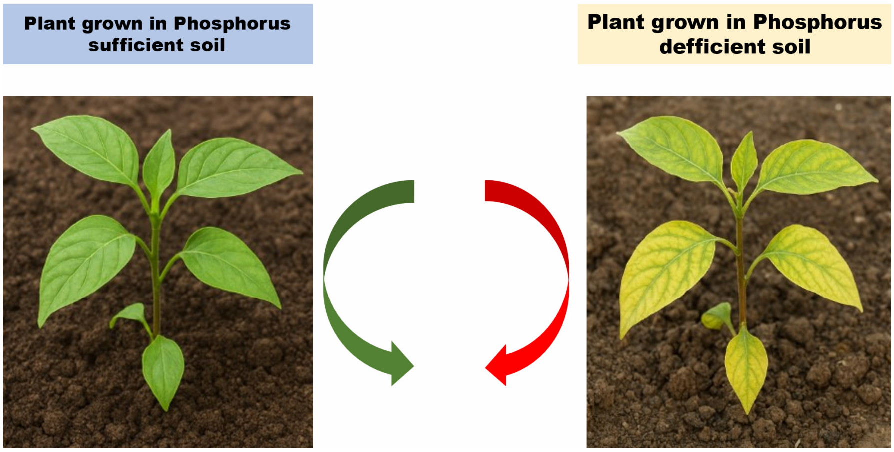

**Fig. 2** : Phenotypic differences in plants grown in low and high Phosphorus.

## Genetics underlying low Phosphorus tolerance

Over time, several approaches such as microarray analysis (Wang *et al.*, 2002) and more recently transcriptomics have been used to study the genetic and phenotypic basis of plant responses to low phosphorus (P). P responsive genes are generally classified into early response genes, which trigger non-specific changes and late response genes which mediate morphological, physiological and biochemical adaptations (Vance *et al.*, 2003). Following P uptake its cellular transport is facilitated by phosphate (Pi) transporters. Pi transport occurs through high and low affinity systems governed by four families of membrane transporter i.e. Pht1, Pht2, Pht3 and Pht4 (Raghothama and Karthikeyan 2005). Among these, Pht1 members are predominantly expressed in the epidermis and outer root cortex (Mudge *et al.*, 2002).

Rice contains 13 members of the Pht1 gene family (OsPht1-1 to OsPht1-13) of which OsPht2, OsPht3, OsPht6 and OsPht7 function as key transporters under low soil P availability (Ai *et al.*, 2009). Unlike the root-localized Pht1 members, OsPht2, OsPht3 and OsPht4 transcripts are linked to subcellular Pi partitioning being localized to the plastid, mitochondrial and Golgi membranes respectively (Cubero *et al.*, 2009; Versaw and Harrison 2002). In addition, OsPT11 and OsPT13 are essential for the regulation of arbuscular mycorrhizal (AM) symbiosis (Yang *et al.*, 2012). Several regulators of Pi signaling have also been characterized including OsPHR1–3, OsSPX1–3 and OsIPS1–2 (Wang *et al.*, 2009; Liu *et al.*, 2010; Secco *et al.*, 2012). Under Pi deficiency, rice exhibits reduced primary root elongation but enhanced lateral root and root hair formation largely due to altered auxin transport and sensitivity (Nacry *et al.*, 2005). Increased activity of the auxin receptor TIR1 promotes lateral root development in coordination with transcription factors ARF7 and ARF19 (Perez-Torres *et al.*, 2008).

Acid phosphatase (APase) secretion represents another key mechanism for P acquisition. In Arabidopsis, Pi deficiency specifically induces the expression of a secreted purple acid phosphatase, AtPAP10 (Wang *et al.*, 2011). Local Pi sensing is mediated by the interaction of *PDR2* (phosphate deficiency response 2) and *LPR* (low phosphate response) genes. The *pdr2* mutant exhibits reduced cell division and primary root growth whereas *lpr1* and *lpr2* mutants show contrasting phenotypes (Ticconi *et al.*, 2004). Moreover, optimal expression of several Pi deficiency inducible genes depends on sufficient sugar availability (Hammond *et al.*, 2011). The phosphate (PHO) regulon, first identified in *Escherichia coli*, coordinates P adaptation by regulating Pi transporters release enzymes and assimilation pathways (Wanner and Chang 1987; Santos-Beneit 2015) and is conserved across prokaryotes and eukaryotes. In plants, PHO1 family members are localized to the trans-Golgi and facilitate Pi transport from roots to shoots. In Arabidopsis, *AtPHO1* is strongly expressed in roots under P limitation and is essential for xylem loading of absorbed Pi.

The PHO1 protein is characterized by a hydrophilic N-terminal region containing an SPX domain with three sub-domains SYG1 (SYnaptoGenesis abnormal), Pho81 and XPR11 which functions as Pi sensors for signal transduction. Its C-terminal region carries a tripartite EXS domain (ERD1, XPR1 and SYG1) along with six transmembrane α-helices, although not directly involved in Pi transport the EXS domain is essential for Pi export and Golgi/trans-Golgi localization (Wang *et al.*, 2004; Wege *et al.*, 2016). In rice, PHO1 orthologues (OsPHO1 and OsPHO2) facilitate P translocation from roots to shoots and *pho1* mutants accumulate excess P in roots relative to shoots (Secco *et al.*, 2010; Arpat *et al.*, 2012). The OsSPX1–OsSPX6 family is localized to multiple organelles, suggesting diverse roles in P homeostasis (Wang *et al.*, 2009). Other PHO genes also play critical roles for example, *pho3* mutants show impaired sucrose loading and reduced expression of Pi-deficiency genes in Arabidopsis (Lei *et al.*, 2011), highlighting the importance of sugar signaling under low P.

Long distance signalling further involves phloem mobile microRNAs. In Arabidopsis, miR399 regulates low P response by targeting *PHO2* mRNA which encodes the ubiquitin conjugating enzyme UBC24 (Pant *et al.*, 2008). In rice, OsmiR827 modulates the expression of OsSPX-MSF1 and OsSPX-MSF2 under P starvation showing reciprocal regulation patterns between P-sufficient and P-deficient conditions (Lin *et al.*, 2010). Transcriptional regulation is further controlled by *PHR1* and *PHL1* which are members of the MYB DNA-binding protein family which activate several Pi starvation inducible genes including *miR399* (Bari *et al.*, 2006).

## QTL studies for the mapping of low Phosphorus tolerance genes

Efforts to understand low P tolerance in rice were advanced significantly by two landmark studies in 1998. The first, by Wissuwa *et al.*, (1998) which involved a cross between Kasalath, a traditional *aus* variety from Assam and the japonica cultivar Nipponbare, while the second study used a cross between IR20 (sensitive) and IR55178-3B-9-3 (tolerant) (Ni *et al.*, 1998). Both identified a major genomic region on chromosome 12 linked with tolerance to low P. Using 98 backcross inbred lines (BILs) of Kasalath/Nipponbare, Wissuwa *et al.* mapped QTLs for P uptake on chromosomes 2, 6, 10 and 12 through composite interval mapping. In contrast, Ni *et al.* employed 42 recombinant inbred lines (RILs) from the IR20/IR55178-3B-9-3 cross under hydroponic conditions, mapping a key QTL for P deficiency tolerance on chromosome 12 using RFLP markers. Initially termed *PHO*, this QTL was later renamed *Pup1* (Phosphorus uptake 1) after fine mapping (Wissuwa *et al.*, 2002). *Pup1* was localized to a 15.31–15.47 Mb interval on the long arm of chromosome 12 (Heuer *et al.*, 2009), with Kasalath carrying a 275 kb region compared to a shorter 157 kb region in Nipponbare spanning three BAC clones.

Sequence analysis of the *Pup1* locus revealed it as a transposon rich hotspot. In Kasalath, this region carried 68 predicted gene models including 16 transposons and over 40 uncertain genes showing partial similarity to other elements (Chin *et al.*, 2011). A unique 120 kb INDEL region located between *OsPupK30* and *OsPupK67* contained 21 gene models, of which 14 were initially considered as candidates. Based on expression under low P, three genes were prioritized: *OsPupK20* (dirigent-like protein), *OsPupK29* (hypothetical protein) and *OsPupK46* (protein kinase). While *OsPupK20* and *OsPupK29* were found in both Kasalath and Nipponbare and were upregulated under P deficiency, *OsPupK46* was unique to Kasalath and also showed strong induction in roots during low P stress (Chin *et al.*, 2011).

Although *Pup1* is present in over 50% of rice accessions from stress prone ecologies it is largely absent in genotypes adapted to irrigated conditions (Chin *et al.*, 2010). Interestingly, more than 80% of drought-adapted rice lines carry *Pup1*, suggesting that breeders have unintentionally selected for it due to its overlap with the drought yield QTL *qDTY12.1*, resulting in co-introgression of both loci (Bernier *et al.*, 2007). Expression studies later identified *OsPupK46*, a protein kinase gene as the key candidate for low P tolerance. This gene was subsequently named *OsPSTOL1* encoding a serine/threonine kinase and is recognized as a root growth enhancer from the seedling stage ultimately contributing to higher grain yield (Gamuyao *et al.*, 2012).

Beyond *Pup1*, several minor QTLs contributing to low P tolerance have been identified. Wissuwa *et al.* (1998) reported QTLs for P uptake on chromosomes 2, 6 and 10 along with a QTL for P-use efficiency on chromosome 4 while Ni *et al.* (1998) mapped minor QTLs for root traits on chromosomes 1 and 6. A DH population from ZYQ8 (indica) × JX17 (japonica) revealed major QTLs on chromosome 6 for relative root dry weight (*qRRDW6*), relative shoot dry weight (*qRSDW6*), total root dry weight (*qRTDW6*) and P uptake efficiency (*qRPUC6a*) (Ming *et al.*, 2000). Chromosome 6 later emerged as a hotspot for P-responsive genes (Heuer *et al.*, 2009) also harboring *OsPTF1*, a bHLH transcription factor linked with P-deficiency tolerance (Yi *et al.*, 2005), and *qREP6*, a root elongation QTL mapped from a Gimbozu × Kasalath cross under P stress (Shimizu *et al.*, 2004). Additional QTLs for root traits including relative dry shoot weight were mapped on chromosomes 1, 2, 5 and 12 in OM2395 × AS996 populations (Lang and Buu 2006). Given the overlap between drought and P deficiency responses the drought-adapted rice varieties such as Shabaghi Dhan, Daggadeshi, Pynthor and Paijong from Northeast India have been identified as promising donors for P deficiency tolerance (Tyagi *et al.*, 2012).

Li *et al.* (2009) mapped 29 additive and 24 epistatic QTLs for P tolerance using 271 introgression lines (ILs) from Yuefu (sensitive) × IRAT109 (tolerant), among which *qRN4* (total root number) was consistently expressed under both low and high P while *qRRS8* conferred tolerance to both low P and drought stress. In the same cross, a doubled haploid (DH) population of 116 lines was evaluated under contrasting P conditions identifying 17 yield-related QTLs, 12 of which explained >10% phenotypic variation with co-localization on chromosomes 3, 6 and 7 (Mu *et al.*, 2008). Using a RIL population from Zhenshan 97 (japonica) × Minghui 63 (indica), 36 QTLs associated with P-use efficiency and 24 epistatic interactions were identified through high-density SNP mapping (Wang *et al.*, 2014). More recently, a QTL-seq approach with an F5 Akamai (tolerant) × Koshihikari (sensitive) population detected a major QTL, *qLPT1* on the long arm of chromosome 12 (Nishida *et al.*, 2018). Since Akamai lacked *OsPSTOL1*, *qLPT1* was proposed as a novel locus associated with enhanced root efficiency under low P stress. The different genes governing Phosphorus starvation tolerance in various crops are given in Table 1.

**Table 1 :** Genes/QTLs affecting Phosphorus starvation tolerance in different field crops.

| Crop | Gene/QTL | Physiological Effect | Remarks |
|---|---|---|---|
| Rice | *Pup1* (Phosphorus uptake 1) | Enhances root growth and P acquisition under low P | Widely studied; Kasalath donor variety |
| Rice | *OsPTs* (*OsPT1–OsPT13*) | Phosphate transporters, uptake and translocation | Regulated under P deficiency |
| Rice | *OsPHR2* | Transcription factor regulating P starvation responses | Controls P signaling pathway |
| Maize | *ZmPT1, ZmPT2* | High-affinity phosphate transporters | Expressed under low P conditions |
| Wheat | *TaPSTOL1* | Enhances root growth and P uptake | Ortholog of rice Pup1 |
| Wheat | *TaPTs* | Phosphate transporters | Multiple members contribute to P uptake |
| Soyabean | *GmPTs* | High-affinity phosphate transporters | Upregulated in roots under P starvation |
| Soyabean | *GmPAPs* | Acid phosphatases aiding P mobilization | Secreted into rhizosphere under low P |
| Barley | *HvPHT1, HvPHT4* | High-affinity phosphate transporters | Expressed under low P |
| Common bean | *PvPAP1, PvPT1* | Phosphate acquisition and mobilization | Contributes to low P adaptation |

## Marker-assisted breeding for low P tolerance

Marker-assisted backcrossing (MABC) is widely recognized as an efficient breeding strategy that utilizes markers linked to genes or QTLs for transferring target traits into elite genetic backgrounds (Hasan *et al*., 2015). Initially applied for developing disease resistant rice cultivars, MABC has been effectively used to introgress resistance genes against bacterial blight and blast (Singh *et al*., 2011). More recently, QTLs such as *Sub1*, *Pup1*, *Saltol* and several drought yield QTLs have also been deployed for cultivar improvement (Singh *et al*., 2019; Muthu *et al*., 2020). This approach is particularly useful for improving elite high yielding or quality rice cultivars that are otherwise stress susceptible. By enabling early selection of backcross progenies carrying the target allele and facilitating assessment of recurrent parent genome recovery, MABC significantly accelerates the breeding pipeline (Gopalakrishnan *et al*., 2008; Ellur *et al*., 2016).

Chin *et al.* (2011) developed a series of molecular markers targeting gene models within the Kasalath *Pup1* region designated with the prefix “K” followed by the gene number. For example, marker K5 was derived from the hypothetical gene *OsPupK05* but also targeted *OsPupK04*, a putative fatty acid α-oxygenase. The dirigent-like gene *OsPupK20* was tagged by two markers, K20-1 and K20-2 with K20-1 detecting a small InDel in Kasalath and functioning as a CAPS marker with *MseI*. Similarly, three markers (K29-1, K29-2, K29-3) were designed for the hypothetical gene *OsPupK29*, targeting InDels across exons and introns. For the Kasalath specific kinase gene *OsPupK46*, two markers were designed: K46-1 (from the conserved kinase domain) and K46-2 (from the 3′ UTR). Both were dominant markers since no corresponding alleles were present in Nipponbare. Markers spanning K41–K59 also showed dominant inheritance reflecting their origin from a large Kasalath-specific InDel region. Based on amplification patterns six markers—K29-1, K29-3, K41, K43, K45 and K46-1 were identified as core markers for assessing the *Pup1* locus in rice germplasm (Chin *et al*., 2011). These markers and their subsets have since been widely used for germplasm surveys (Sarkar *et al*., 2011; Tyagi *et al*., 2012; Pariasca-Tanaka *et al*., 2014; Aluwihare *et al*., 2018; Sundar 2016). For instance, Sarkar *et al.* (2011) recommended Bhutmuri, Gobindabhog and Radhunipagol as donor parents for *Pup1* introgression, while Pariasca-Tanaka *et al.* (2014) identified a novel *PSTOL1* allele from *Oryza glaberrima* in upland NERICA varieties noting that several Kasalath *Pup1* genes were absent in African rice thereby highlighting opportunities for MABC transfer.

The first successful marker-assisted transfer of the *Pup1* QTL was achieved by Chin *et al.* (2011) who introgressed it into two IRRI cultivars (IR64 and IR74) as well as the Indonesian upland varieties Situ Bangendit and Batur resulting in clear yield advantages in the NILs compared to their recurrent parents. Subsequently, *Pup1* was introgressed into MTU1010, a widely grown low-P sensitive mega variety with long slender grains and short duration (released by ANGRAU, Telangana) using Vandana as the donor and markers K20-1 and K46-1 for foreground selection (Anila *et al.*, 2018). Introgression of *OsPSTOL1* via MABC was also reported in the short duration varieties ADT 43 and ASD 16 with IR74-*Pup1* serving as the donor (Chithrameenal *et al.*, 2018). Ongoing efforts at ICAR-IIRR, Hyderabad are focused on transferring *Pup1* into Improved Samba Mahsuri (Sundaram *et al.*, 2018).

## Conclusion and Future Perspectives

Phosphorus (P) is a vital macronutrient for rice (*Oryza sativa*) growth which influences vital life processes such as energy transfer, root development and overall plant metabolism. Despite its importance, P availability in soils is often limited due to factors like soil pH fixation by minerals and organic matter content. Consequently, P deficiency can lead to stunted growth, reduced tillering and lower yields in rice crops. Phosphorus Use Efficiency (PUE) in rice is a critical factor determining how effectively plants utilize available P. Enhancing PUE involves improving both phosphorus uptake efficiency (PUpE) and utilization efficiency (PUtE). Advances in genetic research have identified key genes such as *OsPSTOL1* which is associated with improved P uptake and root development under low P conditions. These genetic insights offer potential pathways for breeding rice varieties with enhanced P efficiency.Rice cultivation faces significant challenges related to phosphorus deficiency affecting approximately 50% of global rice growing soils. This deficiency impacts plant growth, leading to reduced yields and necessitating increased fertilizer application. While traditional breeding methods have made strides in developing P-efficient varieties, the integration of modern molecular techniques holds promise for more precise improvements. Key strategies to address P deficiency in rice include genetic improvement in terms of improved varieties, appropriate soil management stratergies and adequate fertiliser management practises. Looking ahead, the focus should be on integrating genetic, agronomic, and technological approaches to combat P deficiency in rice cultivation. Future research in this direction includes planed MABB programmes for introgression of genes related to Phosphorus starvation tolerance from wild relatives/landraces to the elite varieties in cultivation, genomic selection and using genome editing tools to achieve the same. By adopting a multifaceted approach, it is possible to develop rice varieties and cultivation practices that are more resilient to phosphorus limitations which ensures food security in the face of global challenges.

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## Author Contribution

AT: designed the study; AT: reviewed the literature; AT and NK: analysed the literature and prepared the manuscript.

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